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ELEMENTARY TEXT-BOOK

OF

ZOOLOGY

GENERAL PART AND SPECIAL PART:
PROTOZOA TO INSECTA.

BY

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PREFACE TO THE ENGLISH TRANSLATION.

I UNDERTOOK the translation of Professor Claus' excellent "Lehrbuch der Zoologie" with a view of supplying the want, which has long been felt by teachers as well as students in this country, of a good elementary text-book of Zoology. Professor Claus' works on zoology are already well known in this country ; and I think it will be generally admitted that they take the first place amongst the zoological text-books of the present day.

It has been decided to publish the English translation in two volumes. The second volume, which begins with Mollusca, is in the press, and will, I trust, appear early in the autumn.

The German has been, with one or two unimportant exceptions, closely followed throughout. These exceptions, and the few additions which I have thought it necessary to make, have in all cases been indicated by enclosure within brackets.

I must ask the indulgence of the reader towards the errors and deficiencies of this translation. I trust that they will be found to be neither numerous nor important. I have to thank Mr. Heathcote for the assistance he has given me in the laborious work of translation. I am also indebted to Professors Newton and Foster, Dr. Gadow, and Mr. W. Heape for advice and assistance.

ADAM SEDGWICK.

TRINITY COLLEGE, CAMBRIDGE,
1884.

30497

TABLE OF CONTENTS.

GENERAL PART.

CHAPTER I.

ORGANIZED AND UNORGANIZED SUBSTANCES . . .	Page 9—14

CHAPTER II.

ANIMALS AND PLANTS	15—24

CHAPTER III.

ORGANIZATION AND DEVELOPMENT OF ANIMALS IN GENERAL	24—131
INDIVIDUAL, ORGAN, STOCK	24
Repetition of organs and parts of the body	25
CELLS AND CELL TISSUES	29
Nucleus and Nucleolus	29
Cell-membrane	29
Reproduction of Cells and division of Nucleus	30
1. <i>Cells and Cell-aggregates</i>	32
Isolated cells, <i>e.g.</i> , blood corpuscles, ova, etc.	32
Epithelium	34
Epidermal exoskeleton	34
Glandular tissue	36
2. <i>Tissues of the connective substance</i>	37
Cellular or vesicular	37
Mucous or gelatinous	37
Reticular, adenoid	38
Fibrillar	38
Elastic	39
Cartilage	39
Osseous tissue	40
3. <i>Muscular tissue</i>	43
4. <i>Nervous tissue</i>	45
INCREASE IN SIZE AND PROGRESSIVE DIFFERENTIATION, ETC.	47
Unicellular stage	48
Multicellular stage	49
CORRELATION AND CONNECTION OF ORGANS	50
Doctrine of Final Causes	51
"Type"	52
Scope of Morphology	52
STRUCTURE AND FUNCTION OF THE COMPOUND ORGANS	52
Digestive organs	53
Salivary glands, liver, pancreas	58

	Page
<i>Organs of circulation . . . . .</i>	59
Heart	61
Arteries and veins	62
Heart and vessels of vertebrates	64
<i>Organs of respiration . . . . .</i>	67
Branchiæ	69
Lungs, tracheæ.	69
Tracheal gills	71
Renewal of external medium	72
Venous and arterial blood	73
<i>Animal heat. . . . .</i>	73
<i>Organs of secretion . . . . .</i>	74
Kidneys	75
Water-vascular vessels and segmental organs	75
Vertebrate kidneys	76
Cutaneous glands	77
ORGANS OF ANIMAL LIFE	78
<i>Skeletal structures . . . . .</i>	79
<i>Nervous system . . . . .</i>	79
<i>Sense organs. . . . .</i>	83
Tactile organs	84
Auditory organs	85
Visual organs	85
Facetted eye	88
Simple eye	89
Olfactory organs	91
INTELLIGENCE AND INSTINCT	93
REPRODUCTIVE ORGANS	95
Biogenesis	96
Asexual reproduction	96
Sexual reproduction	97
Hermaphroditism	99
Separation of the sexes	100
Sexual differences	101
Sexual dimorphism	104
Parthenogenesis	105
DEVELOPMENT	107
Fertilisation of the ovum	108
Segmentation of the ovum	110
Food-yolk	111
Blastosphere	113
Formation of gastrula	114
Primitive streak	115
Germinal layers	116
Theory of Gastræa	117
DIRECT DEVELOPMENT AND METAMORPHOSIS	119
Effect of food-yolk on development.	120
Explanation of Metamorphosis	121
ALTERNATION OF GENERATIONS, POLYMORPHISM AND HETEROGAMY	123
Metagenesis	123
Explanation of Metagenesis	124
Polymorphism	126
Heterogamy	127
Pædogenesis	128
Heterogamy of Trematoda	129

CHAPTER IV.

	Page
HISTORICAL REVIEW	131—139
Aristotle	133
Pliny	132
Renaissance of Sciences in Sixteenth century	133
Ray	134
Linnaeus	134
Cuvier	135
St. Hilaire, Goethe, Oken	137
Classification of the present day	138

CHAPTER V. :

MEANING OF THE SYSTEM	139—179
Species	140
Varieties	141
Sterility of hybrids	142
Fertility of hybrids	143
Sterility and fertility of mongrels	143
Lamarck	144
Lyell's influence on Geology	144
THEORY OF DESCENT BASED ON NATURAL SELECTION (DARWINISM) .	144
Darwin	145
Natural selection	145
Origin of varieties, races and species	148
Progressing divergence of characters, and disappearance of intermediate forms	149
Species according to the theory of evolution	150
Natural system.	150
EVIDENCE IN FAVOUR OF THE THEORY OF DESCENT	151
<i>Evidence from Morphology . . . . .</i>	151
<i>from Dimorphism and Polymorphism . . . . .</i>	152
Sexual selection	152
Sexual dimorphism of parasites	153
Polymorphism of animal communities	155
<i>from mimicry . . . . .</i>	155
<i>from rudimentary organs . . . . .</i>	156
<i>from embryology . . . . .</i>	157
Retrogressive metamorphosis	158
<i>from the facts of Geographical Distribution . . . . .</i>	159
Zoological Provinces.	160
<i>from Palæontology . . . . .</i>	163
Incompleteness of the geological record	167—168
Transitional forms between allied species	170
Relation of fossil forms to living species	170
Succession of similar types	171
Extinct Mammalia, transitional between living groups	172
Extinct transitional Reptiles and Birds	175
<i>Progressive perfection . . . . .</i>	177
Fauna of the various geological periods	177
Incompleteness of the explanation	118

SPECIAL PART.

CHAPTER VI.

	Page
PROTOZOA	180
RHIZOPODA	181
Foraminifera	184
Lobosa	185
Reticularia	186
Heliozoa	187
Radiolaria	189
INFUSORIA	191
Flagellata	193
Ciliata	198
Holotricha	204
Heterotricha	205
Hypotricha	205
Peritricha	205
Suctoria	205
Schizomycetidae	205
Gregarinidae	207

CHAPTER VII.

COELENTERATA	209
* Spongiaria = Porifera	
SPONGIA	221
Myxospongia	221
Ceraospongia	221
Halichondriæ	221
Hyalospongia	221
Calcispongia	222
Cnidaria	
ANTHOZOA = ACTINOZOA	223
Rugosa	230
Alcyonaria	231
Hexactinia = Zoantharia	231
POLYPOMEDUSÆ = HYDROZOA	233
Hydromedusæ	236
Eleutheroblastæa	240
Hydrocorallia	240
Tubulariæ	241
Campanulariæ	241
Trachymedusæ	242
Siphonophora	243
Physophorida	248
Physalidæ	249
Calycephorida	249
Discoideæ	250
Scyphomedusæ = Acalepha	251
Calycozoa	257
Marsupialida	258
Discophora (Acraspeda)	259
CTENOPHORA	261

CHAPTER VIII.

	Page
ECHINODERMATA	266
CRINOIDEA	286
Tesselata	289
Articulata	289
ASTEROIDEA	290
Stelleridea	292
Ophiuridea	293
ECHINOIDEA	294
Cidaridea	296
Cypeastridea	296
Spatangidea	297
HOLOTHUROIDEA	297
Pedata	299
Apoda	299
ENTEROPNEUSTA	229

CHAPTER IX.

VERMES	303
PLATYHELMINTHES	309
Turbellaria	309
Rhabdocela	313
Dendrocela	314
Trematoda	316
Distomea	321
Polystomea	322
Cestoda	326
Nemertini	339
Enopla	342
Anopla	342
NEMATHELMINTHES	343
Nematoda	344
Chaetognatha	357
Acanthocephala	359
ANNELIDA	362
Chaetopoda	367
Polychæta	374
Errantia	378
Sedentaria	380
Oligochæta	382
Terricolæ	385
Limicolæ	385
Gephyrea	386
Chaetifera	389
Achæta	392
Hirudinea	394
ROTATORIA	400

* *Porifera* = *Spongia*
 I *Calcarea*

CHAPTER X.		Page
ARTHROPODA . . .	405	
CRUSTACEA . . .	411	
<i>Entomostraca</i> . . .	416	
Phyllopoda . . .	416	
Branchiopoda . . .	418	
Cladocera . . .	419	
Ostracoda . . .	423	
Copepoda . . .	428	
Eucopepoda . . .	435	
Branchiura . . .	436	
Cirripedia . . .	438	
Pedunculata . . .	445	
Operculata . . .	446	
Abdominalia . . .	446	
Apoda . . .	446	
Rhizocephala . . .	446	
<i>Malacostraca</i> . . .	447	
Arthrostraca . . .	449	
Amphipoda . . .	451	
Isopoda . . .	456	
Thoracostraca . . .	460	
Cumacea . . .	469	
Stomatopoda . . .	470	
Schizopoda . . .	472	
Decapoda . . .	475	
Macrura . . .	477	
Brachyura . . .	478	
<i>Gigantostraca</i> . . .	479	
Merostomata . . .	479	
Xiphosura . . .	480	
Trilobita . . .	483	
ARACHNIDA . . .	484	
Linguatulida . . .	487	
Acarina . . .	489	
Pygogonida . . .	495	
Tardigrada . . .	496	
Araneida . . .	498	
Tetrapneumones . . .	504	
Dipneumones . . .	504	
Phalangiidae . . .	505	
Pedipalpi . . .	506	
Scorpionidea . . .	508	
Pseudoscorpionidea . . .	510	
Solifugæ . . .	511	
ONYCHOPHORA . . .	512	
MYRIAPODA . . .	514	
Chilopoda . . .	518	
Chilognatha . . .	520	
HEXAPODA-INSECTA . . .	521	
Thysanura . . .	553	
Orthoptera . . .	534	
Orthoptera genuina . . .	550	
Orthoptera Pseudo-Neuroptera . . .	558	
Neuroptera . . .	562	
Planipennia . . .	563	
Trichoptera . . .	564	
Strepsiptera . . .	565	
Rhynchota . . .	566	
Aptera . . .	567	
Phytophthires . . .	568	
Homoptera-Cicadaria . . .	570	
Hemiptera . . .	571	
Diptera . . .	572	
Pupipara . . .	575	
Brachycera . . .	575	
Nemocera . . .	577	
Aphaniptera . . .	578	
Lepidoptera . . .	579	
Coleoptera . . .	585	
Hymenoptera . . .	590	
Terebrantia . . .	594	
Aculeata . . .	595	

GENERAL PART.

CHAPTER I.

ORGANISED AND UNORGANISED SUBSTANCES.

IN the world, which is perceptible to our senses, we distinguish between living organised and lifeless unorganised bodies. The former (*i.e.*, animals and plants) are endowed with the power of movement, and they remain the same in spite of manifold changes both of themselves as a whole and of their parts, and in spite of continual change of the matter entering into their composition. Unorganised bodies, on the other hand, are found in a condition of constant rest; and although this rest is not necessarily fixed and unchangeable, *yet they are without that independence of movement which manifests itself in metabolism.* In the former we recognize an organisation, a composition of unlike parts (organs), in which the matter exhibits its activity in a fluid and dissolved form; in the latter we meet with a mass which is more uniform, though as far as the position and arrangement of the molecules are concerned, not always homogeneous, and in which the various parts continue in a state of resting equilibrium so long as the unity of the body remains undisturbed. The matter of unorganised bodies (for instance, of crystals) is in a state of stable equilibrium, while through the organised being a stream of matter takes place.

The properties and changes of living bodies are strictly dependent on the physico-chemical laws of matter, and this is recognized more clearly as science advances; yet it must be admitted that we are entirely ignorant of the molecular arrangement of the material basis of a living organism, and it exists under conditions the nature of which is as yet unexplained. These conditions, which we may designate as vital, without thereby calling in question their dependence on material processes, distinguish organisms from all un-

organised bodies. They relate (1) to the mode of origin, (2) to the mode of maintenance, (3) to the form and structure of the organism.

Living bodies cannot be manufactured by physico-chemical means from a definite chemical mixture under definite conditions of warmth, pressure, electricity, etc.; their existence rather presupposes, according to our experience, the existence of like or at least very similar beings from which they have originated. It appears that, in the present state of our knowledge, there is no evidence to show that an independent abiogenetic generation (*generatio æquivoca*, spontaneous generation) actually takes place, even in the simplest and lowest forms of life; although very recently some investigators (Pouchet) have been led by results of remarkable but equivocal experiments to the opposite view. The existence of the *generatio æquivoca* would offer a very important service to our contention for the physico-chemical explanation; *it even appears to be a necessary postulate in order to explain the first appearance of organisms.*

The second and most important characteristic of organisms, and that on which the very maintenance of life depends, is their *metabolic power*, *i.e.*, the power which they possess of continually using up and renewing the matter composing the body. Every phenomenon of growth presupposes the reception and change of material constituents; every movement, secretion, and manifestation of life depend on the exchange of matter, on the breaking down and building up of chemical compounds. On this alternating destruction and renewal of the combinations of the body substance two properties necessary to living things depend, *viz.*, *the reception of food and excretion of waste products.*

It is the *organic* substances (so called on account of their occurrence in organisms), *i.e.*, the ternary and quaternary carbon compounds (the former composed of carbon, hydrogen, and oxygen, the latter of these with the addition of nitrogen, and among the latter are included the albumins) which undergo the exchanges characterising metabolism; they either (in animals) break up under the influence of oxidation into substances of simpler composition; or (in plants) are built up by substitution from simpler inorganic substances. But just as the general fundamental properties (elasticity, weight, porosity) of organisms agree so closely with those of inorganic bodies, that it was possible to construct a general theory of the constitution of matter, so all the elements (fundamental substances which differ qualitatively, and are chemically incapable of further simplification) of organic matter are again found in inorganic nature. A vital

element, *i.e.*, an element peculiar to organisms no more exists than does a vital force working independently of natural and material processes. Also with reference to the method of arrangement of the atoms, *organic and inorganic substances have been erroneously put in sharp contrast*; and the whole of the carbon compounds have been contemplated as the products of organisms only. Now, however, it has been shown for some time not only that the atomic arrangement and constitution of both are explained by the same laws, but also that a great many of the former (urea, alcohol, vinegar, sugar) can be artificially built up by synthesis from their elements. These facts point to the probability that many other organic substances will be synthetically produced, and among them, albumin; and they also permit us to conclude that in the origination of organised bodies the same forces were in action which are sufficient for the formation of unorganised bodies. The functions peculiar to organisms, *viz.*, metabolism, movement, growth, are accordingly to be referred to the properties of the chemical compounds composing them, and particularly to the complicated molecular arrangement of living matter.

Nevertheless, this important property of living things, *viz.*, metabolic action, may under certain conditions be temporarily suppressed, without thereby depriving the organism of the power of existence. By removal of water or of heat it is possible, in the case of many of the lower organisms and their germs, to suspend the vital processes for months and even years; and then to restore the apparently lifeless body to the full exercise of its vital properties by the simple addition of water or warmth (eggs of *Apus*, *Ostracoda*, *Anguillula tritici*, *Rotifera*—frogs, water insects, plant seeds).

Finally, the living body is distinguished by its entire form and by the manner in which its various parts are connected together; in other words, by its organization. The form of a crystal, the inorganic individual, is unchangeable, and is bounded by straight lines meeting at determined angles, and by plane, rarely spherical surfaces, which are capable of mathematical expression. The shape of organisms,* on the other hand, in consequence of the semifluid consistency of the material composing them, is less sharply determinable and is within certain limits variable. Life manifests itself as a connected series of ever-changing states; and the movements of matter are accompanied by growth and change of form.

* The fact that there are a number of solid excretion products of organisms (shells) whose form is mathematically determinable does not of course annul this distinction.

The organism commencing as a simple cell, the egg or germ, develops by a gradual process of differentiation and change of its parts up to a definite point at which it has the power of reproducing itself; finally it dies, and breaks up into its elements. The greater part of the substance composing organised bodies is more or less semifluid and liable to osmotic action,—a condition which appears to be necessary both for the carrying on of chemical changes (*corpora non agunt nisi soluta*), and for the modification of the entire form of the organism; it is not however homogeneous and uniform, but is composed of solid, semifluid, and fluid parts which exist as combinations of elements of a peculiar form. Crystals do not possess heterogeneous units subordinated to one another, which, *like the organs of living bodies, serve as instruments for the performance of different functions*, but are composed of molecules of similar atomic constitution; the absence of uniformity in their structure in different directions (planes of cleavage) being due to the arrangement of the molecules, and not to any difference in the molecules themselves.

Organs again prove, on examination of their finer structure, to be

FIG. 1.—*a*, young ova of a Medusa; *b*, mother-cells of spermatozoa of a Vertebrate; one of them presented amœboid movement.

built up of different parts or tissues (organs of a lower order), and these again are composed of the ultimate unit of cell, *the cell*. The cell, last of all, is to be traced back to

the germ cell (ovum, spermoblast) (fig 1.)

The cell by its properties stands in direct contrast to the crystal, and potentially possesses the properties of the living organism. *It consists of a small lump of a semifluid albuminous substance (protoplasm), containing, as a rule, a dense or vesicular structure, the nucleus, and is frequently surrounded by a peripheral structureless membrane.* If the latter is not developed, the presence of life is indicated by a more or less pronounced amœboid movement, the fluid protoplasm sending out and drawing in processes of a continually changing form.

In this organised fundamental structure, from which all tissues and organs of animals and plants are developed, lie latent all the characters of the organism. The cell is, therefore, in a certain sense the first form of the organism, and indeed the simplest organism. While its origin points to the pre-existence of cells of a similar kind, its maintenance is rendered possible by metabolism. The cell has its

nourishment and excretion, its growth, movement, change of form, and reproduction. With participation of the nucleus it begets by division or endogenous cell formation new units like itself, and furnishes the material for the construction of tissues, for the formation, growth and change of the body. With justice, therefore, is the cell recognised as the special embodiment of life, and life as the activity of the cell.

FIG. 2.—Amœba (Protophyes) porrecta (after Max Schultze)

Nor is this conception of the significance of the cell as the criterion of organisation and as the simplest form of life contradicted by the facts that the nucleus also sometimes fails (so-called cytodes of Hæckel), and that bodies undoubtedly manifesting vital phenomena are known which are structureless under the highest power of the microscope. Many Schizomycetes (Micrococcus) are so small that it is difficult to distinguish them in some cases from the granules of precipitates, especially when they show only molecular motion [Brownian movements] (fig. 3). *Consequently, the living protoplasm, with its unknown molecular arrangement, is the only absolute test of the cell and organism in general.*

While appreciating the essential differences which have been

expressed in the above discussion of the properties of living things and unorganised bodies, we must not in our criticism of the relations between them lose sight of the fact, that in numerous lower forms

FIG. 3.—Schizomycetes (after F. Cohn).
a, Micrococcus; b, Bacterium termo,
Bacteria found in putrefying bodies
both in motile and *Zooglæa* form.

of life, metabolism, and all the activities of life can be completely suppressed by the removal of warmth and water, without thereby injuring the capacity of the organism for continuing to live; and further, that in the smallest organisms, which are proved to be such by their capacity of reproducing themselves by their metabolism, and it is impossible, by means of the very strongest powers of the microscope, to detect any organization. Since, moreover, the organic matter composing such forms consist of combinations which can be produced by synthesis, independently of organization, we must allow that hypothesis a certain justification which asserts that the simplest forms of life

have been developed from unorganised matter, in which the same chemical elements occur as are found in organisms.

Since no fundamental difference has been shown to hold between the matter and force of crystals and those of organised beings, we might look upon the first appearance of life as essentially only the solution of a difficult mechanical problem (with Du Bois Reymond), were we not obliged to conclude that there is present even in the simplest and most primitive organisms the germs of sensation and consciousness, attributes which we cannot regard as simply the results of the movement of matter.

CHAPTER II.

ANIMALS AND PLANTS.

THE division of living bodies into animals and plants rests on a series of ideas early impressed on our minds. In animals we observe free movements and independent manifestations of life, arising from internal states of the organism, which point to the existence of consciousness and sensation. In the majority of plants, which pass their lives fixed in the earth, we miss locomotion and independent activities indicative of sensation. Therefore we ascribe to animals voluntary movement and sensation, and also a mind which is the seat of these.

Nevertheless these conceptions apply only to a proportionately narrow circle of organisms, viz., to the highest animals and plants. With the progress of experience, the conviction is forced upon us that the traditional conception of animals and plants needs, so far as science is concerned, to be modified. For although we find no difficulty in distinguishing a vertebrate animal from a phanerogamous plant, still our conceptions do not suffice when we come to the simpler and lower forms of life. There are numerous instances amongst the lower animals in which power of locomotion and distinct signs of sensation and consciousness are absent; while, on the other hand, there are plants which possess irritability and the power of free movement. Accordingly the properties of animals and plants have to be compared more closely, and at the same time the question has to be discussed, whether there are any absolute distinctive characters which sharply separate the one kingdom from the other.

1. In their *entire form and organization* there seems to be an essential contrast between animals and plants. Animals possess a number of internal organs of complicated structure, lodged within a compact outline; while in plants the nutritive and excretory organs are spread out as external appendages, with a considerable superficial extension. In the one case there is found an inner, and in the other an outer position for the absorbent surface. Animals have a mouth for the entry of solid and fluid nutritive matters, which are digested and absorbed in the interior of an alimentary canal, into which open various glands, (salivary glands, liver, pancreas, etc). The useless solid remains of the food pass out through the anus as fæces. The nitrogenous waste material is excreted by a special urinary

organ (kidney), mostly in a fluid form. For the movement and circulation of the fluid carrying the absorbed nutriment, there is a pulsatory pump (heart) and a system of blood vessels, while respiration is usually carried on in terrestrial animals by lungs, and in aquatic animals by gills. Finally, animals possess internally placed generative organs, and a nervous system, and sense organs for the production of sensation.

In plants, on the contrary, the vegetative organs have a much simpler form. Roots serve to absorb fluid nutriment, while the leaves act as respiratory and assimilating organs, taking in and giving out gas. The complicated systems of organs found in animals are absent, and a more uniform parenchyma of cells and vessels, in which the sap moves, composes the body of plants. The generative organs also are placed in external appendages, and there are no nervous and sense organs.

Nevertheless, the above mentioned differences are not universally found, but rather hold only for the higher animals and plants, and gradually disappear with the simplification of the organization.

Even among vertebrates, and still more is it the case amongst mollusca, and the lower segmented animals, the respiratory and vascular organs are considerably simplified. The lungs or gills may fail as special organs, and be replaced by the whole outer surface of

FIG. 4. Branch of a Polyparium of *Corallium rubrum* (after Lacaze Duthiers). P, Polyp.

the body. The blood vessels are simplified, and sometimes they and the heart are absent, the blood being moved in more irregular streams in the body cavity and in the wall-less spaces in the organs. Similarly, the digestive organs are simplified; salivary glands and liver may no longer be found as glandular appendages of the alimentary canal. The alimentary canal may become a blind, branched, or simple sac (Trematoda), or a central cavity, the walls of which are in contact with the body wall (Cœlenterata). The mouth and alimentary canal may also fail (Cestodes), nourishment being taken in by osmosis through the outer walls of the body as in plants. Finally, nerves

and sense organs are totally absent in many organisms, which are looked upon as animals, *e.g.*, in the whole of the Protozoa.

With such reduction of the internal organs it is easy to understand that the simpler lower animals, such as colonies of polyps and the Siphonophora, should often in their outer appearance and the manner of their growth resemble plants, with which they were formerly confounded, especially when they at the same time lacked the power of free locomotion (Polyps, Hydroids, figs. 4, 5). In these cases it is as difficult to limit the idea of "individuality" as it is in the vegetable kingdom.

2. *Between animal and vegetable tissues* there exists also generally an important difference. While in the vegetable tissues the cells preserve their original form and independence, in the animal tissues they undergo very various modifications at the expense of their independence. Accordingly vegetable tissues consist of uniform cell-aggregates, the individual cells of which have retained sharply-marked boundaries; while in animal tissues the cells give rise to

FIG. 5.—*Physophora hydrostatica*. *Pn*, Pneumatophore; *S*, Swimming-bells; *T*, Dactylozoid; *P*, polypite or stomach with the tentacles, *Sf*; *Nk*, terminal swellings on the latter provided with thread-cells; *G*, Clusters of gonophores

extremely different structures, in which the cells as such do not always remain recognisable. The reason for this unlike condition of the tissues must apparently be sought in the different structure of

the cell itself; the vegetable cell being surrounded outside its primordial utricle by a thick non-nitrogenous cuticle, the cellulose capsule; while the animal cell possesses a very delicate nitrogenous membrane, or instead of this only a more viscous boundary layer of of its own semi-fluid contents. Nevertheless, there are also vegetable cells provided only with a simple naked primordial utricle; and, on the other hand, animal tissues which resemble vegetable tissues in the fact that the cells remain independent and develop a capsule (chorda dorsalis, cartilage, supporting cells in the tentacles of hydroids, fig. 6)

FIG. 6.—*a*, Vegetable parenchyma (after Sachs). *b*, Axial-cells from the tentacles of *Campanularia*.

Neither can we, as has been done by many investigators, regard the multicellular composition of the body as a necessary sign of animal life. For not only are there many unicellular algæ and fungi, but also animal organisms which are composed of one simple or complexly differentiated cell (Protozoa). Finally, it is not possible to see any reason why unicellular animals should not exist, especially when we consider that the cell forms the starting-point for the development of the animal body.

3. Least of all can a test be found in the *reproductive* processes. In plants indeed we find a predominance of the asexual method of increase by spores and buds, but similar methods of increase are widely present amongst the lower and more simply organised animals. Sexual reproduction is effected both in animals and plants by processes which are essentially similar; consisting in both of the fusion of the male element (*spermatozoon*) with the female element (*ovum*); and the form of these elements presents in both kingdoms a great agreement, at any rate they are in every case derived from cells. The structure and position of the generative organs inside the body, or as outer appendages of it, cannot be regarded as a distinguishing mark, inasmuch as in both kingdoms the greatest difference prevails in this respect.

4. *The chemical constituents and the metabolic processes* in animals and plants present, on the whole, important features of difference. Formerly great importance was attached to the fact that plants consist chiefly of ternary (non-nitrogenous) compounds, while animals consist of quaternary nitrogenous compounds; and a greater importance was attached in the former to the carbon, in the latter to the nitrogen. But ternary compounds are found to be largely present in the animal body, *e.g.*, fats, carbohydrates; while, on the other hand, quaternary proteids play an important part in those parts of a plant which are especially active in growth. Protoplasm found in the living vegetable cell is richly nitrogenous, and of an albuminous nature; and it agrees in its micro-chemical reactions with sarcode, the contractile substance of the lower animals. In addition, the modifications of egg albumen, known as fibrin, albumen, and casein, are also found in vegetable cells. Finally, it is not possible to mention any substance which is universally and exclusively found either in animals or in plants. Chlorophyll (green colouring matter of leaves) occurs in the lower animals (*Stentor*, *Hydra*, *Bonellia*), while, on the other hand, it is totally absent in *Fungi*. Cellulose, a peculiar non-nitrogenous substance found in the outer membranes of vegetable cells, occurs in the mantle of *Ascidians*. Cholesterin, and certain substances especially characteristic of nervous tissue, are also found in plants (*Leguminosæ*).

Of far greater importance is the difference in the nourishment and metabolic processes. Plants take up with certain salts (phosphates and sulphates of the alkalies and earths) more especially water, carbonic dioxide (carbonic acid), and nitrates or ammonia compounds, and build up organic compounds of a higher grade from these binary inorganic substances. Animals, in addition to taking up water and salts, require organic food, especially carbon compounds (fat) and nitrogenous, albuminous substances; which, in the cycle of metabolism, break down to nitrogenous waste products (amides and acids), kreatin, tyrosin, leucin, urea, etc.; uric acid, hippuric acid, etc. Plants exhale oxygen, whilst they are decomposing carbon dioxide by means of their chlorophyll under the influence of light, and are forming in their chlorophyll corpuscles organic substances from carbon dioxide and solutions containing combined nitrogen. Animals take up oxygen through their respiratory organs for the maintenance of their metabolism. The processes of metabolism and of respiration, therefore, in the two kingdoms are indeed mutually determinant, but have an exactly opposite result. The life of animals depends on the analysis

of complex compounds, and is essentially an oxidation process, by which potential energy is converted into kinetic (movement, production of heat, light). The vital activity of plants, on the contrary, is based, so far as it relates to assimilation, on synthesis, and is essentially a process of reduction; under the influence of which the energy of warmth and light is stored up, kinetic energy being converted into potential.

FIG. 7.—Leaf of *Drosera rotundifolia*, with partially contracted tentacles (after Darwin).

Nevertheless, this difference also is not applicable as a test in all cases. Recently the attention of investigators has been turned, especially by Hooker and Darwin,* to the remarkable nutritive and digestive processes in a group of plants which were first observed a hundred years ago (Ellis). The plants in question catch, after the manner of animals, small organisms, especially insects, and absorb from them through the glandular surface of their leaves the organic matter after a chemical process resembling animal digestion (leaves of the Sun-dew, *Drosera rotundifolia*, and the fly-catcher, *Dionæa muscipula*. Figs. 7 & 8).

FIG. 8.—Leaf of *Dionæa muscipula* in expanded condition (after Darwin).

Many parasitic plants and almost all fungi have not, however, in general, the power of making organic substances from inorganic, but suck up organic juices; and in taking up oxygen and giving out carbonic acid, they present a respiratory process resembling that found in animals.

It was established by Saussure's observations that all plants require oxygen at certain intervals; that in those parts of plants which are not green, not possessing chlorophyll, and also in the green parts in the absence of sunlight, *i.e.* at night, a consumption of oxygen and exhalation

* Compare especially Ch. Darwin, "Insectivorous Plants." London, 1875.

of carbonic acid goes on. In plants, therefore, together with the characteristic deoxidation process, there is always found a process of oxidation analogous to that occurring in animal metabolism; by which a part of the assimilated substances is again destroyed. The growth of plants is impossible without the consumption of oxygen and the production of carbonic acid. The more energetic the growth, the more oxygen is consumed, as indeed the germinating seed or the quickly unfolding leaf and flower buds rapidly consume oxygen and excrete carbonic acid. In this connection should be mentioned the fact that the movements of protoplasm depend upon the inspiration of oxygen. The production of heat (in germination), also of light (*Agaricus olearius*) is accompanied by an active consumption of oxygen. Finally, there are organisms (yeast cells, Schizomycetes) which indeed manufacture both nitrogenous and albuminous compounds, but do not assimilate the carbon of carbonic acid, but rather derive the necessary carbon from prepared carbohydrates (Pasteur, Cohn).

5. *Voluntary movement and sensation*, according to the common view, is the chief characteristic of animal life. Formerly, the power of free locomotion was looked upon as a necessary property of animals; and as a consequence of this the fixed colonies of Polyps were considered to be plants, until Peyssonnel brought forward proof of their animal nature, a view which by the influence of the great naturalists of the last century has gained general recognition. More recently, on the discovery of the existence of motile spores of algæ, it was first recognised that plants also, especially at certain stages of their development (fig. 9), possessed the power of free locomotion, so that we are compelled to direct our attention to the signs by which the voluntary nature of the movement can be decided for a dis-

FIG. 9.—Zoospores, a, of *Physarum*; b, of *Monostroma*; c, of *Ulothrix*; d, of *Bedogonium*; e, of *Vaucheria* (after Reinke).

distinction between the respective movements of animals and plants. As such for a long time was regarded the contractile nature of the movement as opposed to the uniform movements of plants carried out with rigid bodies.

In the place of muscles, which as a special tissue are absent in the

lower animals, there is present an undifferentiated albuminous substance known as sarcode, the contractile matrix of the body. The

FIG. 10.—Zoospores of *Aethalium septicum* after de Bary. *a*, in condition of hatching; *b*, as mastigopods; *c*, in the amoeboid stage; *d*, a piece of plasmodium.

development of *Myxomycetes*, the contractile power is as intense as in the sarcode of *Infusoria* and *Rhizopoda*. The amoeboid movements of the plasmodium of *Myxomycetes* (fig. 10) are not inferior

FIG. 11.—*Amœba Dactylosphæra polypodia*. N, nucleus. Pv, contractile vacuole (after Fr E. Schulze).

viscous contents of vegetable cells, known as protoplasm, possesses likewise the power of contractility, and resembles sarcode in its most essential properties. Both present the same chemical reactions and agree in the frequent presence of cilia, vacuoles, and streams of granules. Pulsating spaces, the contractile vacuoles, are not exclusively a possession of sarcode, but may also occur in the protoplasm of vegetable cells (*Gonium*, *Chlamydomonas*, *Charophora*). The contractility of the protoplasm of vegetable cells is, as a rule, limited by the cellulose membrane, but in the naked cells of *Volvocina* and *Saprolegnia*, and in the amœba-like forms occurring in the

development of *Myxomycetes*, the contractile power is as intense as in the sarcode of *Infusoria* and *Rhizopoda*. The amoeboid movements of the plasmodium of *Myxomycetes* (fig. 10) are not inferior in intensity to those of a genuine *Amœba* belonging to the *Rhizopoda*, e.g., *Amœba polypodia* (*princeps*), (fig. 11). In these similar phenomena of movement of the lower animals and plants we seek in vain for any test of volition, the interpretation of which will depend upon the individual judgment of the observer.

The faculty of sensation, which is inconceivable as a function of matter and which must be always pre-supposed wherever we have to do with voluntary movement, can by no means be affirmed with

certainty in all animal organisms. Many of the lower animals entirely lack a nervous system and sense organs, and, on stimulation, exhibit

but slight movements not more intense than those of plants. This irritability, however, appears widely present among the higher plants. The sensitive plants move their leaves on the application of mechanical stimuli (*Mimoseæ*), or bend like the sundew (*Drosera*, fig. 7) small knobbed processes of the leaf surface which are comparable to the tentacles of polyps. The fly-catcher (*Dioncæa*, fig. 8) brings the two halves of the leaf together in a valve-like manner when touched by insects. The stamens of the *Centaurea* contract along their whole length on mechanical and electrical stimulation, and according to the same laws as do the muscles of the higher animals. Many flowers open and shut under the influence of light at certain times of the day.

Accordingly *irritability* as well as *contractility* appears to be a property both of vegetable tissue and of the protoplasm of vegetable cells; and it is not possible to determine whether volition and sensation, which we exclude from these phenomena in plants, play a part in the similar sensory and motor phenomena of the lower animals.

In none of the above-mentioned characteristics of animal and vegetable life, then, do we find any absolute test, and we are not in a position to indicate the presence of a sharp line between the two kingdoms.

From the common starting-point of the contractile substance* animals and plants are developed in different directions; at the beginning of their development they present many kinds of resemblance, and it is only on their attaining a more complete organization that the full opposition between them is apparent. In this sense, without wishing to draw a sharp line between the two series of organization, we can define our conception of an animal by putting together all the characteristics distinguishing the direction of animal development.

An animal, therefore, is to be defined as an organism provided with the power of free and voluntary movement, and with sensation; whose organs are internal, and are derived from a development of the internal surfaces of the body; which needs organic food, inspires oxygen, changes potential energy into kinetic under the influence of oxidation processes in metabolism, and excretes carbonic acid and nitrogenous waste products.

* The formation of an intermediate kingdom for the simplest forms of life is neither scientifically justified, nor from practical considerations desirable. On the contrary, the acceptance of the *Protista* would only double the difficulty of determining the limit.

Zoology is the science which has animals for its subject, and which seeks to examine the phenomena of their structure and life, as well as their relations to one another and to the outer world.

CHAPTER III.

THE ORGANIZATION AND DEVELOPMENT OF ANIMALS IN GENERAL.

In the foregoing comparison of animals and plants for the establishment of a correct idea of the meaning of the word "animal," the great variety and the numerous grades of animal structure have been hinted at. Just as the complex organism is built up from the ovum by a process of gradual differentiation, and often during its free life passes through conditions which lead in ascending series to an ever higher development of the parts and to a more complete performance of functions; so, if the animal kingdom be examined as a whole, there is apparent a similar law of gradually progressing development, of an ascent from the simple to the complex, manifest both in the form of the body and in the composition of its parts as well as in the completeness of the phenomena of life.

It is true that the grades of animal structure do not, like those of the developing individual, follow the one upon the other in a single continuous series; and the parallel between the developmental gradation of types in the animal kingdom as a whole and the successive conditions of an individual animal breaks down in so far as we distinguish in the former, as opposed to the latter, a number of types of animal structure often overlapping, but still, in their higher development, essentially different from each other. These we regard as the highest divisions of the system.

INDIVIDUAL—ORGAN—STOCK.

The animal organism, when viewed from a physiological and morphological stand-point, presents itself as an independent and indivisible unit, as a "complete individual." Amputated limbs or excised parts of the body do not develop into new animals; in fact we cannot usually remove a single piece of the body without thereby endangering the life of the organism, for it is only as a complex of all its parts that the body can retain its full vital energy. With reference to the property of the indivisibility of the individual, we understand

by the term organ every part of the body which as a unit subordinate to the higher unit of the organism presents a definite form and structure, and performs a corresponding function; that is to say, an organ is one of those numerous instruments on the combined working of which the life of the individual depends.

There are certainly among the simpler animals many instances in which the term individual in its usual sense cannot be rightly applied. In such cases we have to do with structures which from their development must be termed individuals, and represent individuals, accordingly, in a *morphological* sense. A great many of them are, however, fused to a common stock, forming what is known as a colony, and are related physiologically to this, as organs are to an organism. They are accordingly *incomplete* or *morphological* individuals, which are usually incapable of leading a separate existence; and, when they differ from each other in form and function, dividing amongst themselves the labours, the performance of which is necessary for the maintenance of the whole colony, they always perish if separated from it.

Such polymorphous* stocks of animals present the properties of individuals although they are morphologically aggregations of individuals which behave physiologically as organs (fig. 5). On the other hand, groups of organs can acquire individual independence.

In the animal body organs do not always remain single, but the same organ may be often repeated. The manner of the repetition is dependent on the kind of symmetry, which may be radiate or bilateral. In animals with radiate symmetry, the *Radiata*, it is possible to connect two opposite points of the body by an axis, which may be called the chief axis, and to divide the body by sections passing through this axis into a number of equivalent and symmetrical parts known as *antimeres*. The organs which are not repeated are situated in the chief axis of the body, while the other organs, which are uniformly repeated in each antimere, are situated peripherally. Each antimere contains, therefore, a definite group of organs and represents a secondary unit, which, together with its fellows and the central organs, constitutes the primary unit, *i.e.*, the perfect animal.

In a radiate animal a number of lines can be drawn at right angles to the chief axis, corresponding in number to the antimeres, and each passing along the middle of an antimere; such lines are known as *radial*. Similarly, a corresponding number of *inter-radial* lines

* *Vide* R. Leuckart, "Ueber den Polymorphismus der Individuen und die Erscheinung der Arbeitstheilung in der Natur." Giessen, 1851.

can be drawn, passing between the antimeres. A vertical section through a radial line divides the corresponding antimere into two

FIG. 12*a*.—Sea-urchin (diagrammatic). *J*, inter-radius with the double row of interambulacral plates and the genital organs *G*; *R*, radii with the double row of ambulacral-plates perforated by the ambulacral pores. *A*, anus.

FIG. 12*b*.—Shell of a Sea-urchin seen from above. *R*, radius with the perforated plates; *J*, inter-radius with the corresponding generative organs and their pores.

equal parts, while a similar section through an inter-radial line divides one antimere from its neighbour. Radiate animals may have

FIG. 13.—Star-fish (diagrammatic). *G*, generative organ in inter-radius; *Af*, position of the ambulacral feet in the radii.

two, three, etc., radii; and in animals which possess an uneven number of radii, one radius and one inter-radius always fall in the same vertical plane (fig. 12*a*, *b*, and fig. 13). In animals with an even number of radii, on the contrary, each vertical plane passes through two radii or two inter-radial. A vertical section passing through one radius would, if prolonged, pass through the radius of the opposite antimere (fig. 14*a*). For example, an animal with four radii

possesses four antimeres, each of which will be divided into two, by two radial vertical sections passing at right angles to each other through the chief axis; while they will all be separated from each other by two similarly directed inter-radial sections.

Biradial forms (the Ctenophora) possess, on the contrary, only two radii, which lie in a common vertical plane. A second vertical plane crossing the first at right angles passes through the inter-radial, and

divides the antimeres from each other. The first, in which the greater number of organs are repeated, may be designated the *transverse plane*, while the second, corresponding to the median plane of bilateral animals, is known as the *sagittal plane* (fig. 14b).

FIG. 14a.—Acalepha larva (Ephyra).
Rk, marginal body; Gf, gastric filament. Rc, radial-canal; O, mouth.

FIG. 14b.—Ctenophore seen from above. S, sagittal plane; T, transverse plane; R, vibratile plates; Gf, gastric canals.

In the bilateral arrangement, which is found also in each individual antimeres of the Radiata, only one plane, the *median plane*, can be imagined, which passes through the chief axis and divides the body into two exactly similar parts (right and left). These two halves, as opposed to antimeres, may be termed *parameres*. In bilateral animals we distinguish an anterior and posterior end, a right and a left side, and a dorsal and a ventral surface. The unpaired organs are placed in the middle line, on each side of which, in the two halves of the body, are placed the paired organs. The plane which is placed at right angles to the median plane (passing from right to left) and separates the unlike dorsal and ventral halves of the body, is known as the *lateral plane*. The antimeres of the Radiata also consist of two parameres, and are therefore bilateral, in that the vertical plane passing through the radius like the median plane divides them into two similar parts.

The same groups of organs or similar parts of the same organ may also be repeated in a longitudinal direction. This occurs especially frequently in bilateral, less frequently in radiate animals (*strobila*). The body thus obtains a segmentation, and is divisible into successive sections, the *segments* or *metameres*,

FIG. 15.—Segmented worm (Polychaete). Ph, pharynx; D, alimentary canal; C, cirrus; F, tentacle

which are placed one behind the other, and more or less completely resemble each other in structure (*Annelids*, fig. 15). The successive segments may in structure and function appear completely equivalent, and represent, like the antimeres of the Radiata, individuals of a lower order, which on the severance of their mutual connection can acquire independence and remain alive for a shorter or longer period (*proglottis* of Cestodes).

In animals of higher organization the segments are much more intimately connected, and are mutually dependent, but they lose at the same time their complete homonomy. In the same degree as the metameres acquire an unlike structure, and corresponding to this a varying importance in the life of the organism, they lose their individual independence, and sink more and more to the value of organs.

The metameres in the polymorphous colonies are quite analogous to the segments of the individual. In them there follow, one behind the other, similar groups of different individuals, each of which fulfils singly the conditions necessary for existence, and therefore can continue to live as a colony of a lower order when separated from the stock (*Eudoxia*, *Diphyes*, fig. 16).

FIG. 16.—Portion of *Diphyes* after R. Leuckart). *D*, hydrophyllium; *GS*, gonophore; *P*, Polyp with tentacle. The groups of individual's separate themselves as *Eudoxia*.

The distinction into a higher and lower order also holds for organs. There are organs which are reducible to a single cell, or to an aggregation of equivalent cells (simple organs), and others in the formation of which various cells and tissues (compound organs) participate, and which frequently, in their turn, may be divided into parts different in structure and function. The compound organs of higher order are composed of different parts which function as organs of a lower order. These, again, are composed of various kinds of cells and cell derivatives, which are organs of a still lower order. Finally, in the last analysis, we come to the cell or the area of protoplasm corresponding to it, which is the simplest and ultimate organ. On the other hand, we group together organs of different order, which are intimately connected so far as their chief function is concerned, under the name of *system* (vascular system, nervous system) or *apparatus* (digestive apparatus), although we cannot clearly distinguish them from compound organs.

CELLS AND CELL TISSUES.

The constituent parts of which an organ is made up are known as tissues. They possess a definite structure, visible with the help of a microscope, and have either the form of cells or of structures derived from cells. Tissues have a function corresponding to their special structure, and this function determines the whole function of the organ. They may, therefore, be regarded as organs of a lower order. The ultimate unit, the organ of the lowest order, or elementary organ,* from which all tissues are derived, is the cell. The essential part of a cell is not, as we have already seen, the membrane or the nucleus, but the protoplasm, with its special molecular arrangement, in which reside the functions of independent movement, of metabolism and of reproduction (fig. 1).

The nucleus of a cell is either a solid mass of protoplasm or a more fluid structure enclosed by a firm membrane, and may contain one or more solid bodies (nucleolus). Different as are the forms which the nucleus may take, it always contains a fluid substance, the *nuclear fluid*, and a protoplasmic substance, the *nuclear substance* of a special importance for the functions of the nucleus (fig. 17).

An important and very general property of protoplasm is its power of contractility. The living mass presents, in connection with metabolism, phenomena of movement. These movements are not merely confined to the currents of solid particles suspended in the viscous contents of the cell, but are shown also in the change of form of the whole cell. If the outer part of the protoplasm has condensed so as to give rise to a cell membrane, *i.e.*, if the cell has acquired a distinct wall, the changes in its form are very much restricted. In other cases the movement shows itself in a quick or slow change in the outer form. The cell in this case manifests

FIG 17.—Different forms of nuclei (after R. Hertwig). *a*, nucleus from a cell of a Malpighian tubule of a caterpillar. *b*, nucleus of a *Heliozoon* with a cortical layer and nucleolus in the nuclear fluid. *c*, nucleus from the egg of a Sea-urchin. Nucleolus imbedded in a protoplasmic fibrous network surrounded by nuclear fluid.

* Th. Schwann, "Microscopische Untersuchungen über die Uebereinstimmung in der Structur und dem Wachsthum der Thiere und Pflanzen." Berlin, 1839. Fr. Leydig, "Lehrbuch der Histologie des menschen und der Thiere." Frankfurt a.M. 1857.

the so-called amœboid motion; it sends out processes, draws them in again, and is able by such means to change its position. This capacity of change of form is especially possessed by young undifferentiated cells, which have not developed an outer membrane. Such cells in their later growth usually develop a cell membrane, which accordingly is not, as was formerly supposed, a necessary constituent of the cell, but is merely an indication that the cell has undergone a certain amount of differentiation from its early indifferent condition.

It has been already pointed out that the fundamental properties which distinguish the life of organisms manifest themselves also in the life of their constituent cells. According to our present knowledge, cells always originate from pre-existing cells; a process of free cell formation, as conceived by Schwann and Schleiden, indicated by the precedent origin of nuclei in a formative organic material, has never been proved.

Such a process may, however, take place when the formative matter is the plasma of a cell, or of several cells fused together (plasmodium). In such cases we have a process of free cell formation (*e.g.*, spore formation in *Myxomycetes*) which certainly is not clearly marked off from a process of new formation within the mother cell, and is to be looked upon as a modification of the so-called endogenous cell formation. This leads us to a consideration of the very widely distributed method of cell increase by *division*. When the cell has reached a certain size by the absorption and assimilation of nutrient matter, the protoplasm separates itself into two nearly equal portions, this process being usually preceded by the division of the nucleus. Each portion receives half of the original nucleus.

During its division the nucleus undergoes, as has been recently shown in many instances, peculiar differentiations and changes (fig. 18). It becomes spindle-shaped; its contents take on the form of longitudinally arranged striæ, running from pole to pole of the spindle; the centre of each of the striæ becomes thickened, giving rise to a cross equatorial zone of granular matter, the nuclear plate (thickened zone). The central thickenings constituting the nuclear plate divide. Each half travels towards the poles of the spindle, and becomes there enclosed in a clear fluid mass, which appears in the protoplasm. From these two structures the new nuclei are formed at the poles of the now dumb-bell shaped nuclear spindle, the striæ of which vanish during the constriction of the protoplasm, which has already commenced and quickly progresses. The division

is completed when the young nuclei, proceeding from the two poles of the nuclear spindle and the surrounding clear protoplasm, have attained their definite size, and the remains of the fibres have been absorbed.

During these processes the protoplasm of the cell has gradually become more and more constricted by a furrow which is directed transversely to the long axis of the nuclear spindle, and which after the completion of the division of the nucleus brings about a separation of the cell contents into two masses—the daughter cells (fig. 18).

If the products of the division are unequal, so that the smaller portion may be looked upon as a production of the larger, we give the name "*budding*" to this form of reproduction.

FIG. 18.—Processes of cell division in an embryonic blood corpuscle of a chick (after Bütschli). K, nuclear spindle. Kp, nuclear plate or equatorial thickening.

Finally, the term *endogenous* cell formation is applied to that method of increase in which the cells originate within the mother-cell. In this case the protoplasm does not divide by a progressive constriction and separation into two or more parts, but differentiates itself round the newly formed nuclei, with which the original nucleus may persist.

The ovum which we have to contemplate as the starting-point of the development of the organism produces by these various methods of cell multiplication the material of cells which serves for the formation of the tissues. Groups of originally indifferent and similar cells break up and assume severally a changed appearance. The constituent elements undergo various differentiations, and from them and their derivatives is produced a definite form of tissue, endowed with a function corresponding to the peculiarity of its structure.

The separation of groups of different cells leading to the establishment of various tissues prepares the way for the physiological division of labour between the organs, which, like the tissues composing them, can, according to the functions which they perform, be divided into *organs of vegetative life* and *organs of animal life*.

The former have to do with the nutrition and maintenance of

the body; the latter, on the contrary, serve for movement and sensation, functions which are exclusively the property of animals (as opposed to plants). For the sake of clearness we will divide the vegetative tissues into two groups,—into cells and cell-aggregates (epithelium), and into tissues of connective substance. In the tissues of animal life we distinguish muscular and nervous tissues. This classification of the tissues has no other aim than to facilitate a general review of the different forms of tissue, and to render possible a criticism of their relationships; it lays no claim to establish an absolutely sharp line between the various groups.

1. Cells and cell-aggregates. Cells may either be free and isolated from each other, floating in a fluid medium, or they may be placed near one another forming part of an aggregation of cells spread out superficially. To the former belong the cells of the blood, chyle, and lymph. The blood of invertebrates, which is generally colourless, and

FIG. 19.—Blood-corpuscles (after Ecker). *a*, colourless blood corpuscles from the heart of the fresh water mussel (*Anodonta*). *b*, from the caterpillar of *Sphinx*. *c*, red corpuscles from *Proteus*. *d*, from the smooth adder. *d'*, lymph corpuscles of the same. *e*, red corpuscles of the frog. *f*, of the pigeon. *f'*, lymph corpuscles of the same. *g*, red blood corpuscles of man.

the blood of vertebrates, which is with few exceptions red, consists of a fluid albuminous plasma containing numerous blood-corpuscles in suspension. These corpuscles are in invertebrates irregular often spindle-shaped cells, endowed with the capacity of amœboid movement. In the blood of vertebrates, in addition to such colourless amœboid corpuscles there are found red corpuscles (discovered by Swammerdam in the frog); and these are so numerous as to give the blood a uniformly red appearance to the unaided eye. They are thin discs with an oval, nearly elliptical or circular (*Mammalia* *Petromyzon*) contour, with nuclei in the first case, and without nuclei in the second (except in the embryo) (fig 19). They contain

the red colouring matter of the blood, *hæmoglobin*, which plays so important a part in respiration. They arise in all probability from the colourless corpuscles which are always far less numerous in normal blood. The colourless corpuscles are genuine cells of variable form, and have the power of amœboid motion (migration into tissues, regeneration of tissues, etc.); they come from the lymphatic glands, in which they arise as lymph corpuscles, and eventually pass with the lymph stream into the blood. The ova and spermspores, after

FIG. 20.—Spermatozoa. *a*, of Medusa. *b*, of a Nematode. *c*, of a Crab. *d*, of Torpedo. *e*, of Salamander (with undulating membrane). *f*, of Frog. *g*, of a Monkey (*Cercopithecus*).

they have separated from the epithelial layer in the wall of the ovary and testis, as well as the spermatozoa produced from the spermspores, respectively belong to the category of free cells. The form and size of the spermatozoa present great variations. They always consist of a modified cell, frequently of a very small cell with a long flagellum, nucleus, and remains of protoplasm. In many cases the head is elongated into a fibre-like structure, or is twisted like a corkscrew (Birds, Selachians). Sometimes a distinct head is absent, and the spermatozoon is thread-like (Insects). In the Nematodes the sperm-

atozoon is hat-shaped; while in Crustacea it has the form of a cell, with long radiating processes (fig. 20).

Epithelial tissues consist of aggregations of cells which as simple or stratified layers cover the external and internal surfaces of the body, and line its closed spaces (*endothelium*). According to the different shape of the cells composing it, we distinguish cylindrical, ciliated, and pavement epithelium. In the first case the cells, in consequence of the elongation of the long axis, are cylindrical (fig. 21, *c*); in the second, the free surface of the cells is beset with vibratile cilia or flagella (fig. 21, *d*), which are continuous with the living protoplasm of the cell. If only one flagellum projects from the cell (sometimes a flat cell fig. 21, *b*) then the name flagellate cell is applied (collared cell of sponges, fig. 21, *e*). Finally, in the case of pavement epithelium (fig. 21, *a*) the cells are flattened; and if there

FIG. 21.—Various kinds of epithelial cells. *a*, Flat cells. *b*, flat cells with flagella (from a Medusa). *c*, cylindrical cells. *d*, ciliated cell. *e*, flagellate cell with collar (from sponge). *f*, cylindrical cell with porous border (intestinal epithelium).

is more than one layer the superficial cells are flat, while those in the deeper layers are more and more rounded.

While the cells of the lower layers retain their semi-fluid character, and are occupied in continual cell division and growth; those of the upper layers possess a firmer consistency, gradually become horny, and are thrown off as scales or continuous flakes, to be replaced by the continuous growth of the lower layers. Thick stratified layers of cornified cells, almost fused with one another, give rise to indurated or horny structures (nails, claws, hoofs), which may form a more or less complete coat for the body and function as a protective exoskeleton (fig. 21, *a* to *f*).

There are also cells the free surface of which is distinguished by a

well-marked thickening. The protoplasm of the free surface of such cells becomes hardened so as to give rise to a thick superficial border, perforated at right angles to its surface by a number of fine canals which give it a striated appearance (intestinal epithelium, fig. 21, *f*, epidermis cells of *Petromyzon*). If these thickened borders fuse together so as to form a continuous layer which obtains a certain independence, we obtain cuticular membranes, which, according to their origin, may be homogeneous or stratified (fig. 22, *a*, *b*, *c*), and

FIG. 22c.—*Cu*, cuticle with bristles in the condition of ecdysis. *Cu'*, newly-formed cuticle (*Branchipus*).

FIG. 22.—*a*, Cuticle and hypodermis of the larva of *Corethra*. *b*, cuticle and hypodermis of a *Gastropacha* caterpillar, with two poison glands beneath corresponding bristles.

may exhibit various patterns of different kinds. Very frequently the surfaces of the individual cells are indicated on the cuticle as polygonal figures; and, in addition to the very fine pores, there are also found larger passages produced by out-growth from the cells. These latter lead to the appearance of various cuticular appendages, such as hairs, bristles, scales, etc., which are placed on the cuticular pores, and contain as a matrix their special cell or a process of it. Cuticular membranes may obtain a very considerable thickness, and, by the deposition of calcareous salts, a high degree of firmness (carapace of Crustacea) so that they acquire the value of skeletal tissues, which,

however, it is generally difficult to distinguish from certain connective tissues.

While cuticular structures are solid secretions which are of use in supporting and giving a definite form to the organism, there are, on the other hand, various fluid secretions proceeding from cells which give rise to no structures, and which are often of considerable importance from a chemical point of view. In this case the epithelium becomes glandular tissue. In the simple cases the gland is constituted of a single cell, the secretion of which either passes out through the free surface of the membrane, or a special opening in

FIG. 23.—Unicellular glands. *a*, goblet cells from the epithelium of the small intestine of a vertebrate. *b*, unicellular cutaneous gland of *Argulus* with long duct. *c*, unicellular cutaneous gland of insects with cuticular duct.

the inner or the outer surface of the body, into the subjacent tissue.

From this fundamental form the larger and more complicated glands are to be derived, as the result of continued regular and irregular outgrowth. While their form presents great variations, they are universally characterised by the transformation of their terminal portion into a duct; this differentiation may also appear in the simple glandular tubes, and even in the unicellular glands (figs. 23, 24).

FIG. 24.—Gastric glands. *a*, their origin as invaginations of the epithelium. *b*, perfect gastric glands.

it (fig. 23). If several cells enter into the formation of a gland, they are arranged, in the simplest cases, round a central cavity, which receives the secretion. The gland then has the form of a sack or blind tube, derived from an invagination of the epithelium, either of

2. The tissues of the connective substance. Under this term there are included a great number of different tissues which morphologically resemble each other in the presence of a greater or less amount of intercellular substance, intercalated between the cells (connective tissue corpuscles). They connect and surround other tissues, and serve as supporting and skeletal structures. The intercellular substance arises from the cells as a differentiation of the peripheral part of their protoplasm; it cannot accordingly be genetically clearly distinguished from the cell membrane and its differentiations, which we have considered in connection with epithelial tissue. The cell walls already produced by the protoplasm may also become fused with the intercellular substance, and so contribute to its increase. The intercellular substance is usually secreted by the whole periphery of the cell, and presents great variations both in its morphological and chemical characters.

When the amount of intercellular substance is small, the tissue is called *cellular* or *vesicular* connective tissue. This form is found especially in medusæ, molluscs, and worms, and to a less extent in vertebrates (notochord, fig. 25), and is not sharply marked off from cartilaginous tissue. Embryonic connective tissue, which consists of closely aggregated embryonic cells, evidently closely resembles it.

Mucous or *gelatinous* connective tissue is characterised by possessing a watery hyaline and gelatinous matrix. The condition of the cells in each case is different. Frequently they send out delicate, often branched processes which anastomose with one another and form a network. In addition, however, parts of the intercellular

FIG. 25.—Vertebra of larva of a toad (after Götze). *Ch*, notochord cells; *ChS*, notochord sheath; *Sk*, skeletogenous tissue; *N*, spinal cord.

substance may be differentiated into bundles of fibres (Wharton's gelatine in the umbilical cord). Such forms of tissue are found amongst the Invertebrata, *e.g.*, in Heteropods and Medusæ, whose gelatinous disc, in consequence of the reduction or complete absence of cells, is reduced to a layer of soft or hardened connective tissue but little different in its origin, as a unilateral cell excretion, from cuticular structures (Hydroid Medusæ, swimming bells of Siphono-

phora). The so-called secreted tissue of young Ctenophora, and the gelatinous tissue of Medusæ and Echinoderm larvæ, into which cells eventually migrate, being at first absent, has a similar relation (fig. 26).

FIG. 26.—Gelatinous tissue of *Rhizostoma*. *F*, fibrous network; *Z*, cells with processes; *Z'*, the same in division.

Reticular connective tissue consists of a network of star-shaped and branched cells, the spaces of which contain another kind of tissue element. In the so-called adenoid tissue, which functions as the supporting tissue of the lymph glands, the contents of the intercellular spaces are lymph corpuscles.

FIG. 27.—Fibrillar connective tissue.

A form of connective tissue very widely scattered amongst the Vertebrates is the so-called *fibrillar connective tissue* (fig. 27). This consists of a large proportion of spindle-shaped, or branched cells, and of a solid intercellular substance, which is totally or partially broken up into bundles of fibres and possesses the property of

yielding gelatine on boiling. If the protoplasm of the cells is mostly or entirely used up in the formation of fibres, fibrous tissue is produced with nuclei in the position of the original cells. Very often the

fibres have a wavy outline, and are arranged nearly parallel to one another (ligaments, tendons). In other cases they cross one another at an angle in different directions (dermis), or they present a net-like arrangement (mesentery). Fat tissue consists of ordinary connective tissue in which the cells are for the most part round and contain greater or smaller fat globules.

If the normal fibrillæ and bundles of fibrillæ be treated with acids and alkalis, they swell up, and a second form of fibre, which resists these re-agents, comes into view. These are the *elastic fibres* (fig. 28), so called because they preponderate in tissue which is especially elastic. They present a tendency to branch and to form networks, and often possess great strength (ligamentum nuchæ, arterial walls). They may also be spread out and connected together so as to form a perforated membrane (fenestrated membrane).

Cartilage is another form of connective tissue. It is characterized by the shape of its cells, which are usually spherical, and its firm intercellular substance. The latter contains chondrin, and determines the rigidity of the tissue. Externally, cartilage is covered by a vascular connective tissue-coat, known as the perichondrium. When the intercellular substance is very slightly developed, we get tissues which are transitional between cellular connective tissue and cartilage.

FIG. 28.—Elastic fibres, *a*;
b, network.

FIG. 29.—*a*, Hyaline cartilage with cells. *b*, Fibro-cartilage.

According to its special constitution, three kinds of cartilage may be distinguished, viz., hyaline (fig. 29, *a*), fibrous (fig. 29, *b*), and

elastic cartilage; the latter containing a network of elastic fibres. There are also intermediate forms, approximating to the fibrillar connective tissue, in which cartilage cells may be surrounded by bundles of connective tissue fibres. The cells are placed in spaces, which are usually round, in the intercellular substance, and are surrounded by firm layers which are separated off from the latter, and have the appearance of capsules. These so-called cartilage capsules were formerly looked upon as the membranes of the cartilage cells, analogous to the cellulose capsules of plant cells; a view of them which is not in any way opposed by what is known as to their development as secretions of the protoplasm. Nevertheless, the capsules stand in closer relation to the earlier formed intercellular substance which has been produced in the same way, in that they often fuse with it. The growth of the cartilage is accordingly in the main interstitial. We frequently see in the spaces in the cartilage

FIG. 30.—Incrusted cartilage, or cartilage bone.

several generations of cells surrounded by special capsules placed one within the other. In such cases the secreted capsules have remained separate from the intercellular substance. Certain kinds of cartilage, moreover, have spindle-shaped cells, and sometimes the cells are prolonged into numerous radiating processes.

Calcareous salts may also be deposited in the intercellular substance in a greater or less quantity. In this way arises the so-called incrustated cartilage, or the cartilage bone (fig. 30), which in the sharks is present as a persistent form of skeletal tissue, but in the higher vertebrates only as a transitional structure. Cartilage owes its special usefulness as a skeletal tissue to its rigidity. It is sometimes found in the Invertebrata (Cephalopoda, tubicolous worms such as *Sabella*, *Cœlenterata*), and very generally in the Vertebrata, whose skeleton always contains a certain amount of cartilage, and in fishes may be exclusively constituted of it (cartilaginous fishes).

Osseous tissue possesses a still higher degree of rigidity. The intercellular substance is strengthened and hardened by the deposition of carbonate and phosphate of lime, while the cells (the so-called bone corpuscles) possess numerous fine processes which anastomose with each other (fig. 31 *a, b, c*). The cells occupy spaces in the com-

compact intercellular substance, which is also traversed by numerous canals, known as Haversian canals. These contain the nutritive blood-vessels and correspond exactly in their course and branchings to the latter. The intercellular substance consists of lamellæ, which are arranged concentrically round the canals. The Haversian canals begin on the surface of the bone, which is covered by a vascular and nervous connective tissue layer, known as periosteum, and open into larger spaces (marrow spaces), which in the long bones occupy the axis of the bone, but in the spongy bones have an irregular distribution.

In a second form of osseous tissue the cells themselves remain in the outer part of the excreted intercellular substance, and only their

FIG. 31a.—Longitudinal section through a long bone (after Kölliker). *G*, Haversian canal.

FIG. 31b.—Transverse section through a long bone (after Kölliker). *K*, bone corpuscles; *G*, Haversian canals; *L*, lamellæ.

FIG. 31c.—*K*, spaces containing the bone corpuscles and their processes—they open into the Haversian canal, *Hc* (after Kölliker).

numerous processes, which run parallel to one another and are of great length, are embedded in it. The intercellular substance, which is hardened by the deposition of calcareous salts, is therefore traversed by a great number of fine tubes. It is deposited on one side only of the cells, and in its origin recalls the hard carapace of the Crustacea, which is similarly traversed by prolongations of cells.

This kind of osseous tissue, traversed by fine parallel tubes, is

found in osseous fishes, and quite universally as the dentine of teeth (fig. 32).

FIG. 32.—Section through the root of a tooth (after Kölliker). *C*, cement; *J*, interglobular spaces *D*, dentine with dentinal tubes.

of bones; and a primary was distinguished from a secondary method of bone development. In reality the two processes resemble each other closely. For in the latter case, in conjunction with a precedent deposition of lime, and partial destruction or reduction of the cartilage, there is a new formation of a soft connective tissue-substance (osteogenic substance) from the centre outwards, the cells (osteoblasts) of which give rise to bone corpuscles, and the intermediate tissue becomes the hard basis of bone (fig. 33). Moreover, cartilage bones grow in thickness at the expense of the

With regard to its development, bone is preceded by soft connective tissue or by cartilage. In the first case, it develops by the transformation of the connective tissue cells into bone corpuscles, and by the hardening of the intermediate tissue. More frequently it is preceded by cartilage; and this holds for a great part of the vertebrate skeleton. Formerly great importance was attached to this difference in the origin

FIG. 33.—A section of ossifying cartilage (after Frey). *a*, Smaller marrow spaces placed in the cartilage; *b*, ditto, with cells of the cartilage marrow; *c*, remains of the calcified cartilage; *d*, larger marrow spaces; *e*, osteoblasts.

periosteum, the connective tissue of which is directly transformed into bony substance.

3. Muscular tissue. We ascribe the property of contractility to the protoplasm itself of the active cell; but we observe that, even in the protoplasmic body substance of the Infusoria, a striated arrangement obtains in those parts in which the contractile function especially resides. By a similar differentiation of the protoplasm certain cells and aggregations of cells possess in a much higher degree the power of contractility, and give rise to the so-called muscular tissue which serves exclusively for movement. At the moment of their activity these cells undergo a change of shape; they become shorter and broader than when at rest.

FIG. 34a.—Myoblasts of a Medusa (Aurelia).

In many Cœlenterata, cells are found in which a part only of the cell is developed into a contractile fibre. It is the deeper parts of such cells which give rise to delicate muscular fibres or networks of fibres, while the superficially placed body of the cell * (myoblast), the part which produces the above, performs other functions, and usually bears a cilium. In consequence of their epithelial-like arrangement, the myoblasts receive the name of muscle-epithelium (fig. 34 a, b). In their further development the greatest part of the cell protoplasm appears to give rise to contractile muscle-

FIG. 34b.—Muscle-epithelium of a Medusa (Aurelia).

substance; and sometimes the whole cell becomes elongated into a muscle fibre.

Two kinds of muscles, which are morphologically and physiologically different, are to be distinguished, viz., the *smooth muscles*, or contractile fibre-cells; and the *cross-striped muscle-substance*.

* These cells have been called neuro-muscular cells; a misleading term, since it cannot be shown that they have had anything to do with the origin of ganglion cells.

In the first case we have to do with flat, spindle-shaped, or band-shaped elongated cells, and with layers of such cells. They react slowly to nervous stimuli; they enter the condition of contraction gradually, and remain contracted for some time. The contractile substance appears for the most part to be homogeneous, but it is sometimes longitudinally striated. The smooth muscles have the

widest distribution amongst the Invertebrata; but they are also found in vertebrates, in the walls of numerous organs (vessels, ducts of glands, intestinal wall) (fig. 35).

Cross-striated muscle consists of cells, more frequently of multi-nucleated so-called primitive bundles. It is characterised by the partial or complete transformation of its protoplasm into a cross-

FIG. 35.—*a*, smooth muscle fibres isolated. *b*, piece of an artery (after Frey); 1, outer connective tissue layer; 2, the middle layer formed of smooth muscle fibres; 3, non-nucleated inner layer.

striped substance, consisting of special doubly refracting elements (sarcous elements) connected together by a simply refracting intermediate substance (fig. 36, *a*, *b*). Physiologically, this form of muscular tissue is characterised by the energetic and considerable contraction which immediately follows its excitation, a property which renders it especially suitable for the carrying out of powerful movements (muscles of vertebrate skeleton).

In the simplest cases the cross-striated fibrillæ are produced by the deeper parts of the myoblasts, which form a continuous flat surface epithelium (muscle epithelium) above the layer of delicate fibres (Medusæ and Siphonophora) (fig. 34 *b*). In the higher animals they

FIG. 36.—*a*, Primitive fibre. *b*, cross-striated muscle fibre (primitive muscle bundle) of *Lacerta* with nerve termination.

arise from the transformation of a greater quantity of protoplasm, and almost the whole contents of the cell are concerned in their production. Rarely the cells remain single, and never acquire more than one nucleus, so that the muscle is composed of only a single cell (eye muscles of *Daphnia*). Sometimes the cells become elongated into long fibres, the primitive bundles; the nuclei at the same time increase in number, and a membrane, the sarcolemma, becomes developed on the outer surface of each fibre. More frequently, however, the primitive bundles arise by the fusion of several cells placed in a row. Either the nuclei come to lie close to the sarcolemma in a peripherally-placed layer of finely granular protoplasm, or they are arranged in a row in the axis of the fibre in some finely granular non-contractile protoplasm. The finer and coarser muscular bundles are composed of many primitive bundles (fibres) placed close together and held together by connective tissue. The fibrillation of the muscular bundles corresponds to the direction of the primitive bundles (muscles of Vertebrata). Finally, both the simple cells, and the multi-nucleated muscles which arise from them, may be branched (heart of Vertebrata, intestine of Arthropods, etc).

4. Nervous tissue. As a rule, nervous tissue is found with muscular tissue, and is the means by which stimuli are conveyed to the latter; but above all, it is the seat of sensation and the will. With regard to this important function it would appear probable that in phylogeny the elements of nervous tissue have not arisen in connection with muscular tissue, but in connection with the sense cells found in the skin, *i.e.*, differentiated ectoderm cells, and that then, still remaining connected with the sense-cells, they have travelled inwards into the subjacent tissue; while the connection with the muscle-cells, which at first possessed an independent irritability, is only secondary.

Nerve-tissue contains two distinct structural elements, nerve cells or ganglion cells, and nerve fibres; both possess a distinct minute structure and molecular arrangement, as well as chemical composition.

The ganglion cells act as centres for nerve-stimuli, and are found especially in the central organs which are known as brain, spinal cord, or simply ganglia. They usually possess a finely granular contents, with a large nucleus and nucleolus and one or more processes (unipolar, bipolar, multipolar, ganglion cells), one of which is the root of a nerve fibre (fig. 37, *a*, *b*).

Frequently the ganglion cells are enclosed in connective tissue

sheaths, which are prolonged over their processes and so over the nerve fibres. Very generally several ganglion cells are enclosed in a common sheath.

Nerve fibres are either centrifugal, *i.e.*, they carry nervous impulses from the central organ to the peripheral organs (motor, secretory nerves); or they are centripetal, *i.e.*, they carry them from the periphery to the central organs (sensory nerves). They are prolongations of ganglion cells, and, like them, are fre-

FIG. 37.—*a* bipolar ganglion cell. *b*, nerve cell, from the human spinal cord (anterior cornu), (after Gerlach). *P*, pigment body.

quently enclosed in a nucleated sheath.

The larger and smaller nerves are composed of a number of such fibres bound together. According to the minute structure of the nervous substance we distinguish two kinds of nerve fibres—(1) the so-called medullated nerves, with a double contour; (2) the non-medullated or naked axis cylinders (fig. 38, *a*, *b*, *c*).

The former are distinguished by the fact that, on the death of the nerve and as the result of coagulation, a strongly refractile fatty substance which forms a sheath for the nerve fibre comes into view. This sheath is known as the medullary sheath, and the central fibre as the axis cylinder. The medullary sheath disappears near the ganglion cell, the axis cylinder only entering the protoplasm

FIG. 38.—Nerve fibres (partly after M. Schultze). *a*, non-medullated sympathetic fibre. *b*, medullated fibres, one of them with commencing coagulation of the axis cylinder. *c*, medullated nerve fibre with the sheath of Schwann.

of the latter. They possess in addition an outer sheath, known as the sheath of Schwann (cerebro-spinal nerves of most vertebrates).

In the second form, *i.e.*, in the non-medullated nerve fibres, the medullary sheath is absent, the axis cylinder being either naked or surrounded by a connective tissue sheath. The axis cylinder here also is connected with a ganglion cell (sympathetic nerves, nerves of Cyclostomata and Invertebrates). Very often, however, and this is especially the case with sense nerves, we find that the axis cylinder may break up into very fine nerve fibrillæ, and be, so to speak, resolved into its elements.

Finally, the nerves of Invertebrates very often appear as finely striated bundles of fibrillæ, in which, on account of the absence of a sheath, it is not possible to recognise the limits of the individual axis cylinders.

Peripherally the sensory nerves become connected with accessory structures (end-organs), derived usually from epithelial cells and their cuticular products, or rarely from connective tissue substance (tactile organs). The end-organs are therefore for the most part derived from modified epithelial cells (sensory epithelium). Ganglion cells are frequently found inserted in the course of the nerve fibres close to their termination (fig. 39, *a*, *b*, *c*.)

FIG. 39.—Rod-shaped sense cells from the olfactory organ (after Max Schultze). *a*, from the frog; *Sz*, supporting cell between two ciliated rod-cells. *b*, from man. *c*, from pike. Probable connection between the nerve fibrillæ and the sense cells.

INCREASE IN SIZE AND PROGRESSIVE DIFFERENTIATION, DIVISION OF LABOUR AND PERFECTION.

The lowest organisms possess neither tissues nor organs formed from cells. The whole organism consists of a single cell. The body of such an animal is composed of protoplasm, and its skin of the

cell membrane. The latter is often without an opening for the entrance of solid bodies; the entrance of food being entirely effected by endosmosis. In such cases, *e.g.*, in the Gregarines and parasitic Opalines, the outer body-wall suffices, like the membrane of the cell, for the performance of such vegetative functions as the absorption of food and the removal of the excretory products. The protoplasm (sarcode) constitutes the body parenchyma, and is the seat of the animal and vegetative vital activities.

Accordingly there results a definite connection between the functions of the peripheral layer and of the included mass, in which the processes of animal and vegetative life are carried on. This connection pre-supposes a definite relation between the superficial area of the surface and the size of the mass, and this relation changes as growth proceeds. For while the surface increases by squares, the mass increases by cubes; while the mass increases in three dimensions, the surface only increases in two, and therefore as growth proceeds the relation changes to the disadvantage of the latter. In other words, with increase of size the superficial area becomes relatively smaller. Finally it becomes relatively so small that the vegetative processes cannot be carried on, and it is necessary for the maintenance of life that for a given energy of life it should be increased by the production of new surfaces.

This holds not only for the simple unicellular organisms, which resemble cells in their nutritive processes, but also for cells themselves whose size never exceeds certain fixed limits. Further, as the organism increases in size, not only does it divide into several cells, but these cells arrange themselves in such a way as to give the largest possible extent of surface. The cellular organism accordingly acquires not only an outer but also an inner surface on which the cells are arranged in a regular layer. With the appearance of an inner surface, a division of labour is established. The outer layer carries on the animal functions and such vegetative processes as those of respiration and excretion, while the *inner (digestive cavity) serves for the reception and digestion of food.*

We thus see that increase in size must not only be accompanied by an increase in the complexity of organisation, but must also bring out at the same time the essential characteristics of animal organization.

The numerous cells developed from the original simple organism were at first equivalent to one another, and all endeavoured to take up a peripheral position (colonies of Protozoa—*Volvox*—Blastosphere) (fig. 40, *a, b.*) Then, in consequence of the needs of the growing organism,

it became necessary that they should be divided, so as to bound two surfaces, into an external and an internal layer; the one forming the outer wall of the body and known as ectoderm, and the other lining the central cavity (digestive cavity) known as endoderm; these two layers being continuous with one another at the opening of the central digestive cavity, or mouth opening (fig. 40 *c*). The cells of the two layers, in correspondence with the difference in their function, possess a different structure. Those of the outer layer, which carry on the animal functions, are usually cylindrical ciliated cells containing a pale albuminous substance; those of the inner layer are more rounded and of a darkly granular aspect; they may also bear cilia for the movement of the contents of the cavity which they line. In actual fact we find this form, which from a physiological standpoint is the simplest organism with cellular differentiation that we can conceive of, realised in the two-layered "gastrula," which appears in the development of almost all groups of the animal kingdom as a free-swimming larva, and to which the adult sexually mature Cœlenterate closely approximates.

As the organism increases in size, additional complications ensue. These result partly from a still further increase of surface brought about by secondary invaginations and partly from the appearance of some intermediate tissue placed between the two primary layers. The secondary invaginations perform special functions and give rise to glands; while the intermediate

FIG. 40.—*a*, Cell colony of young *Volvox Globator* (after Stein). *b*, Blastosphere stage of an Acalepha larva (*Aurelia Aurita*). *c*, Gastrula stage of *b*; *Ec*, Ectoderm; *En*, Endoderm; *o*, Blastopore (mouth of Gastrula).

tissue, developed from one or both of the primary layers, primitively serves as a support for the body and forms the skeleton; and it also gives rise to muscles which increase the organism's power of movement and apply themselves, on the one hand, to the ectoderm (somatic muscles), and on the other, to the endoderm (splanchnic muscles). Between the primary layers of the body there is primitively present a space, the primary body cavity.* Subsequently a second space, developed as a split in the intermediate tissue may appear, giving rise to the secondary body cavity.† From the latter the vascular system is developed.

Contemporaneously with the appearance of muscles a nervous system is usually differentiated from modified cells of the outer layer. Outgrowths from the body also are developed, which may have either a radiate or a bilateral arrangement. They take the form either of organs of nutrition (gills) originating from the need for an increase of surface, or of organs of prehension and movement (tentacles, limbs).

The increasing complexity of organization depends, therefore, not only upon the extension of the surfaces endowed with vegetative functions, and on the appearance of the organs of animal life, but also on a progressing process of division of labour; which results in a clearer and more definite localization of the various functions, necessary for the maintenance of life, in special organs. The greater this specialization the more completely will each organ be able to discharge its special functions, and supposing a proper co-ordination between the working of all the organs, a great advantage accrues to the organism, which is thereby rendered capable of a higher and more complete life. Therefore we find, as a general rule, that the larger the body and the more complex the organization, the higher and more perfect is the life. In this relation, however, the form and arrangement of the organs which characterize the various groups (types), as well as the special conditions of life which are limited by them, must be taken into account as compensating factors.

CORRELATION AND CONNECTION OF ORGANS.

The organs of the animal body stand in a mutually limiting relation to one another, not only in their form, size, and position, but also in their actions; for since the existence of an organism depends upon the blending of the individual performances of all its organs to a united manifestation, the various parts and organs must all, in

* Usually known as segmentation cavity.—ED.

† Usually known as "body cavity," or "coelom."—ED.

a definite and regular manner, be adjusted and subordinated to one another. This relation of dependence, necessarily resulting from the conception of the organism, has been very suitably termed "*Correlation*" of organs; and many years ago served for the establishment of several principles, the cautious application of which has been of great service to the comparative method.

Each organ, in order that it may properly discharge the functions which are requisite for the maintenance of the entire machine, must comprise a certain number of working units, and consequently must have a certain size and possess a form dependent partly on its functions and partly on its relation with other organs. If an organ becomes abnormally enlarged it increases at the expense of the surrounding organs, and the form, size, and function of the latter become injuriously modified. From this is deduced the principle to which Geoffroy St. Hilaire gave the name—if he was not the first to recognise it—of the "*principe du balancement des organes*," and this enabled that investigator to establish the doctrine of "Abnormalites" (Teratology).

The organs which are physiologically similar, *i.e.*, organs which perform in general the same function, as, for instance, the teeth or the alimentary canal or the organs of movement, undergo great and various modifications; and the particular methods of nutrition and habits of life, as well as the external conditions which must be fulfilled if the life of any particular genus is to continue, depend upon the special arrangement and action of the individual organs. Given therefore the special form and arrangement of a particular organ or part of an organ, it is possible to arrive at conclusions concerning the special structure, not only of many other organs, but even of the entire organism, and to reconstruct to a certain extent the whole animal so far as its essential features are concerned. This was first done by Cuvier for many extinct Mammalia, with the aid of scanty fragments of fossil bones and teeth, in a masterly manner.

If we regard the life of the animal and its maintenance, not as the result, but as the end sought, as the aim of all the special arrangements and actions of the individual organs and parts, we are led to the "*principe des causes finales*" (*des conditions d'existence*) of Cuvier, and consequently to the so-called teleological doctrine by which we certainly do not attain to a mechanico-physical explanation. However that may be, this theory, if it be regarded merely as an expression of the reciprocal relations which necessarily exist between the form and function of the parts and of the whole, and not in the Cuvierian sense as implying the existence of design, renders important and

indispensable service to the understanding of the complicated correlations and the harmonious adjustments in the organic world.

The same plan of structure and arrangement of the organs is not found, as Geoffroy St. Hilaire asserted in his theory of analogies, in the whole animal kingdom ; but, on the contrary, there are, as Cuvier stated, several plans of organization or *types*. The term 'Type' was applied by Cuvier to the chief, *i.e.*, the most comprehensive and general divisions of his system ; and each type was distinguished by the sum of the characters of its form and structure. In the essential characteristics of their structure, the higher and lower members of the same type agree, while in the unimportant details they present the most marked differences. The different types themselves do not represent absolutely isolated groups, nor groups which are exactly equivalent to one another, but in a greater or less degree they are related to one another ; this is evident after an examination of the lower forms and a careful comparison of the developmental histories.

To *morphology* belongs the task of pointing out the identity of plan under the most diverse conditions of organization and habits of life, not only among animals of the same group but also between those of different groups. This science has for its object the determination of *homologies*, as opposed to *analogies* which concern the similarity of function, *i.e.*, the physiological equivalence of organs found in different groups, *e.g.*, the wing of a bird and that of a butterfly. That is to say, it has to trace back to the same primitive structure parts of organisms belonging to the same or different groups, which with a different structure and under deviating conditions of life discharge different functions ; as, for example, the wing of a bird and the fore-limb of a mammal ; and so to show their morphological equivalence. In the same way the organs of similar structure which are repeated in the body of the same animal, *e.g.*, the fore and hind limbs, are designated as *homologous*.

THE STRUCTURE AND FUNCTION OF THE COMPOUND ORGANS.

The *vegetative organs* comprise the organs of *nourishment* which are necessary for all living organisms, whether animal or vegetable.

In the former, however, they gradually and in the most intimate connection with the progressive development of the animal functions, attain a higher and more complicated structure. In animals, the reception of food is followed by its digestion. The substances to be assimilated, which have been made soluble by digestion, enter a

nutrient fluid (blood) which permeates the body, and is carried in more or less definite tracts to all the organs. To the latter the blood yields its ingredients, and receives from them such decomposition products as have become useless, and carries them away to be excreted in definite organs. The organs which serve for the performance of the different functions of nutrition and excretion

FIG. 41.—*Rotalia veneta* (after M. Schultze) with a diatom caught in the pseudopodial network.

consist of the apparatus for the reception of food and for its digestion, and for blood formation; and of the organs of circulation, respiration, and of excretion.

Digestive organs. Even animals which have only the value of a single cell (Protozoa) swallow solid particles of food. This is effected

in the simplest cases, as in the *Amœbæ* and *Rhizopoda*, by prolongations of the sarcode (pseudopodia) surrounding the foreign body (fig. 41). In the *Infusoria*, which are covered by a firm cuticle, there is a central semi-fluid mass of sarcode (endoplasm), which is distinct from the more compact peripheral layer of sarcode (ectoplasm), and which receives the nutrient substances through the mouth and digests them.

Rows of larger cilia are present, which serve the purpose of procuring food (adoral ciliated zone of the *Ciliata*) (fig. 42).

FIG. 42.—*Stylonychia mytilus* (after Stein) viewed from the ventral surface; *Wz*, adoral zone of cilia; *C*, contractile vacuole; *N*, nucleus; *N'*, nucleolus (paranucleus); *A*, anus.

FIG. 43.—Longitudinal section through the body of an *Anthozoid* (*Octactinia*). *M*, stomachic tube with the mouth opening in the centre of the feather-like tentacles; *Mf*, mesenteric folds; *G*, genital organs.

Among the animals with cellular differentiation (*Metazoa*), the internal cavity of the body in the *Cœlenterata* (morphologically identical with the alimentary cavity and not with the body cavity of other animals) functions as a digestive cavity, and its peripheral adially arranged portions as a system of vascular canals (gastro-

vascular canals). In the larger Polyps (Anthozoa) a tube derived from an invagination of the oral disc projects into the central part of the digestive cavity. This is known as the stomach of the polyp, although it serves entirely for the introduction of food, and should be called rather the buccal or œsophageal tube (fig. 43).

Organs for the prehension of food are found even with this simple digestive system. For near the mouth are placed radially or bilaterally arranged appendages or processes of the body, which set up

FIG. 44.—*Aurelia aurita* seen from the oral surface. *MA*, the four oral tentacles with the mouth in the centre; *Gk*, genital folds; *GH*, opening of the genital pouches; *Rk*, marginal bodies; *RG*, radial canals; *T*, tentacles at the margin of the disc.

currents to convey small particles of food, or as tentacles seize foreign bodies and convey them to the mouth (Polyps, Medusæ) (fig. 44).

Such appendages serving for the capture of prey may also be placed further from the mouth (tentacles of Medusæ, Siphonophora, Ctenophora).

When the digestive cavity acquires a wall distinct from the body wall, and usually separated from the latter by the body cavity (excepting the parenchymatous worms), it appears in the simplest cases as a blind tube, which may be either simple, bifurcated, or branched

(fig. 45), with sharply marked off pharyngeal structures (Trematoda, Turbellaria), or as a tube communicating with the exterior by an anus (fig. 46).

In the last case it becomes divided so as to lead to the distinction of three parts—(1) of the fore-gut (œsophagus) for the reception of the food, (2) of the mid-gut for the digestion of the food, and (3) of the hind-gut for the expulsion of the undigested remains of the food. Sometimes the alimentary canal aborts; and, as in the mouthless Protozoa (Opalina), the mouth opening may be absent

(Acanthocephala, Cestoda, Rhizocephala).

In the higher animals, usually, not only is the number of the divisions greater, but their shape and structure becomes more complicated. The organs for the seizure of food also become more complicated, and the appendages placed nearest the mouth often become modified to subserve this function. A special chamber, the buccal cavity, becomes marked off from the

FIG. 45. — Alimentary canal of *Distomum hepaticum* (after R. Leuckart); *D*, alimentary canal; *O*, mouth.

FIG. 46. — Alimentary canal of a young nematode. *O*, mouth; *Oe*, fore-gut (œsophagus) with pharyngeal dilatation, *Ph*; *D*, mid-gut; *A*, anus.

fore-gut, in front of or within which hard structures, such as jaws and teeth, for the seizure and mastication of the food are placed (Vertebrata, Gastropoda); and into which secretions (salivary) having a digestive function are poured. The masticatory organs are sometimes placed completely outside the body in front of the mouth, and consist of modified limbs (Arthropoda), which in the parasites are metamorphosed into structures for piercing and sucking; or they may have shifted so as to lie entirely within the pharynx (Rotifera, errant Annelids) or in a muscular dilatation of the posterior end of this organ. At this place there is usually developed a widened chamber, the stomach, which by

repeated mechanical action (masticatory stomach of Cray-fish) or by the secretion of digestive fluids (pepsin) furthers digestion; or it may, as in birds, subserve both these functions. From the stomach the food passes into the mid-gut. Dilatations and out-growths of the buccal cavity give rise to cheek and throat pouches, of the œsophagus to the crop, of the stomach to blind sacs which serve as reservoirs for the food (stomach of Ruminants) (figs. 47 & 48).

In the middle section of the alimentary canal, or intestine, the digestive processes, already commenced in the mouth by the action of the salivary secretion and continued in the stomach by the action of the

FIG. 47.—Alimentary canal and accessory glands of a caterpillar. *O*, mouth; *Oe*, œsophagus; *Sp D*, salivary glands; *Se*, spinning glands; *MD*, intestine (mid-gut); *AD*, rectum (hind gut); *Mg*, Malpighian tubes.

FIG. 48.—Alimentary canal of a butterfly. *R*, proboscis (maxillæ); *Sp*, salivary glands; *Oe*, œsophagus; *S*, sucking stomach; *Mg*, Malpighian tubules; *Ad*, rectum.

pepsin of the gastric juice (upon albumins in an acid solution), is completed. The food constituents which have been so far unacted upon (chyme) are in the intestine submitted to the action of the secretions of the liver, pancreas, and intestinal glands, and by them converted into the chyle, which is absorbed by the intestinal walls; the albumins being converted, as in the stomach, into soluble modifications by the action of trypsin (acting, however, only in alkaline solutions). The intestine often attains a great length, and becomes divided into regions possessing a different structure; *e.g.*, in the intestine of

mammals three regions can be distinguished—duodenum, jejunum, and ileum. Its surface is, as a rule, increased by the development of folds and villi, and sometimes of outgrowths. Amongst

the Invertebrata it is often possible to distinguish an anterior especially widened portion of the intestine, which receives the hepatic secretion and is called stomach from the posterior, narrower, and longer section, which is known as intestine.

FIG. 49.—Alimentary canal of a bird. *Oe*, oesophagus; *K*, crop; *Dm*, proventriculus; *Km*, gizzard; *D*, small intestine; *P*, pancreas placed in the loop of the duodenum; *H*, liver; *C*, the two caeca; *U*, ureter; *Ov*, oviduct; *Ad*, large intestine; *Kl*, cloaca.

The hindmost section of the alimentary canal or hind gut, which is not always sharply marked off from the intestine, is especially concerned with the collection and expulsion of the undigested remains of the food, or faeces. It may also possess caecal appendages attached to its anterior part, and possessing a digestive function. In the lower animals it is a small structure, but in the higher animals it attains a much more considerable length, and receives anteriorly one (Mammalia) or two (Birds) caeca, and it may be sub-divided into two parts, known as large intestine and rectum; in the Vertebrata its hind end receives the ducts of various glands (kidney, generative organs, anal glands). It may in addition discharge other functions, *e.g.*, a respiratory (larvæ of Libellulidæ) or a secretory function (larva of Ant Lion).

The salivary glands, liver, and pancreas are to be regarded as outgrowths of the alimentary canal which have become diffe-

rentiated into glands.

The secretion of the salivary glands is poured into the buccal cavity, and there performs two functions—(1) it dilutes the food, (2) it has a chemical action upon it, converting the starch into sugar: they are absent in many aquatic animals and are especially developed in herbivorous animals.

The liver, distinguished in the higher grades of development by its great size, is an appendage of the first part of the small intestine (duodenum). The first trace of it is met with in the lower animals in the form of a characteristically coloured part of the cellular covering of the gastric cavity or intestinal wall (Cœlenterata, worms). In the higher animals it has at first the form of a small blind sac (small Crustacea); this, by a process of branching, is converted into a complicated structure composed of ducts and follicles, which may become connected together in very different ways so as to give rise to an apparently compact organ. Nevertheless, it must be remembered that, in the different groups of animals, glands, which differ both morphologically and physiologically, are included under this term, "liver." While in the Vertebrata the liver, as a bile-producing organ, possesses no known relation to digestion, in the Invertebrata the secretions of many glands, which are generally called "liver," but which would be more appropriately termed *hepatopancreas*, exercise a digestive action upon starch and albumen, and at the same time contain bye-products and colouring matters similar to those found in the bile of Vertebrates (Crustacea, Mollusca).

FIG. 50.- Alimentary canal of Man. *Oe*, œsophagus; *M*, stomach; *L*, spleen; *H*, liver; *Gb*, gall bladder; *P*, pancreas; *Du*, duodenum receiving the bile and pancreatic ducts; *Il*, ileum; *Co*, colon; *Coe*, cæcum with vermiform process, *Pv*; *R*, rectum.

The Organs of Circulation. The nutrient material or chyle resulting from digestion is distributed by a system of spaces to all parts of the body. Excluding the Protozoa, in which the distribution of nutrient material is effected in the same manner as in the cell or tissue unit, the simplest form of vascular system in animals with cellular tissues, *i.e.*, in the Metazoa, is found in the Cœlenterata. In these animals the digestive cavity itself extends to the extreme periphery of the body, and serves to distribute the nutritive fluids

(gastro-vascular system of Polyps, so-called vessels of Medusæ and Ctenophora). The so-called stomach of the Anthozoa is simply an invagination of the body wall into the central cavity of the animal, and functions only as œsophagus.

When a distinct alimentary canal is present, the chyle is absorbed by the walls of the gut, and passed through them into the cœlom or space developed between the gut and body walls (into the general

FIG. 51.—Daphnia with simple heart. *C*, the slit-like opening on one side is seen; *D*, alimentary canal; *L*, liver; *A*, anus; *G*, brain; *O*, eye; *Sd*, shell gland; *Br*, brood pouch placed dorsally beneath the carapace.

tissue of the body in the acœlomate parenchymatous worms), and there gives rise to a fluid, the blood, in which (with some few exceptions) corpuscles (cellular structures produced in the organism) are found. In this space, or in a system of lacunæ derived from it, the blood circulates. Primitively its movements are quite irregular, taking place with each movement of the body (as in many worms), and are effected chiefly by the contractions of the somatic muscles

(*Ascaris*), but also by the movements of other organs, *e.g.*, the alimentary canal (Cyclops). At a higher stage of development a rudiment of the central organ of the circulation appears, in that a special section of the blood path acquires a muscular investment, and as a pulsating heart, comparable to a force and suction-pump.

FIG. 52.—Male of *Branchipus stagnalis* with many-chambered heart or dorsal vessel *Rg*, the lateral openings in which are repeated in every segment. *D*, intestine; *M*, mandible; *Sd*, shell gland; *Br*, branchial appendage of the 11th pair of legs; *T*, testis.

FIG. 53.—Heart of a Copepod (*Calanella*) with an anterior artery, *A*. *Os*, ostia; *V*, valves at the arterial ostium; *M*, muscle.

maintains a continuous circulation of the blood. The heart is either sac-shaped, with two lateral or one anterior slit-like opening (*Daphnia*, *Calanus*) (fig. 51), or elongated and divided into successive chambers and perforated by many pairs of slit-like openings (*Insects*, *Apus*) (fig. 52). As a rule, each chamber possesses a pair of laterally placed

ostia, provided with lip-like valves, which act so as to allow the blood only to enter the organ.

From the heart, as central organ of the circulation, well defined canals, the blood vessels, are then developed, which in the Invertebrata may alternate with lacunæ not provided with walls. In the simplest cases it is only the tracts along which the blood travels from the heart which are provided with independent walls, and developed into blood vessels (marine Copepoda, *Calanella*, fig. 53). At a higher stage of development not only do these efferent vessels acquire a more complicated structure, but a part of the lacuna-system, especially in the neighbourhood of the heart, acquires a membranous investment, and gives rise to vessels which carry the blood back to the

FIG. 54.—Heart and blood vessels and gills of the crayfish. *C*, heart, in a blood sinus; with *Ps* several pairs of ostia; *Ac*, cephalic aorta; *A.ab*, abdominal aorta; *As*, sternal artery.

pericardial sinus, from which it passes through the venous ostia into the heart (Scorpions, Decapods) (fig. 54).

In other cases (Molluscs) the blood flows directly from the afferent vessels into the heart, the walls of the vessel being directly continuous with the walls of the heart. The heart in such cases consists of two chambers, the one known as auricle serves for the reception of the returning blood, the other known as ventricle for its propulsion (fig. 55).

The vessels passing from the ventricle and carrying the blood from the heart are called arteries; those returning the blood to it are called veins, and, in the higher animals, are distinguished from the arteries by their thinner walls. Between the ends of the arteries and the beginning of the veins the body cavity intervenes either as

a blood sinus or as a system of blood-lacunæ; or the arteries and veins are connected by a network of delicate vessels, the capillaries. If the connection between arteries and veins is effected by capillaries in all parts of the vascular system, and the body cavity, as in the Vertebrata, no longer functions as a blood sinus, the vascular system is spoken of as being completely closed.

In the Vertebrates and segmented worms the vascular system obtains a considerable development before a true heart is differentiated in it. At first rhythmically pulsating sections, very frequently the

FIG. 55.—Nervous system and circulatory organs of *Paludina vivipara* (after Leydig). *F*, tentacle; *Oe*, oesophagus; *Cg*, cerebral ganglion with eye; *Pg*, pedal ganglion with adjacent otocyst; *Vg*, visceral ganglion; *Phg*, pharyngeal ganglion; *A*, auricle of heart; *Vc*, ventricle; *Aa*, abdominal aorta; *Ac*, cephalic aorta; *V*, vein; *Vc*, afferent vessel. *Br*, gill.

dorsal vessel, or the lateral vessels connecting this with the ventral vessel (fig. 56), serve for the propulsion of the blood.

Similarly amongst the Vertebrata, the lancelet (*Amphioxus*) possesses no distinctly differentiated muscular heart, the function of that organ being discharged by various parts of the vascular system which are contractile. The arrangement of the vessels supplying the pharyngeal section of the alimentary tract, which has a respiratory function and is known as the branchial sac, admits of a comparison with the vascular arrangement of the segmented worms, and represents the simplest form of the vertebrate vascular system. The longitudinal vessel which runs in the ventral wall of the branchial sac gives off numerous lateral branches, which ascend in the branchial walls. These lateral vessels are contractile at their point of origin

from the ventral vessel. The anterior pair, placed behind the mouth, unite beneath the notochord to form the root of the median body artery (descending or dorsal aorta) which receives the hinder successive pairs of lateral vessels. This dorsal artery gives off branches to the muscles of the body wall and the viscera, from which the venous blood in part is returned to the ventral pharyngeal vessel; part of it, however, before reaching the latter, traverses a capillary network in the liver.

FIG. 56.—Anterior part of the vascular system of an Oligochaete worm (*Sænuris*) (after Gegenbaur). In the dorsal vessel the blood moves from behind forward; in the ventral vessel from before backwards (see arrows). *H*, heart-like dilated transverse lateral vessels.

From the hinder part of the ventral pharyngeal vessel there is developed, in the higher Vertebrata, the heart, which at first has the shape of an S-shaped tube, but later acquires a conical form and becomes divided into auricle and ventricle. The former receives the blood returning from the body and passes it on into the more powerful ventricle, from which arises an anterior vessel, the ascending or cardiac aorta, presenting a swelling at its root, known as the aortic bulb. This vessel leads, by means of lateral vascular arches, the arterial arches, into the dorsal aorta, which passes backwards beneath the vertebral column, and supplies the body. Valves placed at the two ostia of the ventricles regulate the direction of the blood stream; and they are so arranged as to prevent any lackward flow of blood from the cardiac aorta into the ventricle in diastole, and from the ventricle into the auricle in systole.

In consequence of the insertion of the respiratory organs on to the system of the arterial arches, the latter, and at the same time the structure of the heart, assumes various degrees of complication. In fishes (fig. 57), four or five pairs of gills are inserted in the course of the arterial arches, which break up into a respiratory capillary network in the branchial leaflets. From this network the arterialed blood is collected into efferent branchial arches, the branchial veins, corresponding each to a branchial artery; and these unite to form the dorsal aorta. In such cases the heart remains simple, and receives venous blood.

With the appearance of lungs as respiratory organs (Dipnoi, Perennibranchiate Amphibia, larvæ of Salamanders and Batrachians) (fig. 58), the heart obtains a more complicated structure,

in that the auricle becomes divided into a right and left division, the latter of which receives the arterialised blood, returning from the lungs by the pulmonary veins. The septum between the two divisions of the auricle may, however, remain incomplete (Dipnoi, *Proteus*). The advehent pulmonary vessels, the pulmonary arteries, always proceed from the

FIG. 57.—Diagram of the circulatory organs of an osseous fish. *V*, ventricle; *Ba*, aortic bulb with the arterial arches which carry the venous blood to the gills; *Ao*, dorsal aorta into which open the vessels from the gills or branchial veins *Ab*. *N*, kidney; *D*, alimentary canal; *Lk*, portal circulation.

FIG. 58.—Gills (*Br*) and pulmonary sacs (*P*) of a perennibranchiate amphibian. *Ap*, pulmonary artery proceeding from the posterior of the four aortic arches. The other three lead to the three pairs of gills; *D*, alimentary tract; *A*, aorta.

posterior vascular arch, which, as a rule, loses its relation to the branchial respiration.

On the disappearance of the gills, which is completed during the metamorphosis in the *Salamandrina* and *Batrachia*, the pulmonary

arteries obtain a much more considerable size and become the direct continuation of the hindermost pair of vascular arches, while the remaining and primitively most important portions of the latter, *i.e.* the portions leading to the dorsal aorta, are reduced to rudimentary ducts (Ductus Botalli) or completely obliterated. Contemporaneously with these changes there appears a fold in the lumen of the ventral or cardiac aorta, leading to a separation of the posterior vascular

FIG. 59.—Circulatory organs of the frog. *P*, left lung, right lung is removed; *Ap*, pulmonary artery; *Vp*, pulmonary vein; *Vc*, vena cava inferior; *Ao*, dorsal aorta; *N*, kidney; *D*, alimentary canal; *Lk*, portal circulation.

arch (pulmonary artery), which now receives through the ventricle venous blood from the right auricle, from the system of anterior arches which give origin to the cephalic vessels and dorsal aorta and receive arterial blood from the left auricle (mixed, however, with venous blood in the ventricle) (fig. 59).

In Reptiles the separation of the arterial from the venous blood is more complete, in that there is an incomplete ventricular septum which foreshadows the later division of the ventricle into a right and a left half. From the left division arises the right aortic arch,

which gives origin in its further course, to the arteries to the head (carotid arteries). A vessel to the lungs and a left aortic arch may also be distinguished. The left aortic arch and pulmonary artery receive only venous blood, while the right aortic arch, and therefore the carotids which proceed from it, receive principally arterial blood from the left side of the ventricle (fig. 60).

The ventricular septum, and consequently the separation of the right from the left ventricle, is found complete for the first time

in the Crocodilia, and in these animals the right aortic arch arises from the left ventricle. But the separation of the arterial and venous blood is even now not quite complete, for at the point where the two aortic arches cross one another there is a passage (foramen Panizzæ) leading from one into the other, and through which a communication may take place.

It is only in Birds and Mammals, in which, as in the Crocodilia, the right and left ventricle are completely separated, that a separation between the two kinds of blood is completely effected (fig. 61). In Birds the right aortic arch persists, and the left entirely disappears; while in Mammalia the opposite obtains, the left arch persisting and giving rise to the dorsal aorta. In these animals the blood is essentially different from the chyle both in colour and composition, and there is present a special system of chyle and lymph vessels. This system originates in simple tissue spaces, which are without walls, and its main trunks open into the vascular system. The contents are derived from the nutrient material absorbed from the intestine (chyle), and from the fluids which have transuded into the tissues from the capillaries (lymph), and they serve to renovate the blood. In the actual course of the lymph and chyle, *i.e.*, in the lymphatic vessels themselves, are placed peculiar glandular organs, known as lymphatic glands (blood glands), in which the lymph receives its form elements (lymph corpuscles=white blood corpuscles).

Organs of Respiration. The blood needs for the retention of its properties not only this continued renovation by the addition of nutrient fluids, but also the constant introduction of oxygen, with the reception of which is closely connected the excretion of carbonic

FIG. 60.—Heart and great vessels of a Chelonian. *Ad*, right auricle; *As*, left auricle; *Ao.d*, right aortic arch; *Ao.s*, left aortic arch; *Ac*, aorta; *C*, carotids; *Ap*, pulmonary arteries.

acid (and water). The exchange of these two gases between the blood and the external medium is the essential part of the respiratory process, and is effected through organs which are suited for carrying

on this process either in air or in water. In the simplest cases the exchange of these two gases takes place through the general surface of the body; and in all cases, even when special respiratory organs are present, the outer skin also takes part in respiration.

FIG. 61.—Diagram of the circulation in an animal with a completely separated right and left ventricle, and a double circulation (after Huxley). *Ad*, right auricle receiving the superior and inferior venæ cavæ, *Vcs*, and *Vci*; *Dth*, thoracic duct, the main trunk of the lymphatic system; *Ad*, right auricle; *Vd*, right ventricle; *Ap*, pulmonary artery; *P*, lung; *Vp*, pulmonary vein; *As*, left auricle; *Vs*, left ventricle; *Ao*, aorta; *D*, intestine; *L*, liver; *Vp'*, portal vein; *Lv*, hepatic vein.

FIG. 62.—Diagram of the great arteries of a mammal with reference to the five embryonic arterial arches (after Rathke). *c*, common carotids; *c'*, external carotid; *c''*, internal carotid; *A*, aorta. *Ap*, pulmonary artery; *Aa*, aortic arch.

Inner surfaces also may be concerned in this exchange, especially those of the digestive cavity and intestine, or, as in the Echinoderms, in which a separate vascular system is developed, the surface of the whole body cavity.

Respiration in water obviously takes place under far more un-

favourable conditions for the introduction of oxygen than does the direct respiration in air, because it is only the small quantity of

oxygen dissolved in water which is available. Hence this form of respiration is found in animals low in the scale of life in which the metabolic processes are less energetic (worms, molluscs, and fishes).

Organs of aquatic respiration, or *gills*, have the form of external appendages possessing as large a surface extension as possible. They consist of simple or antler-shaped or dendritically branched processes (fig. 63 *a*, *b*), or of

FIG. 63a.—Head and anterior body segments of a *Eunice*, viewed from the dorsal surface. *T*, tentacles. *Ct*, tentacular cirrus. *C*, parapodial cirrus. *Br*, parapodial gill.

lancet-shaped closely-packed leaves with a large surface extension (fig. 64).

FIG. 64.—Transverse section through the gill of a Teleostean fish. *b*, branchial leaflet with capillaries; *c*, branchial artery containing venous blood; *d*, branchial vein containing arterial blood. *a*, branchial bar.

FIG. 63b.—Transverse section through the body of *Eunice*. *Br*, gill; *C*, cirrus; *P*, parapodium with a bundle of setæ; *D*, alimentary canal; *N*, nervous system

The organs of aërial respiration, on the contrary, are internal. They present likewise the condition favourable for an exchange of gases between the air and the blood, viz., a large extent of surface. They have the form either of *lungs* or air-bearing tubes. In the first case (Spiders,

Vertebrates) they consist of spacious sacs with alveolar or spongy

walls, traversed by numerous septa and folds which bear an extremely rich network of capillaries. The *air tubes* or *tracheæ* (fig. 65) constitute

FIG. 65.—Tracheæ with fine branches (after Leydig). *Z*, cellular outer wall; *Sp*, spiral thread.

tute a branched system of canals which extend throughout the whole body, and carry the air to all the organs. Thus instead of the respiratory process being localised, as it is in animals with lungs, it is carried on in all tissues and organs of the body, which are surrounded by a fine

tracheal network. Nevertheless, the air tubes in the case of the modification known as *fan-tracheæ* present an approximation in their structures to lungs, in that the main stems, without further branching, give rise to flat hollow leaves.

FIG. 66b.—Lateral view of head and body of an Acridium. *St*, stigmata; *T*, Tympanum.

Openings in the body wall are present, placing the organs of aerial respiration in communication with the exterior. These openings may be numerous, and paired, placed symmetrically on the sides

FIG. 66a. —Tracheal system of a Dipterous larva. *Tr*, Longitudinal stem of the right side with tufts of tracheæ; *St'*, and *St''*, anterior and posterior stigmata; *Mh*, oral hooks.

of the body (fig. 66 *a, b*) (*stigmata* of Insects, Spiders), or they may be more restricted in number, and communicate also with cavities of complicated structure which are used for other functions (nasal cavities of Vertebrates). In the aquatic larvæ of certain

FIG. 67*a*.—Larva of an Ephemeral fly with seven pairs of tracheal gills
L, slightly magnified; *Tk*, isolated tracheal gill strongly magnified.

FIG. 67*b*.—Tracheal system at the sides of the alimentary canal of an Agrion larva (after L. Dufour). *Tst*, main tracheal trunk; *Kt*, tracheal gills; *Na*, the three simple eyes.

Insects (Ephemeridæ, Libellulidæ) the tracheæ may be without any external openings. In such cases processes of the body filled with a close network of tracheæ, which take up oxygen from the water, and are known as *tracheal gills*, are developed (fig. 67 *a, b*). In rare instances tracheal gills are developed on the wall of the rectum, and

thus acquire a protected position (rectal respiration of *Aeschna*, *Libellula*).

In other respects the branchial and pulmonary respiratory processes are essentially the same. In the pulmonate snails (*Lymnæus*), the pulmonary cavity may be filled with water, and yet continue to function as a respiratory organ (in the young state and also under special conditions in the adult, the animal remaining permanently in deep water). With this fact before us of an air-breathing surface functioning as a gill, it will not surprise us to find that gills and branching folds of skin, which under normal circumstances serve for breathing in water, can, provided they be protected from shrivelling up and desiccation either by their position in a damp space or by their copious blood supply, function as lungs, and allow their possessors to live and breathe on land (Crabs, *Birgus latro*, labyrinthobranchiate Fishes).

A rapid renewal of the medium which carries the oxygen and surrounds the respiratory surfaces is of the greatest importance for the gaseous exchanges. We find, therefore, very often special arrangements, by which the removal of that part of the respiratory medium which has been deprived of oxygen and saturated with carbonic acid and the introduction of another portion containing oxygen and free of carbonic acid, is effected. In the simplest cases this renewal can, although not very efficiently, be brought about by the movements of the body, or by a continuous oscillation of the respiratory surfaces themselves; a method which is especially common when the gills are placed in the region of the mouth and function also as organs of food prehension, *e.g.*, the tentacles of many attached animals (Polyzoa, Brachiopoda, tubicolous Worms, etc.) Very frequently the gills appear as appendages of the organs of locomotion, *e.g.*, of the swimming or ambulatory feet (Crustacea, Annelids), the movement of which brings about a renewal of the respiratory medium around the gills. The movements become more complicated when the gills are enclosed in special chambers (Decapoda, Pisces), or when the respiratory organs are placed within the body, as happens in the case of tracheæ and lungs, in which case also a renewal of the air is effected either by a more or less regular movement of neighbouring parts, or by rhythmic contractions and dilatations of the air-chamber, constituting the so-called *respiratory movements*. The term *respiration* is now not only applied to these movements so obvious to the eye in air-breathing animals, but also to the osmotic processes, secondarily

dependent upon the entrance and exit of *air*, which effect the gaseous exchanges. Taken strictly in this sense it is an incorrect term, inasmuch as in the respiratory movements of animals provided with branchial cavities we have to do with the entrance and exit of *water*.

In the higher animals provided with red blood, the difference in the condition of the blood before and after its passage through the respiratory organs is so striking that it is possible to distinguish blood rich in oxygen from blood rich in carbonic acid, by the colour. The latter is dark red, and is known as venous blood; the former, *i.e.*, blood which has just left the gills or lungs, on the contrary, has a bright red colour, and is known as arterial blood.

While the terms *venous* and *arterial* are used in an anatomical sense to express the nature of the blood-vessel,—those carrying the blood to the heart being called venous, and those carrying it from the heart arterial,—they are also used in a physiological sense as an expression for the two conditions of the blood before and after its passage through the respiratory organs, *i.e.*, to express the quality of the blood. Since, however, the respiratory organs may be inserted in the course of either the venous or arterial *vessels*, it is obvious that, in the first case, there must be venous vessels carrying arterial blood, (Molluscs and some Vertebrates), and, in the latter, arterial vessels carrying venous blood (Vertebrates).

Animal heat. The intensity of respiration stands in direct relation to the energy of the metabolism. Animals which breathe by gills and absorb but little oxygen are not in a position to oxidise a large quantity of organic constituents, and can only transform a small quantity of potential into kinetic energy. They perform, therefore, not only a proportionately smaller amount of muscular and nervous work, but also produce in only a small degree the peculiar molecular movements known as heat. The source of this heat is to be sought, not, as was formerly erroneously supposed, in the respiratory organs, but in the active tissues. Animals in which thermogenic activities are small have no power of keeping independently their own internal heat when exposed to the temperature influences of the surrounding medium. This is also true of those air-breathing animals in which the metabolic and thermogenic activities are great, but which, in consequence of their small size, offer a relatively very large surface for the loss of heat by radiation (Insects). On account of the exchanges of heat which are continually taking place between the animal body and the surrounding medium, the temperature of the

former must in such animals be largely dependent on that of the latter, falling and rising with it. Hence, most of the lower animals are *poikilothermic*,* or, as they have less appropriately been called, *cold-blooded*.

The higher animals, on the contrary, in which, on account of their highly developed respiratory organs and energetic metabolism, the thermogenic activity is great, and which are protected from a rapid loss of heat by radiation by the size of their bodies and by the possession of a covering of hairs or feathers, possess the power of maintaining a constant temperature, which is independent of the rising and falling of the temperature of the surrounding medium. Such animals are designated *homothermic*, or *warm-blooded*. Since they require a high internal temperature, varying only within small limits, as a necessary condition for the normal course of the vital processes, or one may say for the maintenance of life itself, they must possess within themselves a series of regulators whose function is to keep the body temperature within its proper limits, when the temperature of the surrounding medium is high. This may be effected either by diminishing the production of internal heat (diminishing the metabolism) or by increasing the loss of heat from the surfaces of the body (by radiation, evaporation of secretions, cooling in water); and, on the contrary, when the temperature of the outer medium is too low, by increasing the production of internal heat (increasing the metabolic activity by more plentiful food supply, more vigorous movements), or by diminishing the loss of heat by the development of better protective coverings.

When the conditions necessary for the action of these regulators are absent (want of food, small and unprotected bodies), we find either the phenomenon of winter sleep, in which life is preserved with a temporary lowering of the metabolic processes; or, when the metabolic processes of the organism do not enter into abeyance, the remarkable phenomena of migration (migration of birds).

Organs of Secretion. The respiratory organs stand to a certain extent intermediate between the organs of nutrition and those of excretion, in that they take in oxygen and excrete carbonic acid. In addition to this gas a number of excrementitious substances, mostly in a fluid form, which have entered the blood from the tissues, pass out by the lungs. The function, however, of excretion

* Comp. Bergmann, "Ueber die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse," Göttinger Studien, 1847; also Bergmann und Leuckart, "Anatomisch-physiologische Uebersicht des Thierreichs," Stuttgart, 1852.

is mainly discharged by the special *secretory organs*. These have the form of glands of a simple or complex structure which originate from invaginations of the outer skin or of the intestinal wall, and consist essentially of simple or branched tubes, or of racemose and lobulated glands.

Among the various substances which by the aid of the epithelial lining of the walls of glands are removed from the blood and sometimes utilised further for the performance of various functions, the nitrogenous excretory substances are especially important. The organs by which the excretion of these ultimate products of metabolism are effected are the *kidneys*. In the Protozoa they are represented by the contractile vacuoles; in the Worms they appear as the so-called *water-vascular vessels*, and are constituted of a system of branched canals which take their origin in delicate internal ciliated funnels, which open into the spaces in the parenchymatous tissues or into the body cavity. In the latter case the ciliated funnels have a wide opening. In the Platyelminthes (flat worms) the efferent ducts of the system consist of two main lateral trunks (fig. 68, *Ex.*), which frequently open together at the hind end of the body by means of a medium terminal contractile vesicle (fig. 68, *ep*).

FIG. 68.—Young Distomum (after La Valette). *Ex*, main stems of the excretory system; *Ep*, excretory pore; *O*, mouth with sucker; *S*, sucker in the middle of the ventral surface; *P*, pharynx; *D*, alimentary canal.

In the segmented worms the paired kidneys are repeated in every segment, and are known as *segmental organs* (figs. 69 and 70). The *shell-glands* of

Crustacea are in all probability to be traced back to these segmental organs: as are also the paired kidney (organ of Bojanus) of mussels, and the unpaired renal sac of Snails, both of which communicate by means of an internal opening with the *pericardial* division of the body cavity.

In the air-breathing Arthropods and some Crustacea (Orchestia) the urinary organs are tubular appendages (Malpighian vessels) of the hind gut. In the Vertebrata the urinary organs or kidneys obtain a greater independence, and open to the exterior by special

openings which are usually common to the generative organs; they consist essentially of a number of coiled tubes, which in the more primitive types of Vertebrates have a ciliated funnel-shaped opening into the body cavity (Dogfish embryo, fig. 71).

The individual tubules of which the verte

FIG. 69.—Longitudinal section through the medicinal Leech (after R. Leuckart). *D*, alimentary canal; *G*, brain; *Gk*, ventral chain of ganglia; *Ex*, excretory canals (segmental organs, water-vascular system).

FIG. 70.—Diagrammatic representation of the segmental organs of a segmented worm (after C. Semper). *Ds*, dissepiment; *Wtr*, ciliated funnels which lead into the coiled tubes.

brate kidney is composed do not open directly to the exterior, as do the segmental organs of Annelids, but there is present on each side of the body a duct, the kidney duct, which receives the tubules of its own side and opens posteriorly into the cloaca. They also possess an important structure peculiar to the kidney of the Vertebrata known as the "Malpighian body," which consists of a capsular widening of the lumen of each

tubule, into which projects a coil of arterial blood vessels known as the *glomerulus* (fig. 72).

FIG. 71.—Diagrammatic representation of the kidney (segmental organs) of a dog-fish embryo (after C. Semper). *Wtr*, ciliated funnels; *Ug*, kidney duct.

its special covering soft and supple. The coccygeal glands of water-birds are derived from an aggregation of sebaceous glands; their secretion by keeping the feathers oiled preserves them from becoming saturated with water during swimming.

The unicellular and multicellular integumentary glands, which are found so widely present in

Insects, belong, for the most part, to the category of oil and fat glands. Aggregations of cells whose function is to secrete calcareous matters and pigment are especially widely present in the integument of the Mollusca, and serve for the building up of the beautifully

Very generally the outer body surface is the seat of special secretions which frequently play an important part in the economy of the animal, and are used especially as a means of protection and defence. The same is true also of the secretions of the accessory glands opening into the anterior or posterior end of the alimentary canal (salivary glands, poison glands, anal glands) (fig. 73).

To the class of cutaneous glands belong, in the first place, the sweat-glands and the sebaceous glands of Mammalia. The fluid secretion of the former, on account of the ease with which it is evaporated, is of special use in keeping the body cool, while that of the latter keeps the integument and

FIG. 72.—Ciliated funnel and Malpighian body from the anterior part of the kidney of *Proteus* (after Spengel). *Nr*, kidney tubule; *Tr*, ciliated funnel; *Mk*, Malpighian body.

coloured and variously shaped shells of these animals. Integumentary glands and aggregations of glands may also acquire a relation to the acquisition of food (spinning glands of Spiders). Finally, mucous glands are very widely present in the skin of animals which live in damp localities (Amphibia, Snails) and in water (Fishes, Annelids, Medusæ).

FIG. 73.—Alimentary canal with its accessory glands of a beetle (*Carabus*) (after Léon Dufour). *Oe*, oesophagus; *Jn*, crop; *Pv*, proventriculus; *Chd*, chylific ventricle; *Mg*, Malpighian tubules; *R*, rectum; *Ad*, anal glands with bladder.

ORGANS OF ANIMAL LIFE.

Of the so-called animal functions, that of locomotion is the most conspicuous. Animals perform movements for the purpose of procuring food and escaping from their enemies. The muscles used for locomotion are, as a rule, and especially in the simpler forms, intimately united with the skin, and give rise to a muscular body wall (Worms), the alternate shortening and elongation of which brings about a movement of the body. The muscles may also be especially concentrated in parts of the body wall, *e.g.*, in the subumbrellar surface of Medusæ beneath the supporting gelatinous tissue, or in the ventral surface of the body giving rise

to a foot-like organ (Molluscs), or they may be broken up into a series of successive and similar segments (Annelids, Arthropods, Vertebrates). The latter arrangement prepares the way for the rapid and more complete form of movement found in animals in which the hard parts also, whether exoskeletal (Arthropods) or endoskeletal (Vertebrata), have become divided into a series of longitudinally arranged segments or rings, which offer a firm attachment to and are moved by the segments of the muscular system. By this arrangement more powerful muscular actions are rendered possible.

Thus it becomes indispensable that hard parts should be developed to act as a skeletal support for the soft parts, and also to protect them. The skeletal structures may be external, in which case they have the form either of external shells, tubes or successive rings, and are

usually products of the external skin (*chitin*), or they may be internal (*cartilage, bone*) and give rise to *vertebræ* (fig. 74 *a, b*). In either case the body becomes divided at right angles to its long axis into a series of segments, which, in the simpler cases of locomotion, are homonomous (*Annelids, Myriapods, Snakes*). As development progresses some of the muscles required for locomotion gradually lose their relation to the long axis of the body, and acquire a relation to secondary axes; and in this way conditions are acquired for the accomplishment of more difficult and complete forms of locomotion. The hard parts in the long axis of the body then lose their primitive

FIG. 74 *a*—Diagram of the vertebral column of a Teleostean fish with vertebral constriction of the notochord. *Ch*, notochord; *Wk*, bony vertebral bodies; *J*, membranous intervertebral section.

FIG. 74 *b*—Vertebra of a fish. *K*, vertebral body. *Ob*, neural arch (neurapophysis); *Ub*, hæmal arch (hæmapophysis); *D*, neural spine; *D'*, hæmal spine; *R*, rib.

uniform segmentation and partially fuse with one another to form several successive regions, the parts of which are capable of a greater or less amount of movement upon one another (head, neck, thorax, lumbar region, etc.) In this case, however, the parts of the skeleton of the chief axis are usually less movable upon one another, while, on the contrary, a much more perfect locomotion is effected by the extensive movements of the paired extremities or limbs. The limbs likewise possess a solid skeleton, to which the muscles are attached, and which is usually elongated and may be external or internal, and is attached more or less closely to the axial skeleton.

The most essential property of animals is that of *sensation*. This

property, like that of movement, resides in definite tissues and organs which constitute the *nervous system*. For those cases in which a nervous system has not separated from the common contractile basis (sarcode) or from the uniform cell parenchyma of the body, we may suppose that the organism possesses the first beginnings of an irritability serving for perception. This, however, can scarcely be called sensation, for sensation pre-supposes the presence of consciousness of the unity of the body, and this we can scarcely attribute to the simplest animals without a nervous system.

The appearance of muscles is coincident with that of the nervous tissues, which are developed in connection with the sense epithelium of the surface (Polyps, Medusæ, Echinoderms). In such cases

FIG. 75.—Diagram of the nervous system of a star-fish. *N*, nerve ring which connects together the five ambulacral centres.

the nerve fibres and ganglion cells which all lie mingled together keep their ectodermal position and their connection with the sense epithelium. The view that the first differentiation of the nervous and muscular tissues is to be sought in the so-called *neuromuscular* cells of the fresh-water polyps and Medusæ has been shown by later researches to be untenable.

The arrangements of the nervous system can be traced back to three distinct types—(1) the radial arrangement found in the radiate animals; (2) the bilateral arrangement found in segmented Worms, Arthropods, and Molluscs; (3) the bilateral arrangement of the Vertebrata. In the first case the central organs are radially repeated; in the Echinoderms as the so-called ambulacral brains or nerves, which are found in the arms and are connected together by a circumoral nervous commissure containing ganglion cells (fig. 75).

In the second type the nervous system, in the simplest cases, consists of an unpaired or paired ganglionic mass placed in the anterior part of the body above the pharynx, and known as the supra-oesophageal ganglion or brain. From this centre radiate in the simplest cases (Turbellaria) nerves which have a bilaterally symmetrical distribution, and of which two are larger than the others; and take a lateral course (fig. 76).

At a higher stage of development a circum-pharyngeal nerve ring is developed. With the commencing segmentation of the body the number of ganglia increases, and in addition to the brain there is present a ventral nervous system consisting either of ventral cord

FIG. 76.—Alimentary canal and nervous system of *Mesostomum Ehrenbergi* (after Graff). *G*, the paired cerebral ganglia with two eye-spots; *St*, one of the two main lateral nerves; *D*, alimentary canal with mouth and pharynx.

FIG. 77.—Nervous system of the larva of *Coccinella* (after Ed. Brandt). *G*, supra-oesophageal ganglion or brain; *Gfr*, frontal ganglion; *Sg*, suboesophageal ganglion; *G'*, *G''*, the eleven ganglia of the ventral chain of thorax and abdomen.

FIG. 78.—Nervous system of adult *Coccinella* (after Ed. Brandt). *Ag*, optic ganglion. The other letters as in fig. 77.

(Gephyrea) or of a ventral chain of ganglia, which may have a homonomous (Annelids) or heteronomous (Arthropods) arrangement (figs. 77 and 78). The concentration of the nervous system begun

in the latter case may, by the fusion of the brain and ventral cord, be carried to a still further extent, so that in many cases (numerous Arthropods) only a sub-œsophageal ganglion is present. In Molluscs,

FIG. 79.—Brain and spinal cord of a pigeon. *H*, cerebral hemispheres; *Cb*, optic lobes; *C*, cerebellum; *Mo*, medulla oblongata. *Sp*, spinal nerves.

animals in which segments are not developed, the sub-œsophageal ganglion is represented by the pedal ganglion, and there is in addition a third pair of ganglia constituting the visceral ganglia (fig. 55). In Vertebrates, the nervous centres are arranged as a cord, lying on the dorsal side of the skeletal axis, and known as the spinal cord, the segmentation of which is indicated by the regular repetition of the spinal nerves.

This cord, which is traversed by a central canal, is anteriorly widened and (except in *Amphioxus*) differentiated into a complicated ganglionic apparatus, the brain (fig. 79).

The so-called sympathetic or visceral nervous system appears in the higher animals (Vertebrata, Arthropoda, Hirudinea, etc.) as a comparatively independent part of the nervous system. It consists of ganglia and plexuses of nerves which stand in connection with the central nervous system, but are not under the direct control of the will of the animal. It innervates the organs of digestion, circulation, respiration, and generation, and it can carry on its functions for a longer or shorter time after destruction of the sensory and motor centres. In the Vertebrata (fig. 80), the system of visceral nerves consists of a double chain of ganglia, placed on each side of the vertebral column and connected with the spinal nerves and the

spinal-like cranial nerves, by connecting branches, the *rami communicantes*. The ganglia correspond in number with the above-mentioned spinal and cranial nerves, and they send nerves to the

blood vessels and viscera, which there form a complicated network of nervous fibres containing here and there ganglion cells.

The nervous system possesses further peripheral apparatus, the *sense organs*, the function of which is to bring about the perception of certain conditions of the outer world as impressions of a definite mode of sensation (specific energy of nerves* Joh. Müller).

These peripheral organs usually have the form of peculiarly arranged aggregations of hair-shaped or rod-shaped nerve terminations (hair-cells, rod-cells of sensory epithelium) connected by fibrillæ with ganglion cells, through which under the action of external influences a movement of the nervous substance is set up, which travels to the central organ and there affects con-

FIG. 80.—Nervous system of the frog (after Ecker). *Ol*, olfactory nerves; *O*, eye; *Op*, optic nerve; *Vg*, Gasserian ganglion; *Xg*, ganglion of vagus; *Spn 1*, first spinal nerve; *Br*, brachial nerve; *Sg 1-10*, the ten ganglia of the sympathetic system. *Js*, ischial nerve.

* In opposition to the differences in the qualities of the sensations produced by each individual sense organ (colour, tone).

sciousness as a specific sensation. To these end-cells there are often added cuticular structures, whose function is to communicate the external movement to the nervous substance (retinal rods).

The special sensations have quite gradually been developed from the general sensations (comfort, discomfort, pleasure, pain), *i.e.*, nerves of special sense have been derived from sensory nerves which have acquired a special form of peripheral termination, and so become accessible to a special stimulus with which the special sensation is always associated. But it is not till a higher stage of development is reached that the sense-perceptions can be compared according to the nature of the sensations with those of our own body. We can estimate the sense energies of the lower animals exceedingly

vaguely, and only by the insufficient method of comparing them with our own sensations; and it is certain that among the lower animals there are many forms of sensation of which we, in consequence of the specialised nature of our own senses, can have no conception.

Probably of all the senses, that of *touch* is the most widely distributed, and with this we certainly often see a number of special sensations united.

It is generally distributed

FIG. 81.—Nerves with ganglion cells (*G*) beneath a tactile bristle (*Tb*) from the skin of *Corethra* larva.

over the whole surface of the body; frequently, however, it is concentrated on processes and appendages of it. Probably the tentacular appendages of the Coelenterata and Echinodermata have this significance. In the Bilateralia with a differentiated head there are contractile or stiff segmented processes on the head, the *antennæ* or feelers which in the worms are repeated as paired cirri on every segment of the body. It is often possible to trace special nerves to the skin and to find touch organs containing their endings. In the Arthropoda the ganglionic end-swelling of a tactile nerve usually lies beneath a cuticular appendage, such as a bristle, which transmits the mechanical pressure on its point to the nerve (fig. 81).

In the Primates amongst the Mammalia there are present papillæ in the skin (especially on the volar surface) in which the structures known as *touch-bodies*, containing the termination of tactile nerves, are placed (fig. 82).

In addition to the general sensibility and the tactile sensations, the higher animals possess, as a special form of sensibility, the capacity of distinguishing different temperatures.

The sensations of *sound* are produced through an organ, the **auditory organ**, which is, in a certain measure, a special modification of a tactile organ. The auditory organ in its simplest form appears as a closed vesicle filled with fluid (*endolymph*) and one or more calcareous concretions (otoliths); and containing in its walls rod or hair cells in which the nerve fibrillæ end (fig. 83). Sometimes the vesicle lies on a ganglion of the central nervous system (Worms), sometimes at the end of a shorter or longer nerve, the auditory nerve (Molluscs, Decapoda). In many aquatic animals the vesicle may be open and its contents communicate directly with the external medium, in which case the otoliths may be represented by small particles such as sand-grains which have entered it from the exterior (Decapod Crustaceans). In Molluscs a delicate sensory epithelium (*macula acustica*, fig. 83 *Cz*, *Hz.*), marks the percipient portion of the inner wall of the vesicle; while in Crustacea the fibres of the auditory nerve end in cuticular rods or hairs which project from the wall of the vesicle, and, like the olfactory hairs of the antennæ, bring about the nervous excitations. In the Vertebrata not only does the auditory vesicle obtain a more complicated form (membranous labyrinth), but there are also added to it apparatuses for conducting and magnifying the sound (fig. 84). The tympanum of Acrideidæ and Locustidæ, which is generally looked upon as an auditory organ, is built upon quite a different type, since here, instead of a vesicle filled with fluid, air cavities serve for the action of the sound waves on the nerve-endings.

FIG. 82.—Tactile papilla from the volar surface with the touch corpuscle and its nerve *N*.

The **visual organs or eyes** * are, after the tactile organs, the most widely distributed, and indeed are found in all possible stages

* Cf. R. Leuckart, "Organologie des Auges," Graefe and Sämisch, Handbuch der Ophthalmologie, Bd. II.

of perfection. In the simplest cases they are known as *eye-spots*, and consist of irritable protoplasm, *i.e.*, nervous substance, containing pigment granules; and in this form they are perhaps scarcely capable of distinguishing light from darkness, but are only susceptible to the warm rays. It is hardly possible to conceive that pigment is indispensable for the sensation of light, because there are many eyes of complicated structure from which pigment may be altogether absent. The view, however, according to which the pigment itself is sensitive to light, *i.e.*, is chemically changed by the light waves and transmits the excitation produced by these movements to the protoplasm or

FIG. 83.—Auditory vesicle of a Heteropod (Pterotrachea). *N*, acoustic nerve; *Ot*, otolith the fluid of the vesicle; *Wz*, ciliated cells on the inner wall of the vesicle; *H_z*, auditory cells; *Cz*, central cell.

the adjacent nervous substance cannot in itself be contradicted, but it is by no means clear that such changes are produced by the light rays as opposed to the heat rays. Of greater importance in this relation appears the special nature of the nerve endings, through which certain movements, progressing in regular waves, the so-called ether waves, are transmitted to the nerve fibres and give rise to a stimulus which travels to the central organ and is by it perceived as light. In all cases in which in the lower animals specific nerve endings cannot be made out, we have probably only to do with a forerunner of the eye, consisting merely of the pigmented termina-

tion of a cutaneous nerve which is sensitive only to gradations of temperature. Although the sensation of light is the function of the nerve centre, the rods and cones at the end of the optic nerve fibres are the elements which convert the external movement of the ether waves into an excitation of the optic nerve fibres adequate for the production of the sensation of light.

For the perception of an image refractile apparatuses in front of the terminal expansion of the optic nerve (retina) are necessary; and further, the elements of the latter must be sufficiently isolated to admit of the stimuli set up in them being carried as separate movements to the nerve centre. Instead of a general sensation of light a complex sensation made up of many separate perceptions is produced, which corre-

spond in position and quality with the parts of the exciting source. For the refraction of the light convex and often lens-shaped thickenings of the body covering (cornea, corneal lens) through which the rays pass into the eye, are developed; refractile bodies are also found behind the cornea (lens, crystalline cone). The rays diverging from the various parts of the source of the

FIG. 84.—Diagram of the auditory labyrinth. I. of a fish. II. of a bird. III. of a mammal (after Waldeyer). *U*, utricle with the three semicircular canals; *S*, sacculus; *US*, alveus communis; *C*, cochlea; *L*, labyrinth; *R*, aqueductus vestibuli; *Cr*, canalis reuniens.

light are, by means of the refractile media, collected and brought to corresponding foci on the retina or peripheral expansion of the optic nerve, which consists of the rod-shaped ends of the nerve fibres and some more or less complicated ganglionic structures. Lately, in consequence of the discovery of the visual purple* in the outer segments of the rods, it has been attempted to reduce the excitation of the end apparatus of the optic nerve to a photo-chemical process taking place in the retina. The fact that the diffuse pigment (visual purple) of the outer segments of the rods is bleached by the

* In addition to the older works of Krohn, H. Müller, M. Schultze, cf. Boll Sitzungsberichte der Akad. Berlin, 1876 and 1877, also Ewald and Kühne.

action of light is of the highest interest, but it cannot be taken as proving a direct participation of the visual purple in the visual process, inasmuch as the visual purple is not present in those parts of the eye in which alone a distinct image is formed, viz., the macula lutea and, generally, the outer segments of the cones.

The pigment of the eye seems to be of importance for absorbing the superfluous rays of light which would be injurious to the perception of an image. It is distributed partly immediately outside the retina, forming the choroid coat of the eye, which extends also inwards between the individual retinal elements; and partly in front of the lens, giving rise to a transversely placed curtain, the *iris*

which is pierced by an opening, the *pupil*, capable of contracting and dilating. In the higher grades of development the whole eye is, as a rule, enclosed in a hard, connective tissue coat, the *sclerotic*, and thus marked off as an eye bulb.

The arrangements by which the shining points of an object act in regular arrangement on corresponding points of the

FIG 85.—Diagrammatic representation of the compound eye of a *Libellula*. *C*, cornea; *K*, crystalline cone; *P*, pigment; *R*, nerve rods of retina; *Fb*, layer of fibres; *Gz*, layer of ganglion cells; *Rf*, retinal fibres; *Fk*, crossing of fibres.

optic nerve and so render possible the perception of an image vary, and are closely dependent upon the whole structure of the eye. Leaving out of consideration the simplest eyes, such as we find in Worms and the lower Crustacea, two types of eye are to be distinguished.

1. The first form occurs in the so-called *faceted eyes** (figs. 85 & 86) of Arthropods (Crustacea and Insects). The retina of such eyes has a hemispherical form, the convex surface being directed outwards, and consists of large compound nerve rods, the retinulæ

* See Joh. Müller, "Zur vergleichenden Physiologie des Gesichtssinnes," Leipzig, 1826. H. Grenacher, "Untersuchungen über das Sehorgan der Arthropoden," Göttingen, 1879.

(figs. 85 & 86 *Rf* & *R*), which are separated from one another by pigment sheaths. In front of these rods are placed the strongly refractile crystalline cones (*k*), and in front of these again the lens-shaped corneal facets (*C* & *F*).

The eye is enclosed by a firm chitinous layer, which, following the sheath of the entering optic nerve, surrounds its soft parts and reaches as far as the cornea. That part of the eye which is known as optic nerve corresponds in a great measure to the retina itself, and contains a layer of ganglion cells and of nerve fibres.

A reversed and reduced picture of the object is thrown behind each convex corneal facet (lying far from the sensitive layer of nervous rods), and only the perpendicular rays can be perceived since all the others are absorbed by the pigment. Accordingly the light impressions caused by these axial rays, whose number corresponds with the separate nerve rods, form a mosaic on the retina which repeats the arrangement of the parts of the external object emitting light. The picture which is here formed lacks, however, brilliancy and distinctness.

2. The second form of eye, which is widely distributed in the animal kingdom (the *simple eye*, Annelids, Insects, Arachnida, Molluscs, Vertebrates) corresponds to a globular camera obscura with collecting lenses (cornea, lens) on its exposed anterior wall on which the light falls and usually with additional dioptric media filling the optic chamber (vitreous humour.) The simple eye of Insects seems to have originated from the simple metamorphosis of part of the integument, beneath which are placed the end organs of the optic nerve (fig. 87). The cuticular covering (*CL*) projects as a lens-shaped thickening into the subjacent layer of transparent, elongated, hypodermis cells (*Gk*), within which are placed elongated rod-like nerve-cells with refractile cuticular portions, closely aggregated to form a retina (fig. 87 *Rz*). The hypodermis cells surrounding the edge of the lens are filled with pigment, and form an iris-like dark ring

FIG. 86.—Three facets with retinulae from the compound eye of a cockchafer (after Grenacher). The pigment has been dissolved away from two of them. *F*, corneal facet. *K*, crystalline cone. *P*, pigment sheath. *P'*, chief pigment cells. *P''*, pigment cells of the second order. *R*, retinulae.

through the opening in which the rays of light enter the eye to fall on the terminal segments of the retinal cells (fig. 87).

In the more highly developed forms of this type of eye, especially in the Vertebrate eye, the peripheral portion of the optic nerve spreads out so as to form a cup-shaped nervous membrane, the retina, placed immediately behind the refractile media and surrounded by a vascular pigmented membrane, the choroid. The choroid, again, is surrounded by a tough supporting membrane composed of fibrous connective tissue, and known as the sclerotic, which is continued over the anterior part of the eye, *i.e.*, that part through which the light passes, as a thinner transparent membrane. Of the refractile media

FIG. 87.—Transverse section through the simple eye of a beetle larva (partly after Grenacher). *CL*, corneal lens; *Gk*, the subjacent hypodermis cells, the vitreous humour of Authors; *P*, pigment in the peripheral cells of the latter; *Rz*, retinal cells. *St*, cuticular rods of the latter.

bulb, *viz.*, the aqueous humour, the lens (fig. 88 *L*), the vitreous humour (*Gl*), the lens is the most powerful. Grasped by the thickened muscular anterior part of the choroid (the ciliary body (*Cc*) and ciliary processes), the peripheral part of its anterior face is covered by a forward continuation of the choroid, the iris (*Jr*), which, as a ring-like contractile border,

forms a kind of diaphragm perforated by a central contractile opening, the pupil, through which the light enters the eye (fig. 88). The reversed image which is formed in the hinder part of the Vertebrate eye on the cup-shaped retina has a very considerable brilliancy and definition.

The eyes of many Cephalopods may be looked upon as a modification of this type of eye. In the eye of *Nautilus* the lens is absent, and the light enters through a small opening. In this case a reversed, but not brilliant, image is formed on the retina placed on the hinder wall of the eye.

To enable the eye to see clearly objects in different directions and

at different distances, special apparatuses for its movement and accommodation are necessary. They are represented by muscles which can in the former case move the optic bulb and modify the direction of sight in obedience to the will of the animal, and in the latter act upon the refractile media, and vary their relation to the retina. In many compound eyes (Decapod Crustacea) that part of the head on which the eye is placed is prolonged so as to give rise to a movable stalk-like process, which bears the eye at its extremity. The eyes of Vertebrata possess in addition special protective arrangements, *e.g.*, eyelids, lacrymal glands.

The position and number of the eyes present very great variations amongst the lower animals.

The paired arrangement on the head appears to be the general rule among the higher animals; nevertheless visual organs sometimes occur on parts of the body far removed from the brain, as for instance, in *Euphausia*, *Pecten*, *Spondylus*, and certain Annelids (*Sabellidæ*). In the Radiata the eyes are repeated at the periphery of the body in each radius. In the star fishes they lie at the extreme end of the ambulacral furrow at the tip of the arms, in the *Acalephæ* as the marginal bodies on the edge of the umbrella.

FIG. 88.—Transverse section through the human eye (after Arlt). *C*, cornea; *L*, lens; *Jr*, iris with pupil; *Cc*, ciliary body; *Gl*, vitreous humour; *R*, retina; *Sc*, sclerotic; *Ch*, choroid. *ML*, macula lutea; *Po*, papilla optica; *No*, optic nerve.

The sense of **smell** appears to be less widely distributed. Its function is to test the quality of gaseous matters and to produce in consciousness the special form of sensation known as "Smell." This sense in aquatic animals which breathe through gills cannot be sharply marked off from that of taste. The small pits, standing in connection with nerves and provided with an epithelial lining of hair-bearing sense cells, are to be looked upon as the simplest form of olfactory organ (*Medusæ*, *Heteropoda*, *Cephalopoda*). Nevertheless scattered hair cells (*Lamellibranchiata*) may also have to do with the same sensation. In the *Arthropoda* the cuticular appendages of the

antennæ in which the gangliated swollen extremities of nerves occur are to be explained as olfactory fibres. In the Vertebrata the olfactory organ usually has the form of a paired pit or cavity placed on the under surface of the head (nasal cavity), on the walls of which the ends of the olfactory nerve are distributed. The higher air-breathing Vertebrata are distinguished by the fact that in them this cavity communicates with the pharynx, and by the great surface extension (in a confined area) of the much-folded olfactory mucous membrane. The fibres of the olfactory nerve terminate in delicate

elongated cells, bearing rods or hairs and placed between the epithelial cells of this mucous membrane.

The special sense of taste is confined to the mouth and pharynx. Its function, from what we know of the higher organisms, is to test the quality of fluid substances, and to bring about the special sensation of taste. The presence of this sense can be demonstrated with certainty in the Vertebrata, and it is connected with the distribution of a special nerve of taste, the glossopharyngeal, which in man supplies the tip, edges, and root of the tongue and also parts of the soft palate, making these parts capable of the taste sensation.

FIG. 89.—*a* Transverse section through a circumvallate papilla of a calf (after Th. W. Engelmann). *N*, nerve; *Gk*, taste buds in the side-wall of the papilla, *Pc*. *b*, isolated taste bud from the lateral taste organs of a rabbit. *c*, isolated supporting cells (*Dz*) and sense cells (*Sz*) from the same.

The so-called taste-buds found in special papillæ (papillæ circumvallatæ), with their central fibre-like cells, are explained as the percipient organs of this sense (fig. 89 *a*, *b*, *c*). Taste is, as a rule, connected with the tactile and temperature sensations of the buccal cavity, and also with the olfactory sensations. Finally, special organs of taste appear to be present also in the Molluscs and Arthropods as a specific sensory epithelium at the entrance to the buccal cavity.

In the lower animals the taste and olfactory organs are still less

clearly distinguishable than in the higher, and there are numerous senses of an intermediate character for the purpose of testing the surrounding medium.

The sense-organs of the lateral line of Fishes and Salamanders, and the organs resembling taste-buds of the Hirudinea and Chætopoda have been described as organs of a sixth sense. They probably bring about certain sensations referring to the quality of the water.

PSYCHICAL LIFE* AND INSTINCT.

The higher animals are not only rendered conscious of the unity of their organization by their feelings of comfort and discomfort, pleasure and pain, but also possess the power of retaining residua of the impressions of the outer world conveyed through the senses, and of combining them with simultaneously perceived conditions of their bodily state. In what manner the irritability of the lower protoplasmic organisms leads by gradual transitions and intermediate steps to the first affection of sensation and consciousness is as completely hidden from us as are the nature and essence of the psychical processes which we know are dependent on the movement of matter.

We are, however, justified in supposing that a nervous system is indispensable for the development of these internal conditions which may be compared with that condition of our own organization called consciousness. Again, as animals have sense-organs capable of receiving impressions of definite quality from external causes, together with a capacity for retaining in their memory residua of their perceptions, and the power of connecting them with present and with the recollection of past states of bodily sensation so as to form judgments and conclusions, they possess all the conditions essential for the operation of the intelligence; and, as a matter of fact, they do manifest in an elementary form nearly all the phenomena which distinguish human intelligence.

The actions of animals are not only voluntary, the result of experience and intellectual activity, but are also largely determined by internal impulses which work independently of consciousness, and cause numerous, often very complicated, actions useful to the organism. Such impulses tending to the preservation of the individual and the

* W. Wundt, "Vorlesungen über die Menschen und Thierseele." 2 Bde. Leipzig, 1863. W. Wundt, "Grundzüge der physiologischen Psychologie," Leipzig, 1874.

species are called *instincts*;* and they are usually regarded as a special property of the lower animals, and contrasted with the conscious reason of Man. But just as the latter must be looked upon as a higher form of the understanding and intellect, and not as something essentially distinct from them, so a closer examination shows that instinct and the conscious understanding do not stand in absolute contrast, but rather in a complex relation, and cannot be sharply marked off from one another. For if, according to the general view, we recognise the essence of instinct in the *unconscious* and the *innate*, still we find that actions which were at first performed under the direction of conscious intelligence become, by constant practice, completely instinctive and are performed unconsciously; and that, in accordance with the theory of descent, which the whole connection of natural phenomena renders so probable, instincts have been developed from small beginnings, and have only been able to reach the high and complicated forms which we admire in many of the more highly organised animals (Hymenoptera), when assisted by a certain amount, however small, of intellectual activity.

Instinct accordingly may be rightly defined as a mechanism which works unconsciously, and is inherited with the organization, and which, when set in motion by external or internal stimuli, leads to the performance of appropriate actions, which apparently are directed by a conscious purpose. We must not, however, forget that while the intellectual activities are the direct means whereby higher and more complicated instincts arise from simple ones, they themselves depend upon mechanical processes. We may well suppose that the simplest form of instinct is identical with the definite reaction of living matter following a stimulus, or, in other words, with that special form of molecular change which is caused by an external action (as, for instance, the contraction of an *Amœba* when brought into contact with a foreign body).

By the theory of partly instinctive, partly intellectual processes, we may explain the phenomena of association in societies so often found among the higher animals,† *i.e.*, the association of numerous

* Compare H. S. Reimarius, "Allgemeine Betrachtungen über die Triebe der Thiere," Hamburg, 1773. P. Flourens, "De l'instinct et de l'intelligence des animaux," Paris, 1851.

† The origin of the so-called animal stocks with incomplete or confined individuality among the lower animals is quite different, and merely determined by processes of growth; at the same time the advantage for the preservation of the species gained by the fusion is the same. Cf. the animal stocks of the Vorticellidæ, Polyyps, and Siphonophora, Bryozoa and Tunicata.

individuals into communities—the so-called animal-polities—which may be complicated by the division of labour (Bees, Wasps, Ants, Termites).

In fact here the combined action appears to be mutually assisting or mutually limiting, as we find in the so-called animal stocks, the individuals of which are bound together by continuity of body. The advantages to be gained by this mutual rendering of service are not merely limited to the greater facilities for nourishment and defence, and therefore for the preservation of the individual; but, above all, tend to the maintenance of the offspring, and hence to the preservation of the species. It is for this reason that the simplest and commonest associations, from which the more complicated communities, subdivided by partition of labour, are derived, are generally communities of both sexes of the same species.

REPRODUCTIVE ORGANS.

On account of the limit set to the duration of the life of every organism, it appears absolutely necessary for the preservation of the animal and vegetable kingdoms that new life should originate. The formation of new organisms might be due to spontaneous generation (*generatio equivoca*); and formerly this was supposed to take place, not only in the simpler and lower organisms, but also in the more complicated and higher. Aristotle thought that Frogs and Eels arose spontaneously from slime; and the appearance of maggots in putrefying meat was, till Redi's time, explained in the same manner. With the progress of science the limits within which this supposition could be applied became ever narrower, so that they soon came to include only the Entozoa and small animals found in infusions. Finally it has been shown by the researches of late years that these organisms also must, for the most part, be withdrawn from the region of the *generatio equivoca*; so that at present, when the question of spontaneous generation is discussed, it is only the lowest organisms, those found in putrefying infusions, that are considered. The greater number of investigators,* supported by the results of

* Cf. especially Pasteur, "Memoire sur les corpuscules organisés qui existent dans l'atmosphère" (Ann. des. Sc. Nat.), 1861; also "Expériences relatives aux générations dites spontanées" (Compt. rend. de l'Acad. des Sciences, tome 50).

numerous experiments, have rejected, even for the latter animals, the idea of spontaneous generation, which, however, still finds in Pouchet* a prominent and zealous supporter.

Biogenesis, as opposed to abiogenesis, or spontaneous generation, must be regarded as the usual and normal form of reproduction. Fundamentally it is nothing else than a growth of the organism beyond the sphere of its own individuality, and can be always reduced to a separation of a part of the body, which develops into an individual resembling the parent organism. Nevertheless the nature and method of this process differ extraordinarily; and various kinds of reproduction can be distinguished, viz., *fission*, *budding* (*spore-formation*), *sexual reproduction*.†

Reproduction by fission, which, with that by *budding* and *spore-formation*, is included under the term *monogenous asexual reproduction*, is found widely scattered in the lowest animals, and is also of special importance for the reproduction of the cell. It consists simply of a division of the organism into two parts by means of a constriction which gradually becomes deeper, and eventually leads to the separation of the whole body of the organism into two individuals of the same kind. If the division remains permanently incomplete, and its products do not completely separate from each other, compound colonies of animals arise. The number of individuals in such colonies increases by a continuation of the process of incomplete and often dichotomous division of the newly-formed individuals (*Vorticella*, *Polyp* stocks). The division may take place in various directions—longitudinal, transverse, or diagonal.

Budding differs from fission by a precedent disproportionate and asymmetrical growth of the body, giving rise to a structure not absolutely necessary to the parent organism which is developed to a new individual, and by a process of constriction and division becomes independent. If the buds remain permanently attached to the parent, we have here also the conditions necessary for the formation of a colony (*Polyp* colonies). Sometimes the budding takes place at various parts of the outer surface of the body, irregularly or obeying definite laws (*Ascidians*, *Polyps*); sometimes it is localised to a definite part of the body, separated off as a *Germ-stock* (*Salpa*, *stolo prolifer*). The cell-layers distinguished as germinal

* Pouchet, "Nouvelles expériences sur la génération spontanée et la résistance vitale," Paris, 1864.

† Cf. R. Leuckart's article, "Zeugung" in R. Wagner's "Handwörterbuch der Physiologie."

layers are repeated in the commencing buds, and from them the organs are differentiated.

The reproduction by spores is characterised by the production within the organism of cells, which develop into new individuals *in situ* or after leaving the organism. But this conception of spores, which is taken from the vegetable kingdom, can only be applied to the Protozoa and coincides with endogenous cell-division. The cases of so-called spore-formation amongst the Metazoa (germinal sacs of Trematodes) are probably identical with egg formation, and are to be reduced to a precocious maturation and spontaneous development of ova (Parthenogenesis, Pædogenesis).

The digenous or sexual reproduction depends upon the production of two kinds of germinal cells, the combined action of which is necessary for the development of a new organism. The one form of germ cells contains the material from which the new individual arises, and is known as the *egg-cell*, or merely *egg* (*ovum*). The second form, the *sperm-cell* (*spermatozoon*), contains the fertilising material, *semen* or *sperm*, which fuses with the contents of the egg-cell, and in a way which is not understood gives the impetus to the development of the egg. The cell structures from which the eggs and sperm arise are called *sexual organs*, for reasons which will be evident in the sequel; the eggs being produced in the *female* organ or *ovary*, and the semen in the *male* organ or *testis*. The *egg* is the *female*, and the *semen* the *male* product.

The structure of the sexual organs presents extraordinary differences and numerous grades of progressive complication. In the simplest cases, both products arise in the body wall, the cells of which give rise at determined places to ova or spermatozoa (Cœlenterata). Sometimes they arise in the ectoderm (Hydroid-Medusæ), sometimes in the entoderm (Acalepha, Anthozoa). A similar arrangement

FIG. 90.—Generative organs of a Heteropod (*Pterotrachea*) after R. Leuckart. *a*, Male-organs; *T*, testis. *Vd*, vas deferens. *b*, female organs; *Ov*, ovary; *Ed*, albumen gland; *Rs*, receptaculum seminis; *Va*, vagina.

obtains in the marine Polychæta, in which the ova and spermatozoa are developed from the epithelium of the body-cavity (mesoderm), and dehiscent into the body cavity. Usually, however, special glands, the ovaries and testes, are developed, which perform no other function than that of secreting ova and spermatozoa (Echinoderms).

As a rule, however, there are found associated with the male and female generative glands accessory structures and a more or less complicated arrangement of ducts, which discharge definite functions in connection with the development of the generative products subsequent to their separation from the glands, and ensure a suitable meeting between the male and female elements (fig 90). The ovaries are provided with ducts, the oviducts, which are not rarely derived

FIG. 91, *a*.—The female organs of *Pulex* (after Stein). *Or*, ovarian tubes; *Rs*, receptaculum seminis; *V*, vagina; *Gl*, accessory gland. *b*, The male generative organs of a water-bug (*Nepa*) (after Stein). *T*, testis; *Vd*, vasa deferentia; *Gl*, accessory glands; *D*, ductus ejaculatorius.

from structures serving quite another purpose (segmental organs). The oviducts, in their course, may receive glandular appendages of various kinds which furnish yolk for the nourishment of the ovum, or albumen to surround it, or material for the formation of a hard egg-shell (chorion). These functions may be sometimes discharged by the ovarian wall (Insects), so that the egg when it enters the oviduct has taken up its accessory yolk and acquired its firm egg-shell. Very often the ducts also discharge these various functions, and are divided into corresponding regions; they are often dilated at part of their course to form a reservoir for the retention of the

eggs or of the developing embryos (uterus). Their terminal section presents differentiations subserving fertilization (receptaculum seminis, vagina, copulatory pouch, external generative organs). The efferent ducts of the testis, the vasa deferentia, likewise frequently give rise to reservoirs (vesiculæ seminales) and receive glands (prostate), the secretion of which mixes with the sperm fluid or surrounds aggregations of the spermatozoa with a firm sheath (spermatophors).

The terminal section of the vas deferens becomes exceedingly muscular, and gives rise to a ductus ejaculatorius, which, as a rule, is accompanied by an external organ of copulation to facilitate the conveyance of the semen into the female generative organs. The generative organs present either a radial (Coelenterata, Echinodermata) or a bilaterally symmetrical arrangement (fig. 91), a contrast which is visible in the typical arrangement of all the systems of organs.

The simplest and most primitive condition of the generative organs is the *hermaphrodite*. Ova and spermatozoa are produced in the body of one and the same individual, which thus unites in itself all the conditions necessary for the preservation of the species, and alone

represents the species. Instances of hermaphroditism are found in every group of the animal kingdom. But they are especially numerous in the lower groups, and also in animals in which the movements are slow (Land-snails, Flat-worms, Hirudinea, Oligochæta), or which live singly (Cestoda, Trematoda), or in attached animals which are without power of changing their position (Cirripedia, Tunicata, Bryozoa, Oysters). The hermaphrodite arrangement of the generative organs presents great variation, which, to a certain extent, forms a gradual series tending towards the separation of the sexes.

In the simplest cases, the points of origin of the two kinds of generative products lie close to one another, so that the spermatozoa and ova meet directly in the parent body (Ctenophora, Chrysaora).

FIG. 92.—Sexual organs of a Pteropod (*Cynbulia*) (after Gegenbaur.) *a*, *Zd*, hermaphrodite gland with common duct; *Rs*, receptaculum seminis; *U*, uterus. *b*, Acinus of the hermaphrodite gland of the same. *O*, ova; *S*, spermatozoa.

The elements of both sexes arise in layers of cells which have a definite position beneath the entodermal lining of the gastro-vascular canals, and can be traced back to growths of the ectoderm. At a higher stage the ovaries and testes are united in one gland, the hermaphrodite gland (Synapta, Pteropoda), provided with a single duct common to the ova and spermatozoa (fig. 92), but which, as in *Helix* (fig. 93), may partially separate into vas deferens and oviduct. In other cases the ovaries and testes appear as completely separated glands with separate ducts, which may still open into a common cloaca (Cestoda,

FIG. 93.—Sexual organs of the Roman Snail (*Helix pomatia*). *Zd*, hermaphrodite gland; *Zg*, its duct; *Ed*, albumen gland; *Od*, oviduct and seminal groove; *Vd*, vas deferens; *P*, protrusible penis; *Fl*, flagellum; *Rs*, receptaculum seminis; *D*, finger-shaped gland; *L*, Spiculum amoris; *Go*, common genital opening.

Trematoda, rhabdocœle Turbellarians, fig. 94), or may possess separate openings (Hirudinea, fig. 95).

Two hermaphrodite individuals may, and this appears to be the rule, mutually fertilise each other at the same time, or cases may occur in such hermaphrodites in which self-fertilization is sufficient for the production of offspring. But this original condition of self-fertilization appears to be the exception in almost all hermaphrodites. In those animals in which the ovary and testis are not completely separated from one another cross-fertilization is rendered necessary, and self-fertilization prevented by the fact that the male

and female elements are matured at different times (Snails, Salps).

From this form of complete hermaphroditism the generative organs pass through a stage of incomplete hermaphroditism, in which, though the organs of both sexes are present, one of them is rudimentary, to reach the dioecious condition in which the sexes are completely separated (*Distomum fillicolle* and *haematobium*). Animals in which the sexes are distinct not unfrequently present traces of an

hermaphrodite arrangement; such, for instance, as may be seen in the arrangement of the generative ducts of the Vertebrata. In the Amphibia both male and female generative ducts, which are secondarily derived from the urinary ducts, are developed in each individual. The oviduct (Müllerian duct) in the male atrophies, and is only represented by a small rudiment (fig. 96*b*, *Mg*); while, on the contrary, in the female, the vas deferens (Wolffian duct) is rudimentary, or, as in Amphibia, functions as the efferent duct for the kidney secretion (fig. 96*a*, *hg*).

FIG. 94.—Generative apparatus of a rhabdocoele Turbellarian (*Vortex viridis*) (after M. Schultze). *T*, testis; *Vd*, vas deferens; *Vs*, seminal vesicle; *P*, protrusible penis; *Ov*, ovary; *Va*, vagina; *M*, uterus; *D*, yolk gland; *Rs*, receptaculum seminis.

With the separation of the male and female generative organs in different individuals the most complete form of sexual reproduction, so far as concerns division of labour, is reached; but at the same time a progressing dimorphism of the male and female individuals becomes apparent. This is due to the fact that the organization in bisexual animals is more and more influenced by the deviating functions of the sexual

FIG. 95.—Generative apparatus of the medicinal leech. *T*, testis; *Vd*, vas deferens; *Nh*, vesicula seminalis; *Pr*, prostate; *C*, penis; *Ov*, ovaries with vagina and female generative opening.

organs, and with the increasing complication of sexual life becomes modified for the performance of special accessory functions connected with the production of ova and spermatozoa.

In the first place, the modification of the generative ducts of the two sexes in accordance with the function they have to perform determines the development of secondary sexual characters and of sexual dimorphism. Other organs as well as the generative appa-

ratus present differences in the two sexes, being modified for the

FIG. 96a.—Left urinary and generative organs of a female Salamander without the cloaca. *Ov*, ovary; *N*, kidney; *hg*, urinary duct corresponding to the Wolffian duct; *Mg*, Müllerian duct as oviduct.

FIG. 96b, Left urinary and generative organs of a male Salamander, more diagrammatic. *T*, testis; *Ve*, vasa efferentia; *N*, kidney with its collecting tubules; *Mg*, Müllerian duct as a rudiment; *Wg*, Wolffian duct or vas deferens; *Kl*, cloaca with accessory glands *Dr*, of the left side.

performance of special functions in the sexual life. The female is

the passive agent in copulation, merely receiving the semen of the male; the female possesses material from which the offspring

FIG. 97a.—Male of *Aphis platanoides*. *oc*, ocelli; *Hr*, honey tubes; *P*, copulatory organ.

develop, and accordingly takes care of the development of the fertilised egg and of the later fate of the offspring. Hence the female usually possesses a less active body and numerous arrangements for the protection and nourishment of her offspring, which develop either from eggs laid by the mother and sometimes carried about with her, or in the maternal body and are born alive. The function of the male is to seek, to excite, and to hold the female during copulation; hence, as a rule, he possesses greater vigour and power of movement, higher development of the senses, various means of exciting sexual feeling, such as brighter colouring, louder and richer voice, prehensile organs, and external organs for copulation (fig. 97, *a*, *b*).

FIG. 97b, Apterous oviparous female of the same.

In exceptional cases, the functions relating to the maintenance of

the offspring may be discharged by the male, *e.g.*, *Alytes* and the *Lophobranchia*. Male birds also often share with the female the labour of building the nest, of bringing up and protecting the young. But it is a rare exception to find, as in *Cottus* and the *Stickleback* (*Gasterosteus*), that the care and protection of the young fall exclusively upon the male, that he only bears the brood pouch and alone builds the nest,—an exception which bears strong witness to the fact that the sexual differences both in form and function were first acquired by adaptation.

In extreme cases, the sexual dimorphism may lead to so great a difference in the sexes that without a knowledge of their development

FIG. 98.—*Chondracanthus gibbosus*, magnified about 6 times. *a*, female from the side. *b*, female from the ventral surface with the male (*F*) attached. *c*, male isolated, under strong magnification. *An'*, anterior antenna; *An''*, clasping antennæ; *F'* and *F''*, the two pairs of feet; *A*, eye; *Ov*, egg sacs; *Oe*, œsophagus; *D*, intestine; *M*, mouth parts; *T*, testis; *Vd*, vas deferens; *Sp*, spermatophore.

and sexual relations, the one sex would be placed in a different family and genus to the other. Such extremes are found in the *Rotifera* and parasitic *Copepoda* (*Chondracanthus*, *Lernæopoda*, fig. 98, *a*, *b*, *c*), and are to be explained as the result of a parasitic mode of life.

The difference in the two kinds of individuals representing and maintaining the species, whose copulation and mutual action was known long before it was possible to give a correct account of the real nature of reproduction, has led to the designation “sexes,” from which the term *sexual* has been taken to apply to the organs and manner of reproduction.

In reality sexual reproduction is nothing else than a special form of growth. The ova and spermatoblasts represent the two forms of germinal cells which have become free, and which, after a mutual interaction in the process of fertilization, develop into a new organism. Nevertheless under certain conditions the egg can, like the simple germ cell, undergo spontaneous development; numerous instances of this mode of development, which is known as *parthenogenesis*, are found in Insects. The necessity of fertilization therefore

FIG. 99.—Viviparous form of *Aphis platanoides*. *Oc*, ocelli; *Hr*, honey tubes.

no longer enters into our conception of the egg-cell, and no absolute physiological test is left to enable us to distinguish it from the germ-cell. It is usual to regard the place of origin in the *sexual organ* and in the *female* body as a feature distinguishing the ovum from a germ cell, but even with this morphological test we do not in each individual case arrive at the desired result (*Bees, Bark-lice, Psychidæ*). We have already given prominence to the fact that ovaries and testes, in the simplest cases, consist of nothing more than groups of cells of the epithelium of the body cavity or of the outer skin. These, however, do not acquire the character of sexual organs until, at a higher stage of differentiation, the contrast between the two

sexual elements has made its appearance. When the male elements, and with them the necessity of fertilization, are absent, and when, at the same time, the organ which produces the germ cells possesses, in its full development, a structure similar to that of an ovary, it becomes very difficult to distinguish whether we have to do with a pseudovary (germ-gland), and with an animal which reproduces asexually; or with an ovary and a true female, whose eggs possess

FIG. 100.—Viviparous *Cecidomyia* (*Miastor*) larva (after Al. Pagenstecher). *Tl*, Daughter larvæ developed from the rudimentary ovary.

the capacity of developing spontaneously. It is only a comparison with the sexual form of the animal which makes the distinction possible. To take the case of the Plant-lice or Aphides; in these animals we find a generation of viviparous individuals, easily distinguishable from the true oviparous females, which copulate and lay eggs. They resemble the latter in the fact that they are provided with a similar reproductive gland, constructed upon the ovarian type; but they differ from them in this important peculiarity, that they are without organs for copulation and fertilization (in correspondence with the absence of the male animal) (fig. 99). The reproductive cells of the organs known as *pseudovaries* have an origin precisely similar to that of eggs in the ovaries, and only differ from ova in the very early commencement of the embryonic development. The viviparous individuals will therefore be more correctly regarded as *agamie* females peculiarly modified in the absence of organs for copulation and fertilization; and the reproductive cells are by no means to be relegated to the category of germ-cells (as formerly was done by Steenstrup). We must therefore speak of the reproductive processes in the Aphides as being sexual and parthenogenetic and not sexual and asexual. A comparison of the mode of reproduction of the Bark-lice with that of the Aphides, especially of the species *Pemphigus terebinthi*, puts the correctness of this supposition beyond the sphere of doubt.

A similar condition is found in the viviparous larva of *Cecidomyia*. Here the rudiment of the generative glands very early assumes a structure resembling that of the ovary, and produces a number of

reproductive cells which resemble ova in their method of origin, and at once develop into larvæ. The pseudovary is clearly derived from the rudiment of the sexual gland, but without ever reaching complete development (fig. 100). The ovary acquires to a certain extent the signification of an organ for producing germ-cells, and it is not improbable that many products (*Redia*, *Sporocyst*) regarded as spores or germ-cells correspond to embryonic ovaries which produce ova capable of spontaneous development.

FIG. 101.—Ovum of *Nephelis* (after O. Hertwig). *a*, the ovum half-an-hour after deposition. a projection of the protoplasm indicates the commencing formation of the first polar body; the nuclear spindle is visible. *b*, The same an hour later, with polar body extruded, and after entrance of the spermatozoon. *Sk*, male pronucleus. *c*, The same another hour later without egg membrane, and with two polar bodies and male pronucleus (*Sk*); *d*, the same an hour later with approximated female and male pronuclei; *Rk*, polar bodies.

DEVELOPMENT.

It follows from the facts of sexual reproduction that the simple cell must be regarded as the starting-point for the development of the organism. The contents of the ovum spontaneously or under the influence of fertilization enter upon a series of changes, the final result of which is the rudiment of the body of the embryo. These changes consist essentially in a process of cell division which implicates the whole protoplasm of the ovum, and is known as *segmentation*.

For a long time the behaviour of the germinal vesicle at the commencement of segmentation and its relation to the nuclei of the first formed segments were obscure, and the knowledge of the changes and fate of the spermatozoa which enter the ovum in the process of fertilization was, in like manner, in a very unsatisfactory state. Of late years, numerous investigations, especially those of Bütschli, O. Hertwig, Fol, etc., have thrown some light on these hitherto completely obscure processes. It was supposed that in a ripe ovum preparing itself for segmentation the germinal vesicle disappeared,

FIG. 102, a, b.—Parts of the ovum of *Asterias glacialis* with spermatozoa, embedded in the mucilaginous coat (after H. Fol.) c, upper part of the ovum of *Petromyzon* (after Calberla). Am, micropyle; Sp, spermatozoa; Jm, path of the spermatozoon; Ek, female pronucleus; Eh, membrane of ovum; Eh2, prominences of the same.

and a new nucleus was formed quite independently of it; and that the persistence and the participation of the germinal vesicle in the formation of the nuclei of the first segmentation spheres were exceptional (*Siphonophora*, *Entoconcha*, etc.) Thorough investigations carried out on the eggs of numerous animals have, however, shown that as a matter of fact the germinal vesicle of the ripe ovum only experiences changes in which the greater part of it, together with some of

the protoplasm of the ovum, is thrown out of the egg as the so-called *directive bodies* or *polar cells* (fig. 101). The part of it, however, which remains in the ovum retains its significance as a nucleus, and is known as the female pronucleus. This fuses with the single spermatozoon (male pronucleus) which has forced its way into the ovum (fig. 102); and the compound structure so formed constitutes the nucleus of the fertilized ovum, or as it is generally called, the first segmentation nucleus.

FIG. 103.—Development of a Star-fish, *Asteracanthion berylinus* (after Alex. Agassiz). 1, Commencing segmentation of the flattened egg—at one pole are seen the polar bodies; 2, stage with two segments; 3, with four; 4, with eight; 5, with thirty-two segments; 6, later stage; 7, blastosphere with commencing invagination; 8 and 9, more advanced stages of invagination. The opening of the gastrula cavity becomes the anus.

This new nucleus, which divides to give rise to the nuclei of the first segmentation spheres, would appear therefore to be the product of the fusion or conjugation of the part of the germinal vesicle, which remains behind in the ovum, with the male pronucleus, which is a derivative of the spermatozoon which has entered the ovum. *Fertilization would appear, therefore, to depend upon the addition*

of a new element bringing about the regeneration of the primary nucleus of the ovum or germinal vesicle, and would have impressed its influence on the constitution of the conjugated nucleus. The regenerated ovum is therefore the starting-point of the subsequent generations of cells which build up the embryonic body.

Both the origin of the polar bodies which takes place in the ripe ovum *independently* of fertilization, and the division of the segmentation nucleus are accompanied by the appearance of the nuclear spindle and star-shaped figures at the poles of the spindle which are so characteristic of the division of nuclei. The male pronucleus, before it fuses with the female pronucleus, also becomes surrounded by a layer of clear protoplasm, around which a star-shaped figure appears (fig. 101). In those cases in which segmentation takes place without a precedent fertilization (*parthenogenesis*), the female pronucleus appears to possess within itself the properties of the first segmentation nucleus.

The fertilization is followed by the process known as segmentation, in which the ovum gradually divides into a greater and greater number of smaller cells. Segmentation may be *total*, *i.e.*, the whole ovum segments (fig. 103), or it may be *partial*, in which case only a portion segments (fig. 105).

Total segmentation may be regular and *equal*, the resulting segments being of equal size (fig. 103); or it may sooner or later become irregular, the resulting segments being of two kinds—the one smaller and containing a preponderating amount of protoplasm, the other larger and containing more fatty matter. In these cases the segmentation is said to be *unequal*. The process of division proceeds much more quickly in the smaller segments, while in the larger and more fatty segments it is much slower, and may eventually come to a complete standstill. The development of the frog's egg will serve as an example of unequal segmentation, of which there are various degrees (fig. 104). In this egg a dark pigmented and protoplasmic portion can be distinguished from a lighter portion containing much fatty matter or food yolk. The former is always turned uppermost in the water, and is therefore called the upper pole of the egg. The axis which connects the upper pole with the lower is known as the chief axis. The planes of the two first segmentation furrows pass through the chief axis and are at right angles to each other. They divide the egg into four equal parts. The third furrow (fig. 104, 4) is equatorial, taking place in a horizontal plane, and cutting the chief axis at right angles. It lies, however, nearer

the upper pole than the lower, and marks the line of division between the upper and smaller portion of the egg from the lower

FIG. 104.—Unequal segmentation of the Frog's egg (after Ecker) in ten successive stages.

and larger portion, in which the segmentation proceeds much more slowly than in the former.

In *partial* segmentation we find a sharply marked contrast between the formative and nutritive parts of the egg, inasmuch as the latter does not segment. The terms *holoblastic* and *meroblastic* therefore have been applied to total and partial segmentation respectively.

Nevertheless, in total segmentation also, either groups of segments of a definite quality, or, at any rate, a fluid yolk material may be used for the nourishment of the developing embryo. In fact, the

FIG. 105. Segmentation of the germinal disc of a Fowl's egg, surface view (after Kolliker). *A*, germinal disc with the first vertical furrow; *B*, the same with two vertical furrows crossing one another at right angles; *C* and *D*, more advanced stages with small central segments.

contents of every egg consists of two parts—(1) of a viscous albuminous protoplasm; and (2) of a fatty granular matter, the *deutoplasm*, or food yolk. The first is derived from the protoplasm

of the original germinal cell, while the yolk is only secondarily developed with the gradual growth of the first; and not unfrequently it is derived from the secretion of special glands (yolk glands, *Trematodes*); it may even be added in the form of cells.

In the Ctenophora and other Cœlenterata we see already in the first-formed segments the separation of the formative matter or peripheral ectoplasm from the nutritive matter or central endoplasm.

In eggs undergoing a partial segmentation the formative matter usually lies on one side of the large unsegmenting food yolk. In accordance with this, the segments of such eggs, known as *telolecithal*, arrange themselves in the form of a flat disc (germinal disc); hence this kind of segmentation has been called discoidal (eggs of Aves, Reptilia, Pisces) (fig. 105). The food yolk may, however, have a central position. In such *centrolecithal* eggs the segmentation is

FIG. 106.—Unequal segmentation of the centrolecithal egg of *Gammarus locusta* (in part after Ed. van Beneden). The central yolk mass does not appear till a late stage and undergoes later an “after-segmentation.”

confined to the periphery, and is sometimes equal (*Palæmon*) and sometimes unequal (fig. 106). The central yolk mass may at first remain unsegmented, but later it may undergo a kind of after-segmentation and break up into a number of cells (fig. 106). Again, in other cases the food yolk, at the commencement of segmentation, has a peripheral position, so that the cleavage process is at first confined to the inner parts of the egg, and only in later stages, when the food yolk has gradually shifted into the centre of the egg, appears as a peripheral layer on the surface. This is found especially in the eggs of Spiders (fig. 107). The first processes of segmentation in these at first *ectolecithal* ova are withdrawn from observation, since they take place in the centre of an egg covered by a superficial layer of food yolk, until the nuclei with their protoplasmic invest

ment reach the periphery, and the fatty and often darkly-granular food yolk comes to constitute the central mass of the egg (Insects).

As various as the forms of segmentation are the methods by which the segments are applied to the building up of the embryo. Frequently in cases of equal segmentation the segments arrange themselves in the form of a one-layered vesicle, the *blastosphere*, the central cavity of which not rarely contains fluid elements of the food yolk; or they are at once divided into two layers around a central cavity containing fluid; or they form a solid mass of cells without

FIG. 107.—Six stages in the segmentation of a spider's egg (*Philodromus limbatus*) after Hub Ludwig. *A*, egg with two deutoplasmic rosette-like masses (segmentation spheres); *B*, the rosette-like masses with their centrally placed nucleated protoplasm without egg membrane; *C*, egg with a great number of rosette-like masses; *D*, the rosette-like masses have the form of polyhedral deutoplasmic columns, each of which has a cell of the blastoderm lying immediately superficial to it; *E*, stage with blastoderm completely formed; *F*, optical section through the same. The yolk columns form within the blastoderm a closed investment to the central space.

any central cavity. In numerous cases, especially when the food yolk is relatively abundant (unequal and partial segmentation) or the food supply continuous, the embryonic development is longer and more complicated. The embryonic rudiment in such cases has at first the form of a disc of cells lying on the yolk; it soon divides into two layers, and then grows round the yolk.

The two-layered gastrula is, as a rule, developed from the blastosphere by invagination (embolic invagination). In this process the one half (sometimes distinguished by the larger size and more granular nature of its cells) of the cell wall of the blastosphere is pushed in upon the other half (fig. 108), and on the narrowing of the

FIG. 108.—*A*, Blastosphere of *Amphioxus*; *B*, invagination of the same; *C*, gastrula, invagination completed; *O*, blastopore (after B. Hatschek).

aperture of invagination (*blastopore*, mouth of gastrula) becomes the endodermal layer (*hypoblast*) lining the gastrula cavity. The outer layer of cells constitutes the ectoderm or *epiblast*. This mode of formation of the gastrula, which is very common, is found, *e.g.*, in Ascidians, and amongst the Vertebrata in *Amphioxus* (fig. 108).

More rarely the gastrula arises by *delamination*. This process consists of a concentric splitting of the cells of the blastosphere into an outer layer (*epiblast*), and an inner (*hypoblast*) (fig. 109).

FIG. 109.—Transverse sections through three stages in the segmentation of *Geryonia* (after H. Fol.) *A*, stage with thirty-two segments, each segment is divided into an external finely granular protoplasm (ectoplasm) and an inner clearer layer (endoplasm); *B*, later stage; *C*, embryo after delamination; with ectoderm slightly separated from the endoderm, which is composed of large cells surrounding the segmentation cavity.

The central cavity of the gastrula in this case is derived from the original segmentation cavity, and the gastrula mouth is only secondarily formed by perforation. This method of development

of the gastrula has hitherto only been observed in some hydroid Medusæ (Geryonia).

Finally, when the inequality of the segmentation is very pronounced, the gastrula is formed by a process known as epibole. In this process of development the epiblast cells, which are early distinguishable from the much larger hypoblast cells, spread themselves over the latter as a thin layer (fig. 110); and in this, as in the second method of development of the gastrula, the cavity of the gastrula is, as a rule, a secondary formation in the centre of the closely-packed mass of hypoblast cells. The blastopore is usually found at the point where the complete enclosure of the hypoblast is effected.

It sometimes happens that a part of the primary blastosphere is developed more rapidly than the remainder, and gives rise to a

FIG. 110.—*A*, Unequal segmentation of the egg of *Bonellia*; *B*, epibolic gastrula of the same (after Spengel).

bilaterally-symmetrical stripe-like thickening placed on the dorsal or ventral surface of the embryo. Frequently, however, such a *germinal* or *primitive streak* is not developed, and the rudiment of the embryo continues to develop uniformly. Formerly great importance was attached to these differences, the one being distinguished as an *evolutio ex una parte*, and the other an *evolutio ex omnibus partibus*. It is not, however, possible to draw a sharp line between these two methods of development, nor have they the significance which was formerly ascribed to them, for closely allied forms may present great differences in this respect according to the amount of food yolk and the duration of the embryonic development.

The Cœlenterata, the Echinoderms, the lower Worms and Molluscs, Annelids, and even Arthropods and Vertebrates (*Amphioxus*) present us with examples of regular development of all parts of the

body of the embryo which, if the yolk membrane fails, has no need of a special protective envelope. In this latter group, however, the formation of the germinal streak, which is in close relation with the formation of the nervous system, is accomplished later, during the post-embryonic development, when the larva is free-swimming and can procure its own food. In like manner many Polychætes and Arthropods (Branchipus) only acquire a germinal streak in the course of their later growth as larvæ.

In all cases in which the embryonic development begins by the formation of a germinal streak, the embryo only becomes definitely limited after the yolk has been gradually surrounded, as a result of processes which are connected with the complete entry of the yolk into the body cavity (Frogs, Insects), or with the origin of a yolk sac from which the yolk passes gradually into the body of the embryo (Birds, Mammals). The progressive organization of this latter, up to its exit from the egg membranes, presents in each group such extraordinary variations that it is not possible to give a general account of them.

Of primary importance is the fact that in the rudiment of the germ two cell layers first make their appearance—one the ectoderm, which gives rise to the outer integument; and the other the endoderm, from which arises the lining membrane of the digestive cavity and of the glands opening into it. Between these two layers there is formed, either from the outer or the inner layer, or from both layers, an intermediate layer, known as the mesoderm. From the mesoderm arise the muscular system and the connective tissues, the corpuscles of the lymph and blood, and the vascular system. The body cavity may either be derived from the persisting segmentation cavity, *i.e.*, the primitive space between the ectoderm and endoderm (primary body cavity), or it may be developed secondarily as a split in the mesoderm (cœlom), or as outgrowths from the rudiment of the alimentary canal (archenteron), in which case it is known as an enterocœle body cavity.

The nervous system and organs of sense are probably in all cases derived from the ectoderm, very frequently as pit- or groove-like invaginations which are subsequently constricted off. On the other hand, the urinary and generative organs arise both from the outer and inner layers as well as from the middle layer, which is itself derived from one of the primary layers or from the walls of the primary single-layered blastosphere.

Accordingly, as a rule the rudiments of the skin and glandular

lining of the alimentary canal are the first differentiations in the embryo; and many embryos, the so-called *Planulæ* and *Gastrulæ*, on leaving the egg, have only these two layers and an internal cavity, the archenteron. Then follows the development of the nervous and muscular systems,—the latter taking place sometimes contemporaneously with or after the first appearance of the skeleton,—especially in cases in which a germinal streak is developed. The urinary organs and various accessory glands, the blood-vessels and respiratory organs do not appear till later.

The degree of difference between the offspring on attaining the free condition (*i.e.*, at birth or hatching) and the sexually mature adults, both as regards form and size as well as organization, varies considerably throughout the animal kingdom.

It is a very striking fact that an embryo provided with a central cavity and a body wall composed of only two layers of cells appears in different groups of animals as a freely moveable larva capable of leading an independent life. Having recognized this fact, it was not a great step, especially as Huxley* some time ago had compared the two membranes of the body wall of the *Medusæ* (called later by Allman *ectoderm* and *endoderm*) with the outer and inner layers of the vertebrate blastoderm (epiblast and hypoblast), to arrive at the conclusion that there was a similar phylogenetic origin for the similar larvæ of very different animal types, and to trace back the origin of organs functionally resembling each other to the same primitive structure.

It was A. Kowalewski† who, by the results of his numerous researches on the development of the lower animals, first gave this conception the groundwork of fact. He not only proved the occurrence of a two-layered larva in the development of the *Cœlenterata*, *Echinoderms*, *Worms*, *Ascidians*, and in *Amphioxus* amongst *Vertebrates*, but also on the ground of the great agreement in the later developmental stages of the larvæ of *Ascidians* and *Amphioxus* and in the mode of origin of equivalent organs in the embryos of *Worms*, *Insects*, and *Vertebrata*, protested against the hitherto universally received view implied in Cuvier's conception of types, that the organs of different types could not be homologous with one another.

* Th. H. Huxley, "On the Anatomy and Affinities of the family of *Medusæ*." *Philosophical Transactions*. London, 1849.

† Cf. A. Kowalewski's various papers in the "*Mémoires de l'Acad. de Petersbourg*," on *Otenophora*, *Phoronis*, *Holothurians*, *Ascidians*, and *Amphioxus*, 1866 and 1867.

Inasmuch as Kowalewski,* from the results of his embryological work, drew the conclusion that the nervous layer and embryonic skin of Insects and Vertebrates are homologous, and that the germinal layers of Amphioxus and Vertebrates correspond with those of Molluscs (Tunicata) or worms, he was in agreement with the long recognised fact that anatomical transitional forms and intermediate links between the different groups or types of animals exist, and that these latter do not represent absolutely isolated planes of organization, but the highest divisions in the system, and he only gave in reality an embryological expression to the claims of the descent theory. In fact, the conclusion which Kowalewski reached was completely correct—viz., that the homologies of the germinal layers in the different types afford a scientific basis for comparative anatomy and embryology, and must be recognised as the starting-point for the proper understanding of the relationships of the types. For this position we find amongst the vertebrata proofs at every step.

But while his own comprehensive embryological experiences inspired Kowalewski, the founder of the theory of the germinal layers, with a prudent reserve, other investigators, inclined to bold generalization, appeared at once with ready theories, in which the results of embryological investigations were interpreted in accordance with the theory of descent. Among these E. Haeckel's gastræa theory is especially prominent, which raises no less a claim "than to substitute, in the place of the classification hitherto received, a new system based on phylogeny, of which the main principle is homology of the germinal layers and of the archenteron, and secondarily on the differentiation of the axes (bilateral and radial symmetry) and of the cœlom." E. Haeckel† designated the larval form used as the point of departure the *Gastrula*, and believed to have found in it the repetition in embryonic development of a common primitive form, to which the origin of all Metazoa may be traced back. To this hypothetical prototype, which is supposed to have lived in very early times during the Laurentian period, he gave the name of *Gastræa*, and called the ancient group, supposed to be widely scattered and to consist of many families and genera, by the name *Gastræadae*. From this supposition was deduced the complete homology of the outer and inner

* A. Kowalewski, "Embryologische Studien an Würmern und Arthropoden." Petersburg, 1871, p. 58-60.

† E. Haeckel, "Gastræatheorie," Jen. nat. Zeitschrift, 1874." For criticism see C. Claus, "Die Typenlehre und Haeckel's sogenannte Gastræatheorie," Vienna, 1874.

germinal layers throughout the whole Metazoa; the one being traced back to the ectoderm and the other to the endoderm of the hypothetical *Gastræa*; while for the middle layer, which is only secondarily developed from one or both of the primary layers, only an incomplete homology was claimed. It cannot, however, be said that this theory, which is essentially an extension of the Baer-Remak theory of the germinal layers from the Vertebrata to the whole group of Metazoa, with its pretentious and hasty speculation has created a basis for comparative embryology; such a basis can only be obtained as the result of comprehensive investigations.

DIRECT DEVELOPMENT AND METAMORPHOSIS.

The more complete the agreement between the just born young and the adult sexual animal, so much the greater, especially in the higher animals, will be the duration of the embryonic development and the more complicated the developmental processes of the embryo. The post-embryonic development will, in this case, be confined to simple processes of growth and perfection of the sexual organs. When, however, embryonic life has, relatively to the height of the organization, a quick and simple course; when, in other words, the embryo is born in an immature condition and at a relatively low stage of organization, the post-embryonic development will be more complicated, and the young animal, in addition to its increase in size, will present various processes of transformation and change of form. In such cases, the just hatched young, as opposed to the adult animal, is called a *Larva*, and develops gradually to the form of the adult.

FIG. 111.—Larval stages of the Frog (after Ecker). *a*, embryo some time before hatching, with wart-like gill papillæ on the visceral arches. *b*, Larva some time after hatching, with external branchiæ. *c*, Older larva, with horny beak and small branchial clefts beneath the integumentary operculum, with internal branchiæ; *N*, nasal pit; *S*, sucker; *K*, branchiæ; *A*, eye; *H_z*, horny teeth.

sexual animal. The development of larvæ, however, is by no means direct and uniform, but is complicated by the necessity for special contrivances to enable them to procure food and to protect themselves; sometimes taking place in an entirely different medium, under different conditions of life. This kind of post-embryonic development is known as metamorphosis.

Well-known examples of metamorphosis are afforded by the developmental histories of the Insecta and Amphibia. From the eggs of Frogs and Toads proceed larvæ provided with tails, but without limbs, the so-called Tadpoles (fig 111). These, with their laterally compressed tails and their gills, remind one of fishes, and they possess organs of attachment in the form of two small cervical suckers by which they can anchor themselves to plants. The mouth is provided with horny plates; the spirally coiled intestine is surprisingly long; the heart is simple; and the vascular arches have the piscine relations. Later, as development proceeds, the external branchiæ abort, and are replaced by new branchiæ covered by folds of the integument, the caudal fin is enlarged, and the fore and hind limbs sprout out; the fore limbs remain for some time covered by the integument, and only subsequently break through it to appear on the surface. Meanwhile the lungs have developed as appendages of the anterior part of the alimentary canal, and supplant the gills as respiratory organs, a double circulation is developed, and the horny beak is cast off. Finally the tail gradually shrinks and atrophies; on the completion of which the metamorphosis of the aquatic tadpole into the frog or toad suited for life on land is accomplished (fig. 112).

We have then to consider two kinds of development, viz., development with a metamorphosis and direct development, which in extreme cases are distinctly opposed to each other, but are connected by intermediate methods. The size of the egg, or, in other words, the amount of food yolk available for the use of the embryo in proportion to the size of the adult animal appears to be a factor of primary importance in any explanation of these two distinct processes (R. Leuckart). Animals with a direct development require—generally in proportion to the height of their organization and the size of their bodies—that their eggs should be provided with a rich endowment of food yolk, or that the developing embryo should possess a special accessory source of nutriment; they arise therefore either from relatively large eggs (Birds), or they are developed inside, and in close connection with the maternal body, by which arrangement they have a continual supply of food material (Mammals). Animals,

on the contrary, which pass through a metamorphosis always arise from eggs of relatively small size, are hatched in an immature condition as larvæ, and obtain independently, by their own activity, the materials which have been withheld from them while in the egg, but which are necessary for their full development. The number of embryos produced in the case of a direct development is, in proportion to the total weight of the material applied by the mother for reproductive purposes, far smaller than in the case of a development with metamorphosis. The fertility of animals whose young

FIG. 112.—Later stages in the development of *Pelobates fuscus*. *a*, larva without limbs with well developed tail; *b*, older larva with hind limbs; *c*, larva with two pairs of limbs; *d*, young frog with caudal stump; *e*, young frog after complete atrophy of tail.

undergo a metamorphosis, or, in other words, the number of offspring produced from a given mass of formative material, is increased to an extraordinary degree, and has, in the complicated relations of organic life, a great physiological significance, though systematically it is of little importance.

Some time ago it was attempted to explain these indirect metamorphoses, in which both processes of reduction and new development take place, as the result of the necessity which the simply organized

larva, hatched at an early stage of development, laboured under of acquiring special arrangements for its protection and nourishment (R. Leuckart). The proof that such relations do exist between the special larval organs and the peculiar methods of nutrition and protection is an important factor for the full understanding of these remarkable processes, but still is by no means an explanation of them. It is only by aid of the Darwinian principles and the theory of descent that we can get nearer to an explanation. According to this theory, the form and structure of larvæ are to be considered in relation to the development of the race, *i.e.* phylogeny, and are to be derived from the various phases of structure through which the latter has passed in its evolution, and in such a way that the younger larval stages would correspond to the primitive, and the older, on the other hand, to the more advanced and more highly organized animals, which have appeared later in the history of the race. In this sense the developmental processes of the individual constitute a more or less complete recapitulation of the developmental history of the species, complicated, however, by secondary variations due to adaptation, which have been acquired in the struggle for existence* (Fritz Müller's fundamental principle, called by Haeckel the fundamental law of biogenesis).

The greater the number of stages, therefore, through which the larva passes, the more completely is the ancestral history of the species preserved in the developmental history of the individual; and it is the more truly preserved the fewer the peculiarities of the larva, whether independently acquired, or shifted back from the later to the earlier periods of life (Copepoda.) On the other hand, there are certain larval forms without any phylogenetic meaning which are to be explained as having been secondarily acquired by adaptation (many Insect larvæ).

The historical record preserved in the developmental history becomes, however, gradually defaced by simplification and shortening of the free development; for the successive phases of development are gradually more and more shifted back in the life of the embryo, and run their course more rapidly and in an abbreviated form, under the protection of the egg membranes, and at the cost of a rich supply of nutrient material (yolk, albumen, placenta). In animals with a direct development, therefore, the complicated development within the egg membranes is a compressed and simplified

* Fritz Müller, "Für Darwin." Leipzig. 1863, p. 75—81.

metamorphosis, and hence the direct development, as opposed to the metamorphosis, is a secondary form of development.

ALTERNATION OF GENERATIONS, POLYMORPHISM AND HETEROGAMY.

Both in direct development and indirect development by means of a metamorphosis, the successive stages take place in the life-history of the same individual. There are, however, instances of free development, in which the individual only passes through a part of the developmental changes, while the offspring produced by it accomplishes the remaining part. In this case the life-history of the species is represented by two or more generations of individuals, which possess different forms and organization, exist under different conditions of life, and reproduce in different ways.

Such a manner of development is known as alternation of generations (metagenesis), and consists of the regular alternation of a sexually differentiated generation with one or more generations reproducing asexually. This phenomenon was first discovered by the poet Chamisso* in the Salpidæ; but the observation remained for more than twenty years unnoticed. It was rediscovered by J. Steenstrup,† and discussed in the reproduction of a series of animals (Medusæ, Trematoda) as a law of development. The essence of the process consists in this, that the sexual animals produce offspring, which through their whole life remain different from their parents, but can give rise by an asexual process of reproduction to a generation of animals which resemble in their organization and habits of life the sexual form, or again produce themselves asexually, their offspring assuming the characters of the original sexual animal. So that in the last case the life of the species is composed of three different generations proceeding from one another, viz., sexual form, first asexual form, and second asexual form. The development of the two, three, or more generations may be direct, or may take place by a more or less complicated metamorphosis; similarly the asexual and the sexual generations sometimes differ but little from each other (*e.g.* Salpa), and sometimes present relations analogous to those which exist between a larva and the adult animal (*e.g.*

* Adalbert de Chamisso, "De animalibus quibusdam e classe vermium Linnæana in circumnavigatione terræ auspicante comite N. Romanzoff duce Ottone de Kotzebue annis 1815, 1816, 1817, 1818 peracta." Fasc. I. De salpa Berolini 1819.

† Joh. Jap. Sm. Steenstrup, "Ueber den Generationswechsel, etc," übersetzt von C. H. Lorenzen. Kopenhagen, 1842.

Medusæ). Accordingly we have to distinguish different forms of alternations of generations, which have genetically a different origin and explanation.

The latter form of alternations of generations resembles metamorphosis; and we have in most cases to explain it as having arisen in the following way:—The asexual form corresponds to a lower stage in the phylogenetic history, from which it has inherited the capacity of asexual reproduction, while the sexual reproduction belongs entirely to the higher form. To take as an example the alternation of generations of the Scyphomedusæ. The animal is hatched as a free-swimming ciliated planula (gastrula with closed blastopore) (fig. 113 *a*). After a certain time it fixes itself by the pole of its body,

FIG. 113.—Development of the planula of *Chrysaora* to the Scyphistoma stage, with eight arms. *a*, Two layered planula with a narrow gastric cavity; *b*, the same after its attachment with just-formed mouth (*O*), and commencing tentacles; *c*, four-armed Scyphistoma polyp; *Csk*, excreted cuticular skeleton; *d*, eight-armed Scyphistoma polyp with wide mouth; *M*, longitudinal muscles of the gastric ridges; *Csk*, excreted cuticular skeleton.

which is directed forward in swimming, and acquires at its free extremity a new mouth, round which 1, 2, 4, 8, and finally 16 long tentacles soon make their appearance; while the broad oral region projects as a contractile cone (fig. 113 *b*, *c*, *d*). Inside the gastric cavity there project four gastric ridges with longitudinal muscular bands extending from the foot or point of attachment to the base of the oral cone. When the polyp, which has now become a Scyphistoma, has under favourable conditions of nutrition reached a certain size (about 2 to 4 mm.), ring-like constrictions are formed at the

anterior part of the body, giving rise to a series of segment-like divisions. The anterior part of the body bearing the tentacles is first marked off; and following this a greater or less number of sections, the new segments appearing continuously in the direction from before backward. The hindmost or basal swollen club-shaped end of the polyp's body remains undivided. The Scyphistoma has

FIG. 113. —e, Stage of Scyphistoma with sixteen arms (slightly magnified); Gw. gastric ridges. f, Commencing strobilization.

now become the *Strobila*, which itself passes through various developmental phases. The tentacles abort; the successive segments, separated from each other by constrictions and provided with lobe-like continuations and marginal bodies, become transformed into small flat discs, which become separate, and, as *Ephyrae*, represent the larvæ of the Scyphomedusæ (fig. 113 b-h).

In the other cases in which the sexual and asexual forms morphologically resemble each other, as in *Salpa*, the origin of the alternation of generations may, as in the case of the origin of the dioecious from the hermaphrodite state, be traced back to the tendency towards the establishment of a division of labour acting upon an animal which possessed the capacity of sexual and asexual reproduction. It was advantageous for the formation of the regular chain of buds (*stolo prolifer*) that the power of sexual reproduction should

be suppressed, and that the generative organs should become rudimentary and finally vanish in the budding individuals; while, on the other hand, in the individuals united in the chain, the generative organs were early developed, and the *stolo prolifer* was aborted and completely vanished.

Special forms of alternation of generations may be distinguished in which colonies are formed as the result of the asexual reproduction by budding from a single animal, the buds remaining attached and developing into individuals which differ considerably in structure and appearance, and each of which performs special functions in maintaining the colony (nutritive, protective, sexual, etc.) Such a form of alternation of generations is

FIG. 113.—*g*, Fully developed Strobila with separating Ephyrae. *h*, Free Ephyra (of about 1.5 to 2 mm. diameter).

known as *polymorphism*,* and reaches a great complication in the polymorphous colonies of the Siphonophora.

A form of reproduction which closely resembles metagenesis, but which genetically has quite a different explanation, is the lately

* R. Leuckart, "Ueber den Polymorphismus der Individuen oder die Erscheinung der Arbeitstheilung in der Natur." Giessen, 1851.

discovered process known as *heterogamy*. It is characterised by the succession of differently organized *sexual* generations living under different nutritive conditions.

Heterogamy, which was first discovered in certain small Nematodes (*Rhabdonema nigrovenosum* and *Leptodera appendiculata*), can scarcely be explained otherwise than as an adaptation to changed conditions. For when the embryo is developed as a parasite in conditions favourable for the acquisition of nutriment, it gives rise to a sexual form so different in size and structure from that which arises if the

FIG. 114.—A, *Rhabdonema nigrovenosum* of about 3.5 mm. in length at the stage when the male organs are ripe. *G*, genital gland; *O*, mouth; *D*, alimentary canal; *A*, anus; *N*, nerve ring; *Drz*, gland cells; *Z*, isolated spermatozoa. B, Male and female *Rhabditis*, length from about 1.5 to 2 mm.; *Or*, ovary; *T*, testis; *V*, female genital opening; *Sp*, spicula.

embryo leads a free existence in damp earth or dirty water (*i.e.*, in conditions not so favourable for the acquisition of nutriment), that we should, from the difference in their structure, place the two forms in different genera. *Rhabdonema nigrovenosum* from the lungs of Batrachians and the free-living *Rhabditis* follow each other in a strictly alternating manner (fig. 114, A, B). Other cases of heterogamy are afforded by the Bark-lice (*Chermes*), and the Root-lice

(Phylloxera), in that one or more (winged and apterous) female generations are characterised by parthenogenetic reproduction, and consist only of oviparous females; while the generation of females, which lay fertilised eggs, appears with the males only at certain times of the year, and can be distinguished by their small size, and by the reduction of their mouth parts and digestive apparatus.

Such forms of heterogamy lead back apparently to alternations of generations, especially when the parthenogenetic generations present, in the structure of their generative apparatus, essential differences from the females which copulate.

The *plant-lice* and *gall-flies* afford instances of this. The reproductive processes of these animals, on the authority of Steenstrup and V. Siebold, were regarded for a long time as instances of alternations of generations, until the view, which was supported by the reproductive processes of the allied bark-lice, that they came under the head of heterogamy, received general assent. According to this view, the viviparous forms of the plant-lice (Aphides) are merely modified females adapted for parthenogenetic reproduction, and their reproductive gland is nothing more than the modified ovary. There are also cases of heterogamy in which, in the parthenogenetic generations, the development of the egg commences in the ovary of the larva, reproduction being shifted back into larval life. This form of heterogamy, which resembles alternations of generations, was shown to occur in the larva of *Cecidomyia* (Miastor) by Nic. Wagner and by O. Grimm in the larva of a species of *Chironomus*, and is to be looked upon as a case of precocious development of the egg in the parthenogenetic generation. The morphologically undeveloped larva has acquired the power of reproducing itself by means of its rudimentary ovary, a phenomenon which, following the proposal of C. E. v. Baer, has been designated *Pædogenesis*.

If the reproductive gland of the *Cecidomyia* larva be looked upon as a germ-gland, and the cells contained in it as germ cells or spores, the reproduction of the *Cecidomyia* falls into the category of alternations of generations. But the idea involved in the term "spore" is borrowed from the vegetable kingdom, and there is no reason for looking upon these or any other structures in the Metazoa as spores. The above explanation, therefore, is untenable. The reproductive cells in the Metazoa, which have been regarded in this light, have much more probably originated from masses of cells which represent the rudiment of the ovary, and which are usually visible in early stages of development.

Further it cannot be doubted that the development of the Distomeæ, which has hitherto been regarded as a case of alternation of generations really represents a form of heterogamy allied to pædogenesis. After the completion of the segmentation and embryonic development, the ciliated embryos (fig 115, *a*, *b*) pass from the egg into the water, where they swim about, and eventually make their way into the body of a Snail, in which they give rise to sac-like or branched Sporocysts (fig 115, *c*) or to Rediæ provided with an alimentary canal (fig. 115, *d*).

These stages in the development of Distomum which are apparently

FIG. 115.—Developmental history of Distomum (in part after R. Leuckart). *a*, Free-swimming ciliated embryo of the liver fluke.—*b*, the same contracted, with rudiment of alimentary canal *D*; and aggregations of cells; *Ov*, rudiment of genital gland; *Ex*, ciliated apparatus of the excretory system.—*c*, Sporocyst, which has proceeded from Distomum embryo, filled with Cercariæ *C*; *B*, spine of a Cercaria.—*d*, Redia with pharynx *Ph*; alimentary canal, *D*; *Ex*, excretory organs; *C*, contained Cercariæ.—*e*, free Cercaria; *S*, sucker; *D*, gut.

comparable to larvæ, produce by means of the so-called germ granules or spores a generation of offspring known as Cercariæ (fig. 115, *e*), which become free, and then make their way into the body of a new host, and, after the loss of the oral spine and caudal appendage, encyst (fig 115 *f*). Hence they are carried into the body of the permanent host to develop into the sexual adult form.

It is, however, extremely probable that the masses of cells from which the Cercariæ arise represent the rudiments of ovaries, the elements of which develop parthenogenetically without the addition of spermatozoa. The so-called germ sacs (Sporocysts or Rediæ) would in this case be larvæ, which possess the power of reproduction; and the development of the Distomæ would come under the head of heterogamy. The Cercariæ, however, represent a second and more advanced larval phase. Provided with a motile tail, frequently with eyes and buccal spine, their organization, save in the absence of developed generative organs, presents great similarities to the sexually mature adults into which they develop.

This development, however, takes place only in the body of another and usually more highly organized host after the loss of the larval organs.

If the conception of a spore as an asexual reproductive product be maintained, it becomes impossible in practice to draw a sharp line between alternation of generations and heterogamy; since there is no test which enables us to distinguish between a spore and an ovum which develops parthenogenetically. On the other hand, if we interpret, as we are justified in doing, the so-called spores as precociously developed ova, alternation of generations and heterogamy can be clearly distinguished from one another, since in the former one generation is asexual, and increases entirely by budding and division; while in the latter both generations are sexual, though in one of them the ova may possess the power

FIG. 115. *f*.—Young Distomum (after La Valette). *Ex*, main trunk of excretory system; *Ep*, excretory pore; *O*, mouth opening with sucker; *S*, sucker on middle of ventral surface; *P*, pharynx; *D*, limb of alimentary canal.

of spontaneous development.

An essential characteristic both of heterogamy and alternation of generations depends upon the different form of the individuals appearing in the generations which usually occur in a regularly alternating manner in the life-history of the species. But there are cases in which two methods of reproduction may follow each other in the life-history of one individual. This form of the

reproductive process is of the greatest interest as throwing light upon the way in which the phenomena of alternation of generations and heterogamy may have arisen in that it appears in a certain degree as the precursor of the alternating sequence of two or more generations of individuals. The so-called alternation of generations in the stone-corals (*Blastotrochus*), which in early life reproduce themselves by budding, without thereby losing the power of acquiring sexual organs at a later period of life, forms an example of this method of reproduction.

In this category of incomplete heterogamy should be placed the reproductive processes of the Phyllopoda and Rotifera, in which the female produces summer eggs capable of parthenogenetic development, and later winter eggs requiring fertilization (*Daphnidae*).

[In the above account the term alternation of generations, or metagenesis is applied to those cases in which sexual and asexual generations alternate; while heterogamy is applied to those cases in which two sexual generations or a sexual and parthenogenetic generation alternate.]

CHAPTER IV.

HISTORICAL REVIEW.*

THE origin of Zoology extends far back into antiquity. Aristotle (4th century B.C.), who scientifically and in a philosophic spirit worked up the experiences of his predecessors with his own extended observations, must be looked upon as the founder of this science. The most important of his zoological works† treat of the "Reproduction of Animals," of the "Parts of Animals," and of the "History of Animals." The last and most important work is, unfortunately, only incompletely preserved.

We must not expect to find in Aristotle a descriptive zoologist, nor in his works a system of animals followed out into the smallest

* Victor Carus, "Geschichte der Zoologie." München, 1872.

† Compare Jürgen Bona Meyer's "Aristoteles' Thierkunde" (Berlin, 1855).—Frantzius, "Aristoteles' Theile der Thiere" (Leipzig. 1853).—Aubert und Wimmer, "Aristoteles' Fünf Bücher von der Zeugung und Entwicklung der Thiere, übersetzt und erläutert" (Leipzig. 1860).—Aubert und Wimmer, "Aristoteles' Thierkunde." Band I. und II. (Leipzig, 1868).

details; a one-sided treatment of science was not the object of this great thinker.

Aristotle contemplated animals as living organisms in all their relations to the external world, according to their development, structure, and vital phenomena, and he created a comparative Zoology, which in several respects constitutes the basis of our science. The distinction of animals into *animals with blood* (ἔναιμα) and *animals without blood* (ἄναιμα), which he in no wise used as a strictly systematic conception, certainly depends, according to the meaning of the word, upon an error, since all animals possess blood; and the red colour can by no means be taken, as Aristotle believed, to be a test of the presence of blood; but as the possession of a bony vertebral column was put forward as a character of the animals provided with blood, the two groups established by this distinction coincided in their limits with the two great divisions of Vertebrates and Invertebrates.

The eight animal groups of Aristotle are the following:—

Animals with blood, Vertebrates—

(1) Viviparous animals (four-footed, ζωοτοκοῦντα ἐν αἰτοῖς), with which as a special γένος was placed the whale.

(2) Birds (ὄρνιθες).

(3) Oviparous four-footed animals (τετράποδα ἢ ἄποδα ὠοτοκοῦντα).

(4) Fishes (ἰχθύες).

Animals without blood, Invertebrates—

(5) Soft animals (μαλάκια, Cephalopoda).

(6) Soft animals with shells (μαλακόστρακα).

(7) Insects (ἔντομα).

(8) Shelled animals (ὀστρακοδέρματα, Echini, Snails, and Mussels).

After Aristotle, antiquity only possesses one zoological writer of note—Pliny the elder—to point to. He lived in the first century, and, as is well-known, was killed in the great Eruption of Vesuvius (79), while captain of the fleet. The natural history of Pliny deals with the whole of nature, from the stars to animals, plants, and minerals; it is, however, of no scientific value as an original work, but is merely a compilation of facts collected from known sources, and is not by any means implicitly to be trusted. Pliny borrowed to a large extent from Aristotle, often understood him falsely, and also accepted here and there as facts fables, which had been rejected by Aristotle. Without setting up a system of his own, he divided animals according to the medium in which they lived—into Land-animals (Terrestria), Aquatic-animals (Aquatica), and Flying-

animals (Volatilia),—a division which was accepted till Gessner's time.

With the decline of the sciences, natural history also fell into oblivion. The mind of man, fettered by the belief in authority, felt in the middle ages no need for an independent contemplation of Nature. But the writings of Aristotle and Pliny found an asylum within the walls of the Christian cloisters, which preserved the germs of science developed in Heathendom from complete extinction.

In the course of the middle ages, first the Spanish bishop, Isidor of Seville (in the seventh century), and later Albertus Magnus (in the thirteenth century) wrote works on natural history; but it was not until the renaissance of the sciences of the sixteenth century that the works of Aristotle again came to the fore, and the desire for independent observation and research was also roused. Works like those of C. Gessner, Aldrovandus, Wotton, testified to the newly awakening life of our science, whose scope was continually being increased by the discovery of new worlds.

The next century, in which Harvey discovered the circulation of the blood, Kepler the revolution of the planets, and Newton's law of gravitation formed the beginning of a new era in physics, was also a fruitful epoch for Zoology. Aurelio Severino wrote his "Zootomia democritæa" (1645), a work which contained anatomical drawings of various animals, more for the use and advancement of human anatomy and physiology. Swammerdam in Leyden dissected the bodies of Insects and Molluscs, and described the metamorphosis of the Frog. Malpighi in Bologna and Leeuwenhoek in Delft applied the invention of the microscope to the examination of tissues and the smallest organisms (animals from infusions). The latter discovered the blood corpuscles, and first saw the transverse striations of muscular fibres. The spermatazoa also were discovered by a student, Hamm, and called, on account of their movements, sperm-animals. The Italian Redi opposed the spontaneous generation of animals in putrefying matter, proved the origin of Maggots from Flies' eggs, and supported Harvey's famous expression, "omne vivum ex ovo." In the eighteenth century the knowledge of the life-history of animals was enormously enriched. Investigators such as Réaumur, Rösel von Rosenhöf, De Geer, Bonnet, J. Chr. Schaeffer, Ledermüller, etc., discovered the metamorphosis and life-history of Insects and native aquatic animals, while at the same time, by expeditions into foreign lands, a great number of animals from other

continents became known. In consequence of these extended observations and a continually growing eagerness to collect curiosities from foreign countries, the zoological material increased so largely that, in the absence of precise distinctions, nomenclature and arrangement, the danger of error was great, and a general review of the facts almost impossible. Under such conditions, the appearance of the systematiser Carl Linnæus (1707—1778) must have been of the greatest importance for the further development of Zoology.

Ray, who is justly placed in the first rank of Linnæus' predecessors, had earlier endeavoured to acquire a basis for the systematic treatment, and with a certain amount of success, but he failed to organise a thoroughly methodical arrangement. He was the first to introduce the conception of "species" and to consider anatomical characters as the basis of classification. In his work, entitled "Synopsis of Mammalia and Reptilia" (1693), he adopted Aristotle's division of the animal kingdom into animals with and animals without blood. With regard to the first he laid the basis of the definitions of Linnæus' first four classes; the latter he divided into a greater group, containing Cephalopods, Crustacea, and Testacea, and into a smaller containing the Insecta.

The importance of Linnæus' work to the development of science depended not on any far-reaching investigations or important discoveries, but on his acute sifting and exact division of the then existing facts, and on the introduction of a new method of more certain diagnosis, nomenclature, and arrangement.

By erecting for groups of different value a series of categories based on the ideas of species, genus, order, class, he obtained a means of creating a much more precise system of classification. On the other hand, by the introduction of the principle of binary nomenclature, he obtained a fixed and more certain method. Every animal received two names taken from the Latin language—the generic name, which was placed first, and the specific name, which together denote the fact that the animal in question belongs to a definite genus and species. In this way Linnæus not only arranged the facts then known, but also created a systematic framework in which later discoveries would easily find their proper place.

Linnæus's great work, the "*Systema Naturæ*," which in its thirteen editions received many changes, embraced the animal, vegetable, and mineral kingdoms, and in its treatment can only be compared to an exhaustive catalogue, in which the contents of nature, like that of a library, are registered in a definite order with a statement of

their most remarkable characters. Every species of animal and plant obtained a place determined by its properties, and was with the specific name inserted under the genus. After the name followed a short Latin diagnosis, and a list of the synonyms of authors and statements concerning the habits of life, habitat, the native country, and any special characteristics.

Linnaeus created for botany an artificial system of classification founded on the characters of flowers. Similarly his classification of animals was artificial, as it did not depend upon the distinction of natural groups, but took isolated features of internal and external structure as characters. Linnaeus completed the improvements in Aristotle's classification which had been already begun by Ray, by establishing the following six classes, founded on the structure of the heart, the condition of the blood, the manner of reproduction and respiration.

(1) *Mammalia*.—With red warm blood, and a heart composed of two auricles and two ventricles, viviparous. The following orders were distinguished—Primates (with the four genera Homo, Simia, Lemur, Vespertilio), Bruta, Feræ, Glires, Pecora, Belluæ, Cete.

(2) *Aves*.—With warm red blood, and a heart composed of two auricles and two ventricles, oviparous—Accipitres, Picæ, Anseres, Grallæ, Gallinæ, Passeres.

(3) *Amphibia*.—With cold red blood and a heart composed of simple auricle and ventricle, breathing by lungs—Reptilia (Testudo, Draco, Lacerta, Rana), Serpentes.

(4) *Pisces*.—With cold red blood, and a heart composed of simple auricle and ventricle, breathing by gills—Apodes, Jugulares, Thoracici, Abdominales, Branchiostegi, Chondropterygii.

(5) *Insecta*.—With white blood, simple heart, and segmented antennæ—Coleoptera, Hemiptera, Lepidoptera, Neuroptera, Hymenoptera, Diptera, Aptera.

(6) *Vermes*.—With white blood, simple heart, and unsegmented antennæ—Mollusca, Intestina, Testacea, Zoophyta, Infusoria.

While the followers of Linnaeus developed still further this barren and one-sided zoographical treatment and erroneously looked upon the framework of this system as an exact and complete expression of the whole of nature, Cuvier, by combining Comparative Anatomy with Zoology, laid the foundations of a natural system.

George Cuvier, born at Mömpelgard 1762, and educated at the Karlsakademie at Stuttgart, later Professor of Comparative Anatomy at the Jardin des Plantes in Paris, published his comprehensive in-

vestigations in numerous works, especially in his "Leçons d'Anatomie comparée" (1805).

In his celebrated treatise * published in 1812, on the arrangement of animals according to their organization, he established a new and essentially changed classification, which was the first serious attempt to build up a natural system. Cuvier did not, as most zootomists had done, look upon anatomical discoveries and facts as in themselves the aim of his researches, but he contemplated them from a comparative point of view, which led him to the establishment of general principles. By considering the peculiarities in the arrangements of the organs in relation with the life and unity of the organism, he recognised the reciprocal dependence of the individual organs, and appreciating fully the idea of the "correlation" of parts already discussed by Aristotle, he developed his principle of the conditions of existence without which an animal cannot live (*principe des conditions d'existence ou causes finales*). "The organism consists of a single and complete whole, in which single parts cannot be changed without causing changes in all the other parts." By comparing the organizations of many different animals, he found that the important organs are the most constant, and that the less important vary most in their form and development, and even are not universally present.

He was thus led to the principle so important for the systematist of the subordination of characters (*principe de la subordination des caractères*). Without being ruled by the pre-conceived idea of the unity of all animal organization, he became convinced, from a consideration of the differences in the nervous system and in the arrangement of the more important systems of organs, that there were in the animal kingdom four main types (*embranchements*), "general plans of structure on which the respective animals appear to be modelled, and whose individual subdivisions, as they may be called, are only slight modifications based on the development or the addition of some parts, without the plan of the organization being thereby essentially changed."

These four groups (*embranchements* Cuvier, *Typen* Blainville) were the Vertebrata, Mollusca, Articulata, and Radiata.

The views of Cuvier, who in knowledge of anatomical and zoological detail stood far above all his contemporaries, were, however, in opposition to the theories of men of note (the so-called School of

* "Sur un nouveau rapprochement à établir entre les classes qui composent le règne animal." *Ann. des Muséum d'Hist. Nat.*, Tom XIX., 1812.

Natural Philosophy). In France, Étienne Geoffroy St. Hilaire pre-eminently defended the idea, which had been already expressed by Buffon, of the unity of the plan of animal structure, according to which the animal kingdom consisted of an unbroken gradation of animals. Convinced that nature always worked with the same materials, he put forward his theory of analogies, according to which the same parts, though differing in their form and the degree of their development, should be found in all animals; and, further, his theory of connections (*principe des connexions*), according to which the same parts always appear in the same mutual position. A third fundamental principle was that of the equivalence of organs, an increase in the size of one organ being accompanied by the diminution of another organ. The application of this principle had important results, and led to the scientific foundation of Teratology. His generalizations were, however, in the main hasty, in that they were founded on facts taken only from the Vertebrates; and if applied outside that group must lead to many rash conclusions, *e.g.*, that Insects are Vertebrates turned on to their backs.

In Germany, Goethe and the natural philosophers Oken and Schelling pronounced in favour of the unity of animal organization, but it must be confessed without taking account in a comprehensive manner of the actual facts.

The result of this controversy which in France was carried on with considerable vehemence was, that Cuvier's view was victorious, and his principles met with the more undivided assent since it appeared that they were confirmed by C. E. v. Baer's embryological work. Many gaps and errors were certainly discovered by later investigators in Cuvier's classification, and in detail it was much changed, but the establishment of his animal types as the chief groups of the system was retained, and was supported by the results of the developing Science of Embryology.

The most essential of the modifications which it has become necessary to make in Cuvier's system relate chiefly to the increase in the number of types. The Infusoria were some time ago removed from the Radiata, and as Protozoa arranged by the side of the four other groups. Lately the number of groups has been increased by the division of the Radiata into Cœlenterata and Echinodermata, and of the Articulata into Arthropoda and Vermes, and of the Mollusca into three groups.

In our times, however, Cuvier's view has experienced an essential modification in favour of the Natural Philosophers, and the idea of

the absolute independence and isolation of each group must be given up. With a more complete study it has been shown that intermediate forms exist connecting the various types, and that consequently no sharp line of demarcation can be drawn between them. But just as the transitional forms between animals and plants cannot abolish the distinction between these two most important conceptions of the organic kingdom, so the existence of such transitional forms does not in any way affect the value of the idea of groups and types as the chief divisions of the animal system, but only renders it probable that the different groups have developed from a similar or common starting-point.

And to this corresponds the fact, which has become recognised with the progress of embryological knowledge, that similar larval stages and tissue-layers (germinal layers) are found in the developmental history of the different types. This fact points to a genetic connection.

Likewise the results of anatomical and embryological comparison have rendered it probable that the types are by no means absolutely independent, but are subordinated to one another in more or less close relation, that especially the higher groups are genetically to be derived from the Worms, a group which certainly includes extremely dissimilar forms, and eventually will, without doubt, be broken up into several types. We consider it, under such circumstances, convenient, in the present state of science, to distinguish nine types as the chief divisions, and to characterise them in the following manner:—

- (1) *Protozoa*.—Of small size, with differentiations within the sarcode, without cellular organs, with predominating asexual reproduction.
- (2) *Cœlenterata*.—Radiate animals segmented in terms of 2, 4, or 6; mesoderm of connective tissue, often gelatinous; and a central body cavity common to digestion and circulation (gastro-vascular space).
- (3) *Echinodermata*.—Radiating animals, for the most part of pentamerous arrangement; with calcareous dermal skeleton, often bearing spines; with separate alimentary and vascular systems; and with nervous system and ambulacral feet.
- (4) *Vermes*.—Bilateral animals with unsegmented or uniformly (homonomous) segmented body, without jointed appendages (limbs), with paired excretory canals sometimes called water-vascular system.
- (5) *Arthropoda*.—Bilateral animals with heteronomously segmented

bodies and jointed appendages, with brain and ventral chain of ganglia.

(6) *Molluscoidea*.—Bilateral, unsegmented animals with ciliated circle of tentacles or spirally rolled buccal arms; either polyp-like and provided with a hard shell case, or mussel-like with a bivalve shell, the valves being anterior and posterior; with one or more ganglia connected together by a pericæsoophageal ring.

(7) *Mollusca*. Bilateral animals with soft, unsegmented body, without a skeleton serving for purposes of locomotion; usually enclosed in a single or bivalve shell, which is excreted by a fold of the skin (mantle); with brain, pedal-ganglion and mantle-ganglion.

(8) *Tunicata*.—Bilateral unsegmented animals with sac-shaped or barrel-shaped bodies, and a large mantle cavity perforated by two openings; simple nervous ganglion, heart and gills.

(9) *Vertebrata*.—Bilateral animals with an internal cartilaginous or osseous segmented skeleton (vertebral column), which gives off dorsal processes (the neural arches) to surround a cavity for the reception of the spinal cord and brain; and ventral processes (the ribs) which bound a cavity for the reception of the vegetative organs; never with more than two pairs of limbs.

CHAPTER V.

MEANING OF THE SYSTEM.

VERY different opinions have been held in different places and at different times as to the value of the system. In the last century the French Zoologist Buffon held the system to be a pure invention of the human mind; while more recently L. Agassiz thought that a real meaning could be attributed to all the divisions of the system. He explained the natural system founded on relationship of organization as a translation of the thoughts of the Creator into human language, by the investigation of which we become unconsciously interpreters of his ideas.

But it is clear that we cannot call that arrangement, which is derived from the relations of organization founded in nature, an invention of man. Similarly it is preposterous to deny the subjective participation of our intellectual activity, since in every system there is expressed a relation of the facts of nature to our comprehen-

sion and to the state of scientific knowledge. In this sense Goethe appropriately calls a natural system a contradictory expression.

In establishing systems, that which comes into contemplation consists of the individual forms which are the objects of observation. Every systematic conception, from that of the species to that of the type, depends upon the bringing together of similiar properties, and is an abstraction of the human mind.

Species.—The great majority of investigators, till very recently, were agreed in looking upon the *species* as an independently created unit with special properties which were retained in propagation, and were really contented with the fundamental idea in Linnæus' definition of species: *Tot numeramus species quot ab initio creavit infinitum ens.*" This view also accorded with a dogma prevalent in Geology, according to which the flora and fauna of the successive periods of the earth's history were completely isolated, being created afresh at the beginning and destroyed by a vast catastrophe at the end of each period. It was supposed that no living thing could be preserved through one of these catastrophes from one period into the next; that every species of animal and plant was specially created with definite characters, which it retained unchanged until it was destroyed. This idea was confirmed by the difference between the fossil remains of Vertebrates (Cuvier) and Molluscs (Lamarck), and the living forms of these types.

As a matter of fact, however, neither in the animal nor in the vegetable kingdom do offspring resemble exactly the parent forms from which they have originated, but present differences more or less considerable, so that the idea of absolute identity must be removed from our definition of species, and agreement in the most essential particulars introduced in its place. The species would accordingly, in close agreement with Cuvier's definition, include all living forms which *have the most essential properties in common, are descended from one another, and produce fruitful descendants.*

All the facts of natural life, however, can by no means be arranged agreeably to this conception, which has for a fundamental principle that all essential peculiarities must be preserved unaltered by reproduction through all time. The great difficulties in defining species which occur in practice, and which prevent a sharp line being drawn between species and variety, indicate the insufficiency of the conception.

Varieties.—Individuals belonging to the same species do not resemble each other in all particulars, but present differences which,

on closer investigation, suffice to distinguish the individual forms. Combinations of modified characters are often present in the same species, and occasion important variations (varieties) which can be inherited by the descendants. The more important of such variations which are maintained by reproduction are called *constant varieties* or *subspecies*, or *races*, and are divided into *natural races* and *artificial or domesticated races*.

The former are found in free natural life, and are usually confined to definite localities. They have arisen in course of time in consequence of conditions of climate, and under the influence of variations in manner of life and nourishment. The domesticated races, on the other hand, owe their origin to the care and cultivation of man. They comprise only domestic animals whose origin is still unknown.

Varieties, however, which have arisen from one species may differ very surprisingly from one another; in fact, they may present more important features of difference than do distinct natural species. An example of this is found in the domesticated race of pigeons, whose common descent from *Columba livia* (the rock pigeon) was shown by Darwin to be very probable. They are capable of such striking alterations, that their varieties, known as tumbler pigeons, fantail pigeons, etc., were held by ornithologists, who were without knowledge of their origin, to be real species, and were even divided into different genera.

In the natural state, too, it often happens that varieties cannot be distinguished from species by the quality of their characteristics. It is customary to consider that *the essential* of a character is to be found in the constancy of its occurrence, and to recognise varieties by the fact that their characteristics are more variable than those of species. If forms which are widely different can be connected by a continuous series of intermediate forms, they are held to be varieties of the same species. But if such intermediate forms are absent, they are held to be distinct species, even when the differences between them (so long as they are constant) are less.

Under such circumstances we can understand that in the absence of a positive test, the individual judgment and the natural tact of the observer decides between species and variety;* and how it is that the opinions of different observers have differed so widely in

* The establishment of the conception of sub-species is completely at variance with the common conception of species, and is the most striking proof that systematists themselves recognize that the distinction between species and sub-species is a relative one.

practice. This relation has been excellently and thoroughly discussed by Darwin and Hooker. As an example of the difference of opinion on this subject, Nägeli * divided the *Hieraciæ* found in Germany into three hundred species, Fries into one hundred and six, Koch into fifty-two, while other authors recognise hardly more than twenty. Nägeli indeed says, "There is no genus of more than four species on which all botanists are agreed, and many examples may be cited in which, since Linnæus' time, the same species have been repeatedly divided up and re-united."

We are therefore driven, in order to determine the essential property distinguishing species and variety, to consider the most important characteristic for the conception of species,—a characteristic which has hardly ever been used in practice, *i.e.*, the community of descent and the capacity for fruitful interbreeding. This means of determination, however, is also insufficient.

It is a commonly known fact that animals which belong to different species pair with one another and produce hybrids, *e.g.*, horse and ass, wolf and dog, fox and dog. Widely differing species, which are placed in different genera, have even been known to cross with one another, and to produce progeny, such as the he-goat and sheep, and the she-goat and ibex. The hybrids however are, as a rule, sterile. They are intermediate forms with imperfect generative system, without the power of propagation; and even in those cases where there is a power of reproduction (such cases are most frequently met with amongst female hybrids), there is a tendency to revert to the paternal or maternal species.

There are, however, exceptions to the sterility of the hybrid which appear to afford weighty proof against immutability of species. The experiments in breeding between the hare and rabbit, made on a large scale in Angoulême by Roux, have shown that their progeny, the hare-rabbit, is perfectly fertile. Half-bred hybrids of the rabbit and hare have been bred, and have been reproductive through many generations of pure in-breeding. In like manner careful inquiries into the hybridism of plants, especially the investigations of W. Herbert, lead to the conclusion that many hybrids are as perfectly productive among themselves as genuine species.

In a state of nature, too, hybrids of various kinds are found. Such hybrids have frequently been taken for independent species, and have been described as such (*Tetrao medius*, hybrid of *Tetrao*

* C. Nägeli, "Entstehung und Begriff der naturhistorischen Art." München, 1865.

urogallus and *Tetrao tetrix*; *Abramidopsis Leuckarti*, *Bliccopsis abramorutilus*, and others are, according to von Siebold, hybrids.) Sterility of hybrids is not the rule here, for a great number of wild plants have been recognised as hybrid species (Kölreuter, Gärtner, Nägeli—*Cirsium*, *Cytisus*, *Rubus*). This seems to render it the less doubtful that amongst animals which have been domesticated by man, persistent transitional forms can be obtained from originally different species, by gradual alteration brought about by cross breeding.

Pallas, adopting this view, gave it as his opinion that closely allied species, though at first they may refuse to breed together, or may produce sterile offspring, will, after long domestication, produce fertile progeny. And in fact, it has been shown to be probable that some of our domestic animals have originated in prehistoric times as the result of the unintentional crossing of different species. Rüttimeyer especially endeavoured to prove this mode of origin for the domestic ox (*Bos taurus*), which he regarded as a new race resulting from the crossing of at least two ancestral forms (*Bos primigenius*, *brachyceros*). It may be looked upon as certain that the domestic pig and cat, and the numerous breeds of dogs, have originated from several wild species.

In connection with the exceptional cases which have just been discussed, we may lay great stress upon the perfect reproductive capabilities of mongrels, that is, of the progeny produced by the crossing of different varieties of the same species; though here also we meet with exceptions. Disregarding those cases in which mechanical causes render the interbreeding of different varieties impossible, it seems, according to the observations of breeders whose word may be depended upon, that certain varieties have difficulty in crossing with one another; and further that certain forms which have been bred by selection from a common stock are altogether incapable of fertile intercourse. The domestic cat introduced into Paraguay from Europe has, according to Rengger, become essentially altered in process of time, and has acquired a marked aversion to the European ancestral form. The European guinea pig does not breed with the Brazilian form, from which it is probably descended. The Porto-Santo rabbit, which was exported from Europe to *Porto-Santo* near Madeira in the fifteenth century, is so much altered that it can no longer breed with the European race of rabbits.

The evident difficulty of precisely defining the conception of species, in presence of the existence of a gradual, almost uninterrupted series

of animal forms, and of the results of artificial selection, had already, in the beginning of this century, induced illustrious and highly esteemed naturalists to dispute the dominant views on the immutability of species. In the year 1809, Lamark, in his "*Philosophie Zoologique*," broached the theory of the descent of species from one another. He referred the gradual alterations in some degree to changing conditions of life, but mainly to use and disuse of organs.

Geoffrey St. Hilaire, too, the advocate of the idea of unity of organization of all animals and the opponent of Cuvier, expressed his conviction that species had not existed unaltered from the beginning. While agreeing essentially with Lamark's theory of the origin and transmutation of species, he ascribed a less influence to the inherent activity of the organism, and believed that he could explain the alterations through the direct operation of changes in the environment (*monde ambiant*).

The change in the fundamental views of Geology which took place at a later period must be ascribed to the opinions of these investigators. Lyell endeavoured (*Principles of Geology*) to explain geological alterations by means of the forces in operation at the present day, working gradually and without interruption through extended periods of time, and rejected the Cuvierian theory of mighty revolutions and catastrophes which destroyed all life. When the geologists with Lyell had given up the hypothesis of periodic disturbance of the course of natural events, they were obliged to assume the continuity of organic life during the successive periods of the formation of the earth, and to endeavour to account for the immense alterations of the organic world by slight influences operating gradually and without interruption throughout long periods of time. The variability of species, the origin of new species from previous ancestral forms in the course of ages, has become, accordingly, since the time of Lyell, a necessary postulate of geology in order to explain naturally the differences of animals and plants in successive periods without the supposition of repeated acts of creation.

THE TRANSMUTATION THEORY, OR THEORY OF DESCENT, BASED ON
THE PRINCIPLE OF NATURAL SELECTION (DARWINISM).

Nevertheless a more securely grounded theory based upon a firmer standpoint was needed in order to give more force to the Transmutation hypothesis which had remained disregarded; and this

service was effected by the English naturalist, Charles Darwin, who employed a mass of scientific material to found a theory of the origin and mutation of species. This theory, which is closely connected with the views of Lamarck and Geoffroy and in harmony with Lyell's doctrines, has received an almost universal recognition, not only on account of the simplicity of its principle, but also because of the objective and convincing way in which his genius expounded it.

Darwin* starts from the principle of heredity, according to which the characteristics of parents are transmitted to their offspring. But side by side with this, there is an adaptation determined by the peculiar conditions of nourishment, a limited variability of form, without which individuals of like descent would be identical. While heredity tends to reproduce identical characteristics, individual variations appear in the descendants of the same species, and in this way modifications arise, which in their turn are submitted to the law of heredity. Cultivated plants and domestic animals, the individual forms of which vary far more than do those living in a state of nature, are especially disposed to alteration; and capability of domestication is in reality nothing else than the capability of an organism to subordinate and adapt itself to altered conditions of nourishment and way of life.

The so-called artificial breeding, by which man succeeds by judicious choice in cultivating in plants and animals definite properties corresponding to his requirements, depends on the interaction of heredity and individual variation; and it is probable that the numerous races of domestic animals were in this way bred *unconsciously* by man, just as in our own days large numbers of new varieties are bred by judicious choice of the male and female parents. Similar processes are also at work in natural life, calling into existence new alterations and varieties. Here also we find a selection which is occasioned by the struggle of organisms for existence, and may be called *a natural selection*. All plants and animals are engaged, as Decandolle and Lyell had asserted ten years previously, in a mutual struggle for existence among themselves and with external conditions.

A plant has to fight against circumstances of climate, season, and soil; and has also to compete for existence with other plants which, by their superabundant increase, endanger the possibility of its preservation. Plants serve as food for animals, which themselves are engaged in a mutual struggle with each other; the carnivorous

* Ch. Darwin, 'On the Origin of Species by means of Natural Selection,' London, 1859.

feeding very largely upon herbivorous animals. Then again, all are struggling to multiply in great numbers. Each organism produces far more descendants than can in general be preserved. With a definite degree of fertility, a corresponding amount of destruction must take place; for in the absence of the latter the number of individuals would so increase in geometrical progression that no locality would suffice for the sustenance of their progeny. If, on the contrary, the protection afforded by fertility, size, special organization, colour, etc., were removed, the species would soon vanish from the earth. Amongst the complex conditions and interactions of life, even the most remotely connected organisms struggle with each other for existence (*e.g.*, the clover and the mice); but the most violent strife is waged between individuals of the same species, which seek the same food and are exposed to the same dangers. In this strife it necessarily happens that those individuals which are placed in the most favourable situation, through their special properties, have the greatest chance of maintaining themselves and of multiplying, and, in consequence, of reproducing the modifications useful to the species and of preserving them in their descendants, or even sometimes of increasing them.

Just as in the breeding of domesticated animals, an artificial selection is made by man to perpetuate and increase advantageous variations; so in the natural breeding of wild animals, in consequence of the struggle for existence, a selection is made by nature which leads to the preservation of modifications useful to the species.

Since, however, the struggle for existence in closely related forms must be the more violent the more nearly they resemble one another, the most divergent types will have the greatest chance of enduring and of producing descendants. Hence a divergence of characters and an extinction of intermediate forms is the necessary consequence. Thus by the combination of useful properties and by the accumulation of hereditary peculiarities, which were primitively of little importance, varieties gradually arise which ever diverge more and more; and this is what Dārwin sought to prove by happily chosen examples. We can now comprehend why everything in the organism is directed towards one end, which is to ensure existence in the most perfect way. *The great series of phenomena which could hitherto only receive a teleological explanation are thus brought into causal relation, and can be explained as the inevitable result of efficient causes, and their natural connection is thus rendered intelligible.*

This principle of *natural selection*, which is the basis of the Darwinian theory, rests, on the one hand, on the interaction of adaptation and heredity, and on the other, on the *struggle for existence* which can be shown to occur everywhere in nature.

In its fundamental idea the natural selection theory is essentially an application of the doctrine of Malthus to plants and animals. Developed simultaneously by Darwin and Wallace,* it received from the former a most comprehensive scientific foundation.

We must certainly admit that Darwin's selection theory, although supported by what we know of biological processes and of the operation of the laws of nature, is very far from discovering the final causes and physical connection of the phenomena of adaptation and heredity, since it is unable to explain why such or such a variation should appear as the necessary consequence of a change in the vital conditions, and how it is that the manifold and wonderful phenomena of heredity are a function of organised matter.

It is clearly a great exaggeration when enthusiastic supporters of the Darwinian theory† say that it ranks as equal to the gravitation theory of Newton, because "it is founded upon a single law, a single effective cause, namely, upon the interaction of adaptation and heredity." They overlook the fact that we have here only to do with the proof of a mechanical and causal connection between series of biological phenomena, and not in the remotest degree with a physical explanation. Even if we are justified in connecting the phenomena of adaptation with the processes of nourishment, and in conceiving heredity as a physiological function of the organism, we still stand and regard these phenomena as "the savage who sees a ship for the first time." While the complicated phenomena of heredity‡ remain completely unintelligible, we are only in a position to explain in general terms certain modifications of organs, on physical grounds, by the altered conditions of metabolism. It is only rarely—as in the case of the operation of use and disuse—that we are able more directly to relate the development or the atrophy of organs to the increase or decrease in their nutritive activity, *i.e.*, to give a chemico-physical explanation.

Darwin has been unjustly reproached with having left chance to

* Compare also A. R. Wallace, "Contributions to the Theory of Natural Selection."

† Compare E. Haeckel, "Natürliche Schöpfungsgeschichte. 4. Auflage. Berlin, 1873.

‡ It is clearly a misuse of the word "Law" to represent the numerous partially opposed and limiting phenomena of heredity as so many "laws of heredity," as E. Haeckel does.

play a considerable part in his attempt to account for the origin of varieties, with having accounted for everything by the struggle for existence, and with having given too little prominence to the direct influence of physical action on the mutation of forms. This reproach seems to arise from a misapprehension. Darwin says himself that the expression "chance," which he often uses to explain the presence of any small alteration, is a totally incorrect expression, and is only used to express our complete ignorance of the physical reasons for such particular variation.

If Darwin has by a series of considerations arrived at the conclusion that the conditions of life, such as climate, nourishment, etc., exercise but a small direct influence upon variability, since, for instance, the same varieties have arisen under the most different conditions, and different varieties under the same conditions, and that the complex adaptation of organism to organism cannot be produced by such influences, still he recognises in the alteration of the vital conditions and the mode of nourishment the primary cause of slight modifications of structure. But it is only *natural selection which accumulates those alterations, so that they become appreciable to us* and constitute a variation which is evident to our senses. It is exactly upon the intimate connection of direct physical action with the consequences of natural selection that the strength of the Darwinian theory rests.

The origin of varieties and races would appear, however, to constitute only the first stage in the processes of the continual changes of organisms. However slowly the process of selection may work, yet there is no limit to the extent and magnitude of the changes, or to the endless combinations of reciprocal adaptations of living beings if we allow a very long period of time for its operation. With the aid of this new factor of duration of time, which, according to geological facts, cannot be rejected, but stands to an unlimited extent at our service, the gap between variety and species disappears. Since the former are continually diverging with the lapse of time—and the more they do so and become differentiated in their organization so much the better will they be fitted to fill different places in the economy of nature and to increase in number—they at length attain the value of species, which in a state of nature do not interbreed, or, at any rate, only exceptionally produce progeny. *Thus, according to Darwin, a variety is a species in process of formation.* Variety and species are connected by continuous series of transitions, and are not absolutely distinct from one another; but are only relatively separated

by the amount of difference in their morphological and physiological characteristics.

This conclusion of Darwin's, which extends the result of natural selection from the production of variety to that of species, is obstinately and often bitterly opposed by those who subordinate the phenomena of nature to traditional ideas.

Even if they do not deny the facts of variability, and even admit the influence of natural selection on the formation of natural varieties, they yet continue true to the belief that there is an absolute separation between species and race-variety. As a matter of fact, however, we are not in a position to draw such a line of separation. Neither the quality of the distinctive characteristics nor the results of crossing afford us a distinctive criterion between species and variety. The fact, however, *that we are not able to give any satisfactory definition of the conception of species, precisely because we are unable clearly to distinguish between species and variety*, adds so much the more weight to Darwin's argument, since neither the variability of the organism and the struggle for existence nor the great antiquity of life upon the globe can be contested.

The variability of forms is a firmly established fact ; so, too, is the struggle for existence. Now if we add the operations of natural selection to these two factors, we are able to understand the origin of varieties. If we imagine the same process which has led to the formation of varieties continued through a greater number of generations and effective through a longer period of time—and we are the more justified in making use of these long periods of time, since with their help astronomy and geology have been enabled to explain many phenomena—the diverging characteristics will become more and more marked, and will at last gain the value of distinctive species-characters.

In still greater periods of time the species will become so far separated from one another by the simultaneous disappearance of the intermediate forms that they will represent different genera. Accordingly the greater differences of organization which are expressed in the higher divisions of the system, such as orders and sub-orders, etc., require a longer interval of time for their accomplishment, and an extinction of a greater number of intermediate forms. Finally, the different ancestral forms of the classes of a group may be referred to a common starting-point ; and since the different groups of animals are connected by many intermediate forms, the number of the ancestral forms becomes much reduced.

The undifferentiated contractile substance, sarcode or protoplasm, was probably the starting-point of all organic life.

If these suppositions are correct, species no longer retain the signification of *independent and immutable units*, and appear, according to the great law of evolution, only as transient groups of forms, capable of change, and confined to longer or shorter periods of time, to definite conditions of life, and preserving, as long as these conditions do not vary, *a constancy in their essential characters*. The different categories of the system show the closer or more remote degree of relationship; and the system is the expression of genealogical relationship founded upon descent. All systems, however, must be imperfect and full of gaps, since the extinct ancestors of organisms living at the present time can only be very imperfectly supplied by the geological record; numerous intermediate forms are wanting and finally no traces of organic remains from the most ancient periods are preserved.

Only the ultimate twigs of the enormously ramified ancestral tree are accessible to us in sufficient number. Only the extreme points of the twigs are completely preserved; while of the numerous ramifications of the branches only the existence of a stump here and there has been demonstrated. Hence it appears quite impossible, in the present state of our knowledge, to attain to a sufficiently sure representation of this natural genealogical tree of organisms; and while we admire the bold speculations of E. Haeckel's genealogical attempts, it must be admitted that at present there is room for innumerable possibilities in detail, and that subjective judgment holds a more conspicuous place than objective certainty of fact. Hence we must be contented for the present with an incomplete and more or less artificial arrangement; although the *conception of the natural system theoretically* is established.

When the fundamental arguments of the Darwinian theory of selection and the transmutation theory founded upon it are submitted to criticism, it is soon apparent that direct proof by investigation is now, and perhaps always will be, impossible; for the theory is founded upon postulates which cannot be submitted to direct inquiry. Periods of time which cannot be brought within the limits of human observation are required for the alteration of forms under natural conditions of life; and the extremely complicated interactions, which in the natural state under the form of natural selection are tending to change plants and animals, can only be grasped in a general sense, while in their details they are practically unknown to us.

Further, plants and animals which are under the influence of

natural selection are entirely inaccessible to the experiments of man, and the relatively few forms which man has, in a greater or less space of time, brought completely within his power, have been and are being altered and modified by the so-called *artificial* selection. The action of the *natural* selection, in Darwin's sense, is therefore in general incapable of direct proof, and even for the origin of varieties can only be illustrated and rendered probable by hypothetical examples. Against this we must, however, set the fact that there is a great probability in favour of the correctness of the theories of descent and transmutation of species, which have never received better support than from the natural selection theory of Darwin; and that this probability is supported, not only by the whole weight of morphological evidence, but also by the testimony of Palæontology and of geographical distribution.

EVIDENCE IN FAVOUR OF THE THEORY OF DESCENT.

If the transmutation of species is to be regarded as an hypothesis, because it is incapable of being demonstrated by direct observation, then its value depends upon its correspondence with the facts and phenomena of nature.

Evidence from Morphology.—The *whole of Morphology* tends to show the correctness of the theory of transmutation of species. The degrees of resemblance between species which was for a long time expressed by the metaphorical term "*relationship*," and which rested upon an agreement in more or less important characteristics, led to the establishment of systematic groups, of which the highest, the kingdom or type, was founded upon a similarity in the most general features of organization and development. The agreement of numerous animals in the general plan of their organization, *e.g.*, the common possession by fishes, reptiles, birds, and mammals of a rigid column forming the axis of the body, and the dorsal position in regard to this of the central nervous system and the ventral position of the organs of nourishment and reproduction, are very well explained, according to the theories of selection and descent, by the derivation of all Vertebrates from a common ancestor possessing the characteristics of the type, while the supposition of a plan of the Creator renounces all explanation. In like manner is explained that similarity of characteristics by which the remaining groups and sub-groups, from class to genus, are distinguished, as well as the possibility of dividing all organized beings into groups subordinated the one to the other.

The impossibility of a sharply defined classification is also rendered comprehensible by the theory of descent. The theory requires the existence of forms transitional between intimately and remotely allied groups; and explains, as a result of the disappearance, in course of time, of numerous types which have been worsted in the struggle for existence, the fact that groups of equal value are of such various extent, and are often only represented by single forms.

It is not only systematic characters, but also the innumerable facts brought to light by the science of Comparative Anatomy which point to a nearer or more remote relationship between the different groups. For example, if we examine the structure of the extremities or the brain of Vertebrates, we find, in spite of considerable differences (sometimes bridged over by intermediate forms) in the various groups, that in all they are built upon a common type of structure. This type is found very variously modified and more or less differentiated in each secondary group, according to the different functions which the organ has to fulfil and according to the exigencies of the mode of life to which each species is subjected. In the fin of the whale, in the wing of the bird, in the anterior limb of the quadruped, and in the human arm it can be shown that there are present the same bones, here short and broad and immoveably connected, there elongated and jointed in different ways to allow of corresponding movements, sometimes with every part fully developed, sometimes simplified in one way or another, and partly or entirely rudimentary.

Evidence from the facts of Dimorphism and Polymorphism.—The phenomena of dimorphism and polymorphism in the same species, and the sexual differences which have been developed in animals originally hermaphrodite, may be quoted as important evidence of the extensive influence of adaptation.

Male and female forms differ not only in the fact that the former produce spermatozoa and the latter ova, but they exhibit numerous secondary sexual characteristics connected with the different functions which the male and female respectively have to perform. The existence of these secondary characteristics can in all cases be satisfactorily explained by means of natural selection. We may therefore, in a certain sense, speak of a sexual selection* by means of which the two sexes have been, in course of time, gradually separated from one another, not only in peculiarities of form and organiza-

* Ch. Darwin, "The Descent of Man, and, Selection in Relation to Sex," Vol. I. and II. London 1871.

tion, but also in habits of life, in such a way as to favour the preservation of the race. Since the male sex generally has to take a more active part in the acts of copulation and fertilization it is comprehensible that the male form should differ more from the young than the female which supplies material for the formation and nourishment of the embryo and is charged with the care of the progeny. Very frequently the male sex is capable of quicker and more facile movements; in many Insects the male alone has the power of flight, while the female remains without wings (fig. 97). In the strife which the males of similar species have to wage for the possession of the females, those individuals which are most favoured by their organization (in respect of strength, capability for motion, prehensile organs, beauty, organs for production of sound, etc.) will prove the conquerors; while those females which possess properties especially favourable to the prosperity of the offspring will best fulfil their task.

At the same time variations in the duration of development, in the mode of growth and structure, may in a more passive way be favourable under the special conditions of life of the species. The secondary *sexual characters* may sometimes acquire such importance as to lead to essential and deeply engrained modification of the organism, and to a true sexual dimorphism (males of *Rotifera* with no digestive tube, dwarfed males of *Bonellia*, *Trichosomum crassicauda*).

It is a significant fact that dimorphism of sex reaches its highest extreme in parasites. In many parasitic Crustacea (*Siphonostoma*) such extreme cases, in which the large shapeless females have lost the organs of sense and locomotion, and even segmentation, while the males are small and dwarfed, are connected by numerous intermediate forms; and the circumstances which have operated as the cause of this sexual dimorphism are not far to seek. The influence of favourable conditions of nourishment which parasites enjoy does away with the necessity of rapid and frequent locomotion, increases in the female the capacity of producing reproductive material, and brings about such an alteration of form that the power of locomotion is diminished and the organs of movement atrophy and may completely vanish. The body acquires an unwieldy, shapeless character in consequence of the enormous size of the ovary which is filled with eggs, and throws out outgrowths and processes into which the ovaries project, or else acquires an unsymmetrical saclike form. The segmentation is lost and the limbs degenerate; the slender moveable abdomen which, when the animal was free-swimming, was an essen-

tial aid to locomotion, is reduced more and more till it becomes a short, unsegmented stump. The appearance of such a parasite is so strange that one can easily comprehend how it was that formerly one of these abnormal groups, the *Lernææ*, was placed among the endoparasitic Worms, or even among the Mollusca.

The more the female remains behind the type of its fully-developed, free-living allies, so much the more do the two sexes become morphologically remote from one another, for the form and organization of the male also are affected by the changed conditions of life, but in a different manner.* In the male sex the more favourable and abundant nourishment may not affect the necessity of locomotion and the development of the locomotive organs in so direct a manner, since the sexual activity of the male and the necessity for locomotion in order to select a female remain unaltered. Even when locomotion is reduced and rendered difficult, parasitism does not, in the case of the male, lead either to a complete loss of segmentation or to such unsymmetrical growths as we observe in many female parasitic Crustacea. The large quantity of generative material produced, which in the female is of the greatest importance for the preservation of the species, and which therefore favours the development of a large, shapeless, unwieldy body, is the less conspicuous in the male because a very small quantity of sperm serves for the fertilization of an enormous number of ova.

Thus, then, the extreme degree of parasitism in the male, even when accompanied by a confined and more creeping mode of locomotion, does not lead to an excessive increase in size nor produce an unsegmented and strange form of body, but, on the contrary, gives rise to the symmetrically formed, dwarfed pigmæan males. This extreme state is, however, connected with the normal state by numerous intermediate steps. Thus we find in the *Lernæopods* that the size of the male *Actheres* is only slightly reduced, while the true dwarfed males of the *Lernæopoda* and *Chondracanthidæ* are attached, like small parasites (fig. 98), to the posterior end of the female body, which is relatively enormously large. The preparation of a large amount of sperm which implies the possession of a large body, would only be a useless expenditure of material and time in the life of the species, and this must have been avoided by the influence of natural selection.

In addition to this sexual dimorphism we find in various groups of animals—especially in the insects which live together in great

* Compare C. Claus, "Die freilebenden Copepoden." 1863.

societies, the so-called animal communities—a third group of individuals (sometimes even divided into several series of forms) which are without generative organs and are incapable of reproduction, but which assume the functions of protecting, of providing nourishment for the community, and of caring for the young. Adaptive peculiarities suitable for the discharge of these functions are apparent in their structure and organization. These sterile individuals are in the *Hymenoptera* aborted females. Among the ants they are divided into workers and soldiers. Amongst the *Termites* they are derived from both males and females, in which the generative organs are reduced. Sterile individuals are also found amongst animals (Fishes) which do not form communities, and were formerly taken for particular species and described as such. Polymorphism is most highly developed in the Hydroids which are united in stocks—the *Siphonophora*.

The numerous cases of dimorphism and polymorphism in either sex of the same species, should be regarded from the same point of view. Dimorphic females among insects have been observed, *e.g.*, in the Malayan *Papilionidæ* (*P. Memnon*, *Pamnon*, *Ormenus*), in certain species of *Hydroporus* and *Dytiscus*, as also in the *Neurotemis*, a genus of the *Neuroptera*. In these cases, as a rule, one of the female forms is more nearly related in form and colour to the male form whose peculiarities it has assumed. In other cases the differences are more connected with climate and season (seasonal dimorphism of butterflies), and also affect the male animal. They may be connected with the different forms of reproduction (parthenogenesis), and lead to the phenomenon of heterogamy (*Chermes Phylloxera*, *Aphis*). Much more rarely we find two kinds of males with dissimilar secondary sexual characters connected with copulation, as in the case of the “smellers” and “claspers”* described by Fritz Müller in the Isopoda (*Tanais dubius*).

Evidence from Mimicry.—Another series of phenomena which may probably be referred to useful adaptation is the so-called *mimicry*. Certain animal forms come to resemble other widely-distributed species; which are protected by any peculiarity of form and colour, so closely that they seem to have copied them. The cases of mimicry which have been principally made known by Bates and Wallace are directly connected with the protective resemblances mentioned above; that is, the resemblance of many animals in colour and body shape to the objects amongst which they

* Fritz Müller, “Facts for Darwin,” p. 22.

live. For example, amongst the butterflies certain *Leptalidæ* resemble in outward appearance and in mode of flight a species of the family *Heliconius* (fig. 116), which appears to be protected from the pursuit of birds and lizards by a yellow disagreeable-smelling fluid, and share the same locality with the above-mentioned species. The most perfect instances of mimicry are found in the Tropics of the Old World, where the *Danaidæ* and *Acræidæ* are imitated by the *Papilionidæ* (*Danaïs niavius*, *Papilio hippocoon*—*Danaïs echeria*, *Papilio cenea*—*Acræa gea*, *Panopæa hirce*). Cases of mimicry frequently occur between insects of different orders; butterflies imitate the form of Hymenoptera, which are protected by the possession of stings (*Sesia bombyliiformis*—*Bombus hortorum*, etc.) In the same way

FIG. 116.—*a*, *Leptalis Theonoë*, var. *Leuconot* (Pieris). *b*, *Ithomia Ilerdina* (the mimicked *Heliconius*). (After Bates.)

certain beetles resemble bees and wasps (*Charis melipona*, *Odontocera odyneroides*), and the Orthopteran genus *Condylodera tricondyloides* from the Philippines is like a genus of *Cicindelæ* (*Tricondyla*). Numerous Diptera have the form and colour of stinging *Sphegidæ* and Wasps. Also among Vertebrates (Serpents and Birds) some examples of mimicry are known.

Evidence from Rudimentary Organs.—*Rudimentary* organs, too, which are so common, are satisfactorily explained by the theory of selection as the result of non-

employment of such organs. Organs which were formerly functional have gradually or even suddenly become functionless as a result of adaptation to special conditions of life, and, through want of exercise, have, after the lapse of generations, become weaker and finally aborted or degraded (Parasites). We cannot, however, assert that rudimentary organs are in all cases useless. They have, on the contrary, often gained secondary functions, though this may be difficult to demonstrate.

We find, for instance, in certain snakes (*Pythonidæ*) that there are small processes armed with claws at the sides of the anus (*anal*

claws). These are the hind limbs which have become rudimentary, and which do not subserve locomotion but, in the male at least, assist in *copulation*. The blind worms possess a rudimentary shoulder girdle and breast bone, although the anterior extremities are wanting: these bones may be connected with the need of protecting the heart, or may aid in respiration. When we see that the upper incisor teeth are developed in the foetus of many ruminants, and that these teeth are never cut, and that the embryos of the whalebone whales have the rudiments of teeth in their jaws, which they soon lose and never make use of in mastication, it is much more rational to ascribe to these structures a part in the growth of the jaw than to hold them for wholly useless. The rudimentary wings of the penguin are employed as oars, those of the ostrich as aids to running and as weapons for protection. The rudimentary stumps of the kiwi, on the contrary, appear valueless. In many cases we are not in a position to assign any function or value to rudimentary organs.

Evidence from Embryology.—The results of *embryology* too, *i.e.*, the *individual* development from the ovum to the fully developed form, are in complete agreement with the Darwinian theories of *selection* and *descent*. The fact that the animals belonging to one type have, as a rule, embryos which are much alike and undergo a similar developmental process, and that the closer the relationship between the adult forms the greater the similarity in their development (with some remarkable exceptions), supports the conception of a common ancestry and the hypothesis of differing gradations of blood-relationship.

If the groups of different value which correspond to the divisions and subdivisions of our classification are genetically derived from more or less remote ancestral forms, then the individual development will present so many the more common features the closer the forms stand to their common ancestor.

The fact that animals which differ much from one another and exist under very different conditions of life show an unusual agreement in their post-embryonic development up to a more or less late period (the free Copepoda, parasitic Crustacea, Cirripedia), is in no wise opposed to the theory, but may be explained by the influence which adaptation has exerted not only during the period of sexual life, but also during each developmental period, causing changes which have been inherited in corresponding periods of life.

The phenomena of metamorphosis afford numerous proofs of the fact that the adaptation of the embryonic form is as complete as

that of the adult; and we can thus understand how larvæ of many insects belonging to different orders can present great resemblances to one another and be unlike the larvæ of insects of the same order. While as a general rule the development of the individual is an advance from a simpler and lower organization to one more complex which has become more perfect by a continued division of labour among its parts—and we shall later find a parallel to this law of perfection of the individual in the great law of progressive perfection in the development of groups—yet the course of development may, in particular cases, lead to numerous retrogressions, so that we may find the adult animal to be of lower organization than the larva. This phenomenon, which is known as *retrogressive metamorphosis* (*Cirripedia* and *parasitic Crustacea*), corresponds to the demands of the selection theory, since under more simple conditions of life, where nourishment is more easily obtained (parasitism), degradation and even the loss of parts may be of advantage to the organism.

Again, the facts of embryonic development, when considered in relation to the gradations expressed in the system are in complete accord with the theory of evolution. Numerous examples may be cited to prove that features, not only of the simple and more primitive, but also of the more perfectly organised groups of the same type, are reflected in the successive phases of foetal life. In the case of a complicated free development by metamorphosis, which is usually correlated with an unusual simplification of the foetal development within the egg-membranes, the relation of the successive larval stages to the allied smaller groups of the system, to the genera, families and orders, is more direct and striking. For example, in the early stages of the embryonic development of mammals certain structures occur, which in the lower fishes endure throughout life. Later stages show peculiarities which correspond to the characters of amphibia. The metamorphosis of the frog begins with a stage which in form and organization and mode of locomotion agrees with the fish type; and this stage is succeeded by numerous other larval stages in which the characters of the other orders of Amphibia (*Perenni-branchiata*, *Salamandrinidæ*) and of individual families and genera of the same are repeated.

This undeniable likeness between the successive stages of individual development and between allied groups of the system allows us to institute a parallel between the former and the evolution of the species. The evolution of the species finds, it is true, a most imperfect expression in the relationship of the systematic groups, and can

only be inferred from the history of the past for which palæontology affords us but slight material.

This parallel, which naturally presents numerous greater or smaller variations in detail, is explained by the theory of evolution, according to which *the developmental history of the individual appears to be a short and simplified repetition, or in a certain sense a recapitulation, of the course of development of the species.**

The historical record preserved in the developmental history of the individual must often be more or less blurred and obscure on account of the many adaptations which have occurred during the embryonic development, or during larval life. Especially in those cases where the peculiar conditions of the struggle for existence demand a simplification, the development will take a more direct course from the ovum to the perfect animal, will be thrown back into an earlier period of life, and finally will be completed before the animal is hatched, until, in absence of a metamorphosis, the historical record is completely suppressed. On the contrary, in the cases of progressive transformation where the larval states are gradually modified and live under similar conditions of life, the history of the species will be less imperfectly reproduced in that of the individual.

Evidence from the Facts of Geographical Distribution.—Unlike the facts of morphology, those of *geographical distribution* raise great difficulties for the theory principally because the phenomena are very complicated and our experiences are still too limited to permit of our establishing general laws. The present distribution of plants and animals over the surface of the earth is clearly the combined result of the earlier distribution of their ancestors and of the geological changes which have since taken place, the modifications in the extent and position of land and water, which must have had an influence on the fauna and flora.

Accordingly the geographical distribution of plants and animals† appears intimately connected with that part of geology which has for its aim the investigation of the most recent occurrences in the formation of the earth's crust and its contents. It cannot, therefore, be confined to an examination of the areas of distribution of the animals and plants of the present day, but must take cognizance of the distribution of the remains, enclosed in the most recent formations, of the nearest relations and ancestors of living forms, in

* Fr. Müller, "Für Darwin," Leipzig, 1864.

† A. R. Wallace, "The Geographical Distribution of Animals," London, 1876.
P. L. Selater, "Address to the Biological Section of the Brit. Association," 1875.

order to find an historical explanation of the known facts of distribution. Although in this sense the science of animal geography is still in its infancy, yet numerous and important phenomena of geographical distribution receive a satisfactory explanation according to the theory of transmutation of species on the supposition of migrations and gradual changes brought about by natural selection.

It is a most important fact that neither the resemblance nor the want of resemblance of the animals inhabiting different localities can be completely explained as the result of climatic and physical conditions. Closely allied species of plants and animals often appear under very different natural conditions, while a completely different fauna and flora can exist in a similar climate and on a similar soil. On the other hand, the extent of the difference between two fauna is closely connected with the limitations of space and the barriers and hindrances to free migration. The Old and New Worlds, which, leaving out of consideration the polar connection, are completely separated, have in part a very different fauna and flora, although with regard to the climatic and physical conditions of existence there are innumerable parallels which would equally favour the prosperity of the same species.

In particular if we compare the districts of South America with regions situated in the same latitude and possessing the same climate in South Africa and Australia, we find three faunas and floras which differ considerably, while the natural productions from different latitudes of South America with entirely different climates are closely allied. Here the northern animals are indeed specifically different from the southern, but belong to similar or nearly allied genera with the peculiar stamp characteristic of South America.

Zoological Provinces.—The surface of the earth can be divided into from six to eight regions according to the general features of the terrestrial and fresh-water fauna. These regions can indeed only be considered as a relative expression for large natural districts of distribution, since they cannot be applied to all groups of animals in the same manner, and it is impossible that they should differ in like degree and in the same direction. There must also be intermediate regions combining the characteristics of the neighbouring regions with peculiarities of their own; and the question must arise whether these should not be taken as independent regions.

The merit of having first established a natural division of the earth into zoological regions and sub-regions belongs to Sclater. This naturalist founded his system on the distribution of birds, and dis-

tinguished six regions, the limits of which agreed fairly well with the distribution of Mammalia and Reptilia. These regions are—

(1) *The Palæarctic Region*—Europe, the temperate part of Asia, and North Africa as far as Mount Atlas.

(2) *Nearctic Region*—Greenland and North America as far as North Mexico.

(3) *The Ethiopian Region*—Africa, south of Atlas, Madagascar, and the Mascarenes with South Arabia.

(4) *The Indian Region*—India south of the Himalayas, to South China, Borneo and Java.

(5) *The Australian Region*—Celebes and Lombok eastward to Australia, and the South Sea Islands.

(6) *The Neotropical Region*—South America, the Antilles, and South Mexico.

Other naturalists (Huxley) have since shown that the four first of these regions have a much greater resemblance to one another than any one of them has to the Australian or South American regions; that New Zealand is entitled by the peculiarities of its fauna to be considered as forming a region by itself; finally, that a circumpolar* province should be formed equal in value to the Palæarctic and Nearctic.

Wallace objects to the establishment either of a *New Zealand* or of a *circumpolar region*, and advocates the adoption of the six regions of Sclater on practical grounds, but suggests the modification that since the South American and Australian are much more isolated, the regions should not be of equal value.

These regions are bounded by extended seas, lofty mountain ranges, or vast sandy deserts, and obviously such boundaries do not constitute effective barriers to the migration of all animals, but allow certain groups to pass from one region to another.

The obstacles to immigration and emigration appear in certain places, at all events in the present time, to be insurmountable;

* Andrew Murray, on the contrary, in his work on the geographical distribution of Mammalia in 1866, distinguishes only four divisions—the Palæarctic, Indo-African, the Australian, and the American. Rüttimeyer recognises in addition to the six provinces of Sclater a Mediterranean and Circumpolar province. J. A. Allen ("Bulletin of the Museum of Comparative Zoology, Cambridge," vol. ii.) proposes to distinguish eight regions, in connection with "the law of circumpolar distribution of life in zones:"—(1) Arctic realm; (2) North Temperate realm; (3) Tropical American realm; (4) Indo-African Tropical realm; (5) Tropical South American realm; (6) Temperate African realm; (7) Antarctic realm; (8) Australian realm.

but in past ages, when the divisions of land and water were different, they must have been, for many forms of life, easily surmountable. The expression "centre of creation," which has long been used in the sense of a tolerably defined district of distribution—or better still, Rüttimeyer's word, "centre of distribution"—has as a fundamental idea the endemic appearance of definite groups of typical species and their gradual extension * towards the boundaries of the said region, a conception which harmonizes well with the theory of the origin of species through gradual alterations.

The same laws apply also to the distribution of the inhabitants of the sea. Great seas studded with islands which serve to confine the land animals may favour the migration of marine species, while extended continents, which allow their inhabitants to wander freely over them, confine the sea animals within limits which cannot be passed. A great number of sea animals live only in the shallow water round the coast, and their distribution thus often coincides with that of the land animals; whereas the animals found on the opposite coasts of great continents are very different. For example, the sea animals of the east and west coasts of South and Central America differ to such a degree that, with the exception of a series of fishes, which, according to Günther, are found on both sides of the *Isthmus of Panama*, only a few forms are common to the two coasts. In the same way we find that the marine inhabitants of the east insular district of the Pacific differ completely from those of the west coast of South America. If, however, we advance to the west of this part of the Pacific till we come to the coast of Africa in the other hemisphere, we find that the fauna of this extensive district cannot be so sharply distinguished. Many species of fish are found from the Pacific to the Indian Ocean. Numerous Mollusca of the South Sea Islands live also on the east coast of Africa, almost beneath the opposite meridian. In this case the limits of distribution are not impassable, as numerous islands and coasts afford a resting place to wandering inhabitants of the sea. In respect of the different haunts of the inhabitants of the sea, we must make a distinction between the *littoral* animals, which are distributed along the coasts, and live under different conditions and at different depths on the bottom of the sea, and the *pelagic* animals, which swim on the surface.

* Compare Rüttimeyer's Essay, "Ueber die Herkunft unserer Thierwelt," Basel and Genf. 1867.

But there also exists, at considerable depths and on the bottom of the sea, a rich and varied animal life. This has only lately been brought to our knowledge principally by the deep-sea explorations from North America, Scandinavia, and England. In place of that want of animal life which we should on *à priori* grounds expect to find, we see that numerous lowly organised animals of the most different groups are able to exist even at the greatest depths. Besides the lowest sarcode animals of the Foraminifera (*Globigerina* ooze), we find especially silicious sponges, certain corals, *Echinoderms*, and *Crustacea*.* The representatives of the latter are in part of low type, but gigantic, and many of them blind. It is also a fact of more than ordinary interest, as showing the continuity of living creatures from successive geological formations up to the present time, that the deep sea animals are allied to ancient types which occur in Mesozoic formations, especially in chalk.

Evidence from Palæontology.—The results of *geological* and *palæontological* inquiry give us a third great series of facts in support of the theory of slow alterations of species and the gradual development of genera, families, orders, etc. The firm crust of our earth is formed of numerous and enormous rock strata, which have been deposited in a definite series by water in course of time, and also of the so-called volcanic or plutonic rocks, masses which have been forcibly ejected from the molten interior of the earth. The former or sedimentary deposits, which have undergone numerous alterations in the originally horizontal arrangement of their strata as well as in the petrographical condition of their rocks, contain a quantity of the fossilized remains of former plants and animals which have become buried in them, and thus afford an historical record of a rich fauna and flora which existed during the earlier periods of the earth's development. Although these so-called fossils have made us acquainted with a very considerable number of ancient organisms presenting great diversity of form, yet they only constitute a very small portion of the enormous quantity of living beings which have at all times existed upon the earth. They suffice, however, to teach us that a different fauna and flora existed at the time when each individual deposit was being formed, and that

* Compare Wyville Thomson, "The depths of the sea. An account of the general results of the dredging cruizes of the *Porcupine* and *Lightning*, during the summer months of 1868, 1869, 1870." London, 1873. Also the results of the *Challenger* expedition 1874-1876.

the deeper a stratum comes in the series, that is, the earlier it appears in the history of the earth, so much the more its fauna and flora differ from those of the present time. The more nearly one stratum follows another in the series, the closer the relationship between their respective fossils. Every sedimentary formation possesses characteristic fossils which appear very frequently; and from these, taking into account the succession of strata and the petrographic characters of the rocks, the place occupied by the stratum in the geological system can be defined with tolerable accuracy.

Without doubt the characters of the fossils and the relative positions of the strata are the most important aids to the determination of the geological age of the deposit; at any rate they furnish a more reliable criterion than does the structure of the rocks. The idea entertained in earlier times that rocks of the same period always possessed a similar, and rocks of a different period a dissimilar structure, has lately been given up as erroneous. Stratified or sedimentary deposits have arisen in every period under similar conditions. In past times, as at the present time, they were caused by the deposition of clay, of fine or coarse sand, of fine and coarse *débris*, by chemical precipitation of carbonates and sulphates of lime and magnesia, of silica and oxide of iron, and by accumulation of solid animal and vegetable remains. These have become transformed only in course of time into such hard rocks as argillaceous and calcareous schists, limestone, sandstone, dolomite, and conglomerates of many kinds; as the result of many causes, such as mechanical pressure of superincumbent masses, increase of temperature, internal chemical processes, and so forth.

Even though the peculiar structure of rocks may in many cases afford good ground for conjecture as to the relative age, yet it is certain that deposits of similar age may show an entirely different petrographical character; and, on the other hand, that deposits of very different ages may have given rise to rock formations that can be scarcely or not at all distinguished from one another.

The old idea that deposits of the same age must everywhere contain the same fossils, could only be maintained as long as geological investigations were confined to small districts. Similarly the idea, closely connected with the former, that the various geological formations, characterised by a series of definite strata, are entirely independent of one another, no longer obtains credit. The various forma-

tions,* as the group of strata of one district of distribution and belonging to one period are named, cannot be divided petrographically or

* The following table may serve for a bird's-eye view of the geological periods and their most important formations :—

QUARTIARY PERIOD (<i>Diluvial and Alluvial Formations</i>).	{ <i>Recent Periods</i> (alluvium, marine and fresh-water formations).	
	{ <i>Postpliocene</i> or <i>Diluvial Period</i> (erratic boulders, glacial period).	
TERTIARY PERIOD (<i>Cainozoic Formations</i>).	{ <i>Pliocene Period</i> (subappenine formations, bone sand of Eppelsheim, etc.)	
	{ <i>Miocene Period</i> (Molasse, Tegel near Vienna, brown coal in North Germany, etc.)	
	{ <i>Eocene Period</i>	{ Flysch, Nummulite formation of the Paris basin.
SECONDARY PERIOD (<i>Mesozoic Formation</i>).	{ <i>Cretaceous Period</i>	{ Maestricht strata, white chalk, upper green sand, Gault, lower green sand, Weald.
		{ Purbeck strata, Portland stone, Kimmeridge clay, Coral Rag, Oxford clay, Great oolite, Lower oolite, Lias (white, brown, and black jura).
SECONDARY PERIOD (<i>Mesozoic Formations</i>).	{ <i>Jurassic Period</i>	{ Keuper or upper new red sandstone, Muschelkalk (upper Muschelkalk, gypsum and anhydrite, Wellenkalk, Bunter Sandstein).
		{ Zechstein, Rothliegendes.—lower new red sandstone.
	{ <i>Triassic Period</i>	
PALÆOZOIC PERIOD (<i>Palæozoic Formations</i>).	{ <i>Permian</i>	
	{ <i>Carboniferous Period</i>	{ Coal Measures of England, Germany, and North America, Kulmformation, Carboniferous limestone.
	{ <i>Devonian Period</i> (Spiriferenschiefer, Cypridinen-schiefer, Stryngocephalenkalk, etc.—old red sandstone.)	
	{ <i>Silurian Period</i> (Ludlow, Wenlock, strata, etc.)	
	{ <i>Cambrian Period</i> (slate, etc.)	
ARCHÆAN PERIOD	{ Thonschiefer, Laurentian formations. Mica schist, Older Gneiss formations.	

According to Professor Ramsay the groups of formations in England have a thickness of 72,584 feet, *i.e.*, about $13\frac{3}{4}$ English miles; that is, formations of the—

Palæozoic period have a thickness of	57,154	} 72,584 feet
Secondary	13,190	
Tertiary	2,240	

palæontologically from each other in such a manner as to lend support to the hypothesis of sudden and mighty revolutions and catastrophes destroying the whole living world. We may rather assert with certainty, that the extinction of old species and the appearance of new ones has not taken place at the same time at all points of the surface of the earth, for many species extend from one formation into another, and a number of organisms persist from the tertiary period to the present time, but little altered or even identical. Just as the commencement of the recent epoch is hard to define, and cannot be sharply separated from the diluvial period by the character either of its deposits or of its fossils, so it is with the remoter periods of the earth's history, which are founded, like periods of human history, upon great and important occurrences, and yet are in direct continuity.

Lyell has proved in a convincing way on geological grounds that there were no sudden revolutions extending over the whole surface of the earth, but that changes took place slowly, and were confined* to separate localities; in other words, that the past history of the earth consists essentially of a gradual process of development, in which the numerous forces which may be observed in action at the present day have, by their long continued operation, had an enormous total effect in transforming the earth's surface.

The reason for the irregular development of strata and for the limitations of formations is principally to be sought in the interruption of depositions, which, though widely distributed, were only of local importance. Were it possible that a single basin of the sea should have persisted during the whole period of sedimentary formation and under singularly favourable circumstances have formed new deposits in persistent continuity, then we should find a progressive series of strata interrupted by no gaps, which we should be unable to classify according to formations. Such an ideal basin would include only a single formation, in which we should find representatives of all the other formations of the surface of the earth.

* "Every sedimentary formation was extended at the time of deposition over a confined territory,—confined on the one hand by the extent of the sea or fresh-water basin, and on the other by the different conditions favourable to the deposition inside the basin. At the same time, in other places entirely or at any rate somewhat differently stratified formations (*i.e.*, formations of the same age, but of different composition) resulted. Thus marine, fresh-water, and swamp formations have been deposited at the same time from different rocks and with different fossils, while the land surface has remained free." Comp. B. Cotta, "Die Geologie der Gegenwart."

In reality this ideal continuous series of strata is interrupted by numerous and often large gaps, which determine the petrographical and palæontological differences, often strongly marked, between successive strata, and correspond to periods of inactivity, or, as may happen, to periods when the results of sedimentary action have been again destroyed. These interruptions of local deposits are explained by the constant alterations of level which the surface of the earth has undergone in every period in consequence of the reaction of the molten contents of the earth against its firm crust.

As we see in the present time that wide tracts of country are gradually sinking (west coast of Greenland, coral islands), while others are being slowly elevated (west coast of South America, Sweden); that strips of coast line are suddenly submerged beneath the sea by subterranean forces, and that islands as suddenly appear; so it was in earlier periods. Elevation and depression were at work, perhaps uninterruptedly, causing a gradual, more rarely a sudden (and then locally confined) interchange between land and sea. Basins of the sea rising with gradual movement became dry land and rose up first as islands, and afterwards as connected continents, the different deposits of which, with their included fossils, bear witness of the sea which once covered them. On the other hand, great continents sank beneath the sea, leaving perhaps their highest mountain peaks appearing as islands, and again became the seat of fresh deposition of strata. In the first case there would be an interruption of deposit, while in the latter there would result, after a longer or shorter period of inactivity, the beginning of a new formation. Since, however, elevations and depressions, even though affecting districts of great extent, must always be locally confined, the commencement and interruption of formations of equal age have not taken place everywhere at the same time. Deposits continued a long time on one tract after they had ceased on another; hence the upper and lower boundary of equivalent formations may show great want of uniformity, according to the different locality. This explains how it is that formations lying one above the other are composed of strata of very variable thickness, and why we can only in rare cases supply the gaps in the series of these strata from strata found in other countries. The whole succession of formations known to us up to the present time is not sufficiently complete to form an entire and uninterrupted series of the sedimentary formations. There are still numerous and important gaps in the geological record which we may expect to

see filled in future days, when knowledge has increased, and perhaps only when formations now beneath the sea have become known to us.

Imperfection of the Geological Record.—After the foregoing discussion we may consider that the continuity of living organisms in the successive periods of the earth's development and their close relationship has been proved partly by geological and partly by palæontological facts. The theory of descent, however, according to which the natural system must be regarded as a genealogical tree, requires still further proof. It requires proof of the presence of numerous forms, transitional not only between the species now existing and those in the more recent formations, but also between the species in all those formations which have immediately succeeded one another in point of time. The theory also demands proof that forms connecting the different groups of plants and animals of the present day have existed. The establishment and limitation of these groups can, according to Darwin, only be explained by the extinction, in the course of the earth's history, of numerous and intimately connected species. Palæontology is only able imperfectly to comply with these demands; for the numerous closely graduated series of varieties which, according to the theory of selection, must have existed, are, for the greater number of forms, entirely wanting in the geological record.

This want, however, which Darwin himself recognised as an objection to his theory, loses its importance when we consider the circumstances under which organic remains were generally deposited in mud, and preserved for succeeding ages in a fossil form; when we recognise the facts which indicate the extraordinary incompleteness of the geological record, and which show that the intermediate forms must have been in part described as species.

First of all we can only expect to find in deposits the remains of those organisms which possessed a firm skeleton supporting the softer parts of the body, since it is only the harder structures of the body, such as the bones and teeth of Vertebrates, the calcareous and silicious shells of Molluscs and Rhizopods, the shells and spines of Echinoderms, the chitinous skeleton of Arthropods, etc., which are able to resist rapid decay, and to undergo gradual petrification. Thus the geological record will fail to provide us with any account of the numerous and principally low organisms which are not provided with firm skeletal structures.

But also among those organisms which are capable of becoming

fossilized, there are large groups which have only exceptionally left traces of their existence: these are the animals which lived on land. Fossil remains of land animals can only have survived when, during great floods or inundations, or for some reason or other their carcasses have been carried away by the water, floated hither and thither, and been surrounded finally by hardening mud. This explains not only the relative scarcity of fossil Mammalia, but also the fact that of the most ancient Marsupials (Stonesfield slate), scarcely anything is preserved but the underjaw, which, as the body decayed, was easily detached, and, on account of its weight, offered most resistance to the current of the water, and was the first part to sink to the bottom. Although it has been shown by such remains that Mammalia existed in the Jurassic period, yet the Eocene forms are the first which give us an insight into the details of their structure.

Circumstances must have been more favourable to the preservation of fresh-water animals, and most of all to that of marine animals, since the marine deposits have a much greater extent than the locally confined fresh-water deposits. Thick formations seem in general to have arisen under one of two conditions: either in a very deep sea, protected from the operation of winds and waves, no matter whether the bottom was gradually rising or sinking—in this case, however, the strata would be relatively poor in fossils, since only the inhabitants of the deep sea, which is comparatively wanting in animal and vegetable life, would be preserved—or in a shallow sea, in which the bottom underwent a gradual and continued depression during long periods of time favourable to the development of a rich and varied fauna and flora. In this case the sea would have retained uninterruptedly its rich fauna so long as the gradual sinking of its bottom was counteracted by the continual supply of sediment deposited upon it. Thick formations, all or most of the strata of which are rich in fossils, must have been deposited in extended and very shallow regions of the sea, during a long period of gradual depression.

Thus the great gaps which occur in the series of palæontological remains are explained by a consideration of the mode of origin of deposits. These remains must necessarily be confined to the more recent formations. The lower, more ancient, and very thick successions of strata in which the remains of the oldest fauna and flora must have been buried, seem to have been so completely altered by the heat of the molten interior of the earth, that the organic

residua which they contain have been completely destroyed, or so altered that they cannot be recognised.

In any case it may be regarded as certain, that only a small part of the extinct animal and vegetable world has been preserved in a fossil state, and that of this we only know a small part. Therefore we cannot conclude that, because the fossil remains of intermediate stages cannot be found, they have never existed.

It is true that transitional forms are wanting in the strata where they should have occurred, that a species suddenly appears in the middle of a series of strata and suddenly disappears, and that whole groups of species make their appearance and quickly vanish, but the value of these facts as arguments against the theory of selection is diminished by the circumstance that in certain cases series of transitional forms between more or less remotely related organisms have been found, and that many species have been developed in course of time as links between other species and genera; and again, that species and groups of species not unfrequently increase very gradually till they attain an unusually wide distribution, extend into later formations, and then gradually disappear again. Such positive facts have a higher value when we consider the incompleteness of fossil remains.

It will suffice here to refer to the Ammonites and Gasteropods, such as *Valvata multiformis*, as examples supplied to us by Palæontology of transitional forms which can be arranged in a gradual series.

Relation of Fossil Forms with Living Species.—The close relationship of the plants and animals of the present time to the fossil remains of recent formations is a fact of great importance. In particular, we find in the diluvial period and in the different tertiary formations the ancestral forms from which numerous living species are directly descended; and further the characteristic features of the fauna of any particular geographical province in the present epoch are foreshadowed by the fauna of the epoch immediately preceding in the same region; a fact which is proved by the fossil remains we find buried in the most recent strata.

Many fossil Mammalia from the diluvial period and the most recent (pliocene) tertiary formations of South America belong to types of the order of *Edentata* which are now distributed in that part of the world. Sloths and Armadillos of immense size (*Megatherium*, *Megalonyx*, *Glyptodon*, *Toxodon*, etc.) formerly inhabited the same continent, the mammalian fauna of which in the present day is so specially charac-

terised by its Sloths, Armadillos, and Anteaters. In addition to these gigantic forms, small and extinct species have been found in the bone caves of Brazil, and some of these are so nearly related to the living forms that we may assume them to have been their ancestors.

This law of the "*succession of similar types*" in the same localities is also exemplified by the Mammalia of New Holland; for in the bone caves of that country are found many species nearly allied to its present Marsupials. The same law holds good for the gigantic birds of New Zealand, and, as Owen and others have shown, for the Mammalia of the Old World, which, indeed, is continuous by the circum-polar region with North America; and ancient types were able, in the tertiary period, to pass into North America, and *vice versa* by that way. The presence of Central American types (*Didelphys*) in the early and middle tertiary formations of Europe is to be explained in the same way. It is even more difficult to distinguish the regions of distribution of the animals of that time than of those of the later tertiary period.

The evolution of the ancient forms into those of the present time was effected in the case of the lower, simply organised animals at a much earlier period than in the case of higher organisms. Rhizopods, indistinguishable from species living at the present time (*globigerina ooze*) were already living in the Cretaceous period. The deep sea explorations* have accordingly yielded the interesting result, that certain Sponges, Corals, Molluscs, and Echinoderms now living in the deep sea existed in the Cretaceous period. We meet with a number of living species of Molluscs in the oldest tertiary period, though the mammalian fauna of this period differs completely from that of the present day. The greater number of species of Molluscs found in the recent tertiary period resemble those of the present day, but the Insects of that time differed considerably from living species.

On the other hand, the Mammalia, even in the post-pliocene (diluvial) deposits, differ in part both in genera and species from those of the present day, although a number of forms have been preserved through the glacial period. On this account, and on account of the relative completeness of the tertiary remains, it is

* (*Rhizocrinus Lofotensis*—*Apiocrinites*, *Pleurotomaria*, *Siphonia*, *Micraster*, *Pomocaris*, etc.) Types of earlier and even of the older geological formations have been found preserved in the depths of the ocean, which, in spite of the great pressure, the want of light and deficiency in gaseous contents of the water, are more suited to the development of animal life than was formerly believed.

especially interesting to trace the recent mammalian fauna back through the pleistocene forms to the forms of the oldest tertiary period. It is possible to trace the ancestry of a number of mammalian species. Rütimeyer was the first to undertake to trace out the ancestral line of the *Ungulata*, and especially of the *Ruminantia*, so as to obtain a palæontological developmental history, and succeeded in obtaining results, by means of detailed geological and anatomical (deciduous teeth) comparison, which leave no room to doubt that whole series of species of existing mammalia are collaterally or directly related with each other and with fossil species. Rütimeyer's investigations have received corroboration in their essential points from the recent comprehensive works of W. Kowalevski, and have resulted in the establishment of a natural classification of the ungulate animals founded on phylogeny.

FIG. 117.—Bones of the feet of the different genera of the *Equidæ* (after Marsh). *a*, Foot of *Orohippus* (Eocene). *b*, Foot of *Anchitherium* (Lower Miocene). *c*, Foot of *Hipparion* (Pleiocene). *d*, Foot of the recent genus *Equus*.

In addition to these works we have the recent researches of Marsh, who has completed to an extraordinary degree our knowledge of the genealogy of the genus *Equus*, by numerous discoveries (fig. 117) in America (*Wyoming, Green River, White River*). The eocene *Orohippus*, in which the small posterior toes were present as well as the three principal toes which rested on the ground, was succeeded in the Lower Miocene formation by *Anchitherium* with three hoofs; and the latter was followed by the *Hipparion* of the Pleiocene formations; and this is the ancestral form of the existing genus *Equus*.

The origin of most orders of Mammalia, such as *Rodentia*, *Cheiroptera*, *Proboscidea*, *Cetacea*, etc., cannot be clearly traced out, but for certain orders, as the *Prosimiæ*, *Carnivora*, *Ungulata*, and *Ro-*

dentia, remarkable transitional forms have been discovered among the remains of extinct types. These also appear most prominently among the tertiary remains of North America. In the Eocene period here (Wyoming) lived the *Tillodontia* with the genus *Tillotherium*,* characterized by having a broad skull like a bear, two broad incisor teeth like a rodent, and molar teeth like *Palæotherium*, and feet having five toes armed with strong claws. It thus united in its skeletal structure peculiarities of Carnivora and Ungulata. The *Dinocerata* (*Dinoceras laticeps mirabile*) were powerful Ungulates with five-toed feet with six horns on their heads, without incisors in the præmaxillary bone, with strong sabre-like canine teeth in the upper jaw and with six molars.

A third type, that of the *Brontotheridæ* attained elephantine proportions, and was provided with transversely placed horns in front of the eyes. In addition to the foregoing there are a number of other groups of Mammals now completely extinct, the remains of which extend back into far earlier strata. Amongst them are the South American *Megatheridæ* (*Mylodon*, *Megatherium*), which belong to the order Edentata, and the *Toxodontia*, whose skull and dentition show relations to the Ungulates, Rodents, and Edentates. Many other types, however, especially of the Ungulates, which during the tertiary period inhabited both hemispheres, are now extinct in America, but still exist in the East. Elephants, Mastodonta, Rhinoceri, and Equi existed in America in the diluvial but not in recent periods. Of the Perissodactyles the group of Tapirs alone is preserved in America. This group has also been preserved in the Eastern hemisphere in the East Indian species.

In the palæarctic region also are found the remains of extinct intermediate groups of Mammals which existed during the tertiary period. In the Phosphorites of Quercy† in the south of France are found the remains of the skulls of Prosimiæ (*Adapis*), the dentition of which is intermediate between the ancient Ungulates and the Lemuridæ (*Pachylemuridæ*), so that the question may be raised whether the Prosimiæ had not a common ancestry with several

* Compare O. C. Marsh, "Principal Characters of the Tillodontia." *Amer. Journal of Science and Art*, Vol. xi., 1876.

O. C. Marsh, "Principal Characters of the Dinocerata." *Amer. Journal of Science and Art*, Vol. xi., 1876.

O. C. Marsh, "Principal Characters of the Brontotheridæ." *Amer. Journal of Science and Art*, Vol. xi., 1876.

† Compare H. Filhol, "Recherches sur les Phosphorites du Quercy, Étude des fossils qu'on y rencontre et spécialement des Mammifères." *Ann. Sciences géologiques*, Vol. vii., 1876.

eocene Ungulates (*Pachydermata*). In the same locality are found the well preserved remains of the bones of peculiar Carnivora which are well worthy of remark. These are the Hyænodonta. It was for a long time doubtful whether they were Marsupials or not, until Filhol showed from the reserve teeth of their permanent dentition that they were probably of the nature of placental Carnivora. The great agreement of the molars of these Hyænodonta with those of

FIG. 118.—*Pterodactylus crassirostris* (after Goldfuss) about one-third natural size.

the carnivorous Marsupials, as well as the small size of the skull cavity and the relatively slight development of the brain, support the view, which is also rendered probable by many other circumstances, that placental Mammalia have developed from the Marsupials of the mesozoic period.

In the oldest strata of the Eocene formations in both hemispheres, the higher placental Mammalia already appear in a rich variety of forms, which contrast markedly with one another (*Artiodactyla*, *Perissodactyla*). There is, however, no ground

for regarding the immeasurable period from the oldest Eocene to the Keuper, in which the oldest Mammalian remains (the teeth and bones of insectivorous Marsupials) have been found, as the period in which this higher development of the Mammalian organism has been effected.

In other cases also the science of palæontology has led to the discovery of intermediate forms between groups and even between

classes and orders. The *Labyrinthodonta*, the most ancient of the Amphibia, found as early as the carboniferous period, present many piscine characters (*ventral exoskeleton*), and have a cartilaginous skeleton. Many fossil orders and sub-orders of Saurians (*Halosauridæ*, *Dinosauridæ*, *Pterodactylidæ* (fig. 118), *Thecodontidæ*) have not left a single representative in the present day; others again are transitional between recent orders. Such a relation has, for example, been recently shown between the "Pythonomorphous" lizards (related to the genus *Mosasaurus*) from the chalk in America, and serpents so far as the structure of the skull and jaw is concerned.

Owen's researches on the fossil Reptiles of the Cape have shown that certain Reptiles (*Theriodonta*) once lived there which showed a close resemblance to carnivorous Mammalia with regard to their dentition and the structure of their feet. The teeth of these animals, though only furnished with one root, can be divided into incisors, canines, and molars, a fact which induces us to believe it possible that the dentition of the most ancient Marsupials hitherto known (Keuper) may have been derived from that of a *Theriodon*-like Reptile.

Even as regards birds, a class so uniform in structure and so sharply defined, a form (*Archæopteryx lithographica*) (fig. 119) transitional between them and Reptile has been discovered in the Solenhofen slate, although the impression was not perfect. In this form the short tail of the bird is replaced by a long reptilian tail composed of numerous (20) vertebræ and provided with two rows of feathers (*Saururæ*). The articulation of the vertebral column and the structure of the pelvis indicated an affinity to the long-tailed Pterodactyls.

The discovery of a second and more perfect specimen of *Archæopteryx* has made known to us its dentition. It had sharp-pointed teeth wedged into the jaws. Other types of birds have also been found in the American chalk, which diverge more widely among themselves and from the Saurians than do the birds of any living order. These were defined as *Odontornithes* by Marsh,* and distinguished as a sub-class; they had teeth in the jaws, which latter were elongated to form a kind of beak. Some of them (Order *Ichthyornithes*) had bicelous vertebræ, a crista sterni, and well

* O. C. Marsh, "On a new sub-class of fossil Birds (*Odontornithes*)."
American Journal of Science and Art, Vol. v., 1873.

O. C. Marsh, "On the *Odontornithes*, or birds with teeth." *American Journal of Science and Art*, Vol. x., 1875.

developed wings (*Ichthyornis*). Others (*Odontolca*) had teeth em-

FIG. 119.—*Archæopteryx lithographica*.

bedded in pits, normal vertebræ, no keel to the breast-bone, and rudimentary wings. They were not capable of flight (*Hesperornis*,

Lestornis). Possibly in future days we shall be able by the discovery of new types to establish the connection with the *Dinosaurians* (*Compsognathus*), the formation of whose pelvis and feet offers a closer relationship to those parts in birds.

Advance towards perfection.—If we compare the animal and vegetable life of the most ancient formations with that of the succeeding periods of the earth's development, it becomes evident that there has been, on the whole, a continual progress from a lower to a higher condition. The oldest formations of the so-called archæan time, the rocks of which are for the most part in a metamorphic state, must from their enormous thickness have occupied immeasurable time in their origin. They contain no fossil remains which can be recognised with certainty as such; although the presence of bituminous gneiss in the old formations is a proof of the existence of organic bodies at that time. All the organisms of these most ancient periods, which were certainly numerous, have been destroyed without leaving any further traces than the Graphite deposits of the crystalline schist. In the most ancient and very extensive groups of strata we find exclusively cryptogamous plants, especially Fuci, which formed extensive forests beneath the sea.

The warm seas of the primary period were inhabited by numerous sea animals of very different groups, such as Zoophytes, Molluscs (especially *Brachiopoda*), Crustaceans (larva-like *Hymenocaris*, *Trilobites*), and Fishes whose peculiar armoured forms (*Cephalaspidæ*) indicate a low stage of organization. In the coal formations we meet for the first time with the remains of land animals, Amphibia (*Apatheon*, *Archegosaurus*), with a notochord and a cartilaginous skeleton; we also find Insects and Spiders; and in the Permian formations we meet with large lizard-like reptilian forms (*Proterosaurus*); while fishes, exclusively Elasmobranchs and Ganoids with a notochord, and vascular cryptogamous plants (Tree-ferns, *Lepidodendra*, *Calamites*, *Sigillaria*, *Stigmaria*) still predominate.

In the carboniferous period isolated instances of the Lizards amongst Vertebrates and of Coniferae and Cycadiæ amongst plants had already made their appearance; but in the secondary period they obtained such a preponderance that the whole period has been named from them the period of Saurians and Gymnosperms. Amongst the first the colossal Dinosaurians living upon the land, the flying Lizards or Pterodactyls, the Halosaurians, with their best known genera *Ichthyosaurus* and *Plesiosaurus*, are entirely peculiar to the secondary period.

Examples of Mammalia, although scarce, are found in the upper Triassic beds, and also in the Jurassic. Such Mammalia belong without exception to the lowest grade of Marsupials. Flowering plants appear for the first time in the chalk, as do the oldest remains of distinctly bony fishes.

Flowering plants and Mammalia—and amongst the latter the highest order of Apes is represented—so preponderated in the tertiary period that it has been called the period of leafy forests and Mammalia. The plants and animals of the upper tertiary beds show a gradually increasing resemblance to those of the present time, the higher we ascend in the series. Numerous lower animals and plants are identical, not only generically but also specifically with those now living, and the genera and species of the higher animals have a greater resemblance to those of the present time. With the transition to the diluvial and recent epoch, the number and area of distribution of the higher types of flowering plants increase, and in every order of Mammalia we find forms whose structure is specialized more and more in definite directions, and which therefore appear more perfect. In the diluvial age we find the first unmistakable traces of the existence of Man. His history and the development of his civilization has occupied only the last portion of the recent period which has been relatively so short.

Despite its great incompleteness the geological record affords sufficient material to prove the existence of a progressive development from simple and lower grades of organization to higher, and to confirm the law of a progress towards perfection in the succession of the groups. We are indeed unable to make use of more than a small period of the time that has been occupied in this progress towards perfection of organisms, since the organic world of the most ancient and extensive periods has completely disappeared from the record.

If, after the above discussion, we consider the hypothesis of Transmutation of Species and of Descent to have a firm foundation on fact, we must concede a high value to Darwin's theory of Selection as an explanation of the manner in which the transmutation of species has been effected.

There are yet natural historians who admit the great changes which the animal and vegetable world have undergone, and yet combat the Darwinian principle of Selection, without being able to give any other explanation. The phenomena of gradual progress towards perfection agree very well with the theory of Selection.

Natural Selection leads, on the whole, to a progressive differentiation of organs (division of labour), since it preserves any peculiarities which are of use in the struggle for existence, and thus tends to the perfection of the organism. We can therefore connect the progress of simple types to higher ones with the principle of utility implied by Natural Selection, without being obliged, with Nägeli, to have recourse to the obscure notion of an inexplicable tendency towards perfection. It is the latter mystical supposition, and not Natural Selection, which is contradicted by the fact that we find a number of Rhizopods, Molluscs, and Crustacea (*e.g.*, the genera *Lingula*, *Nautilus*, *Limulus*) have existed almost without alteration from the earliest formations through all the geological periods to the present time, and by the observation of a retrogression of organization in the course of development (*e.g.*, retrogressive metamorphosis of Parasites).

Nor again can it be objected that on the hypothesis of Natural Selection the lower types should have been long ago suppressed and have become extinct, while, as a matter of fact, there are higher and lower genera in every class, and the lowest organisms are numerous and widely distributed. It is precisely the great variety in the degrees of organization which brings about and is favourable to the greatest development of life, all the forms of which, both the higher and the lower, being best suited to their peculiar circumstances are able, more or less perfectly, to occupy a special place in nature, and in a certain sense to maintain it. Even the most simple organisms occupy a place in the economy of nature which can be filled by no other organisms, and are necessary to the existence of numerous higher grades.

However well grounded we admit the theory of Selection to be, we cannot accept it as in itself sufficient to explain the complicated and involved metamorphoses which have taken place in organisms in the course of immeasurable time. If the theory of repeated acts of creation be rejected and the process of natural development be established in its place, there is still the first appearances of organisms to be accounted for, and especially the definite course which the evolution of the complicated and more highly developed organisms has taken has to be explained. In the many wonderful phenomena of the organic world, amongst others in the origin of Man in the diluvial or tertiary period, we have a riddle the solution of which must remain for future investigators.

SPECIAL PART.

CHAPTER VI.

PROTOZOA.

Animals of simple constitution and small size ; without tissues composed of definite cells. Sexual reproduction by means of ova and spermatozoa unknown.

From a morphological point of view the Protozoa have remained at the stage of cells, in the protoplasm of which one or more nuclei may be present. The phenomena of segmentation of the egg and formation of the germinal layers are therefore absent from their development. The body is always composed of a contractile granular substance, filled with vacuoles ; it may also contain a *pulsating vacuole*, and present the phenomenon of granule currents. The *pulsating vacuole* consists of a space without walls filled with a clear fluid. This space apparently diminishes and disappears through the contraction of the surrounding plasma, and then re-appears.

There exists, however, in the varying differentiations in the interior of the sarcode body, and in the differences in the external boundary, and in the manner of nourishment, a number of modifications which we shall use for the foundation of groups. In the simplest cases, the entire body consists of a small lump of sarcode, the contractility of which is confined by no firm external membrane. This lump of sarcode is sometimes semi-fluid, and protrudes and retracts processes. It is sometimes of tougher consistence in parts, and protrudes hair-like rays and threads (*Rhizopoda*). Nourishment takes place through the intussusception of extraneous bodies, which can be surrounded and enclosed by the protoplasmic substance at any portion whatsoever of the periphery of the body. In other cases the body which sends out slender processes (*pseudopodia*) secretes silicious or calcareous needles, lattice-work shells, or shells perforated

by holes, to shelter and protect the body (*Foraminifera*, *Radiolaria*). In the *Infusoria* the sarcode body is bounded by an external membrane, and is capable of quick and varied locomotion by means of the movements of the cilia, hairs, bristles, etc., which it possesses. The solid nourishing matter is taken in through a mouth, and the remainder, after digestion, passes out through an anal aperture.

CLASS I.—RHIZOPODA.*

Protozoa without external investing membrane, the parenchyma of which protrudes and retracts processes; as a rule, a calcareous shell or silicious skeleton is secreted.

The body-substance of these animals, the shells of which were described as *Foraminifera* or *Polythalamia*, long before their living contents were known, consists of *sarcode*, and is without any boundary membrane.

The body-substance, which is richly granulated and contains pigment, contracts slowly and sends out at the same time fine thread-like rays (fig. 120), for the most part of a semi-fluid consistency

FIG. 120.—Optical section through portion of the sarcode body of *Actinosphaerium Eickhornii* (after Hertwig and Lesser). *N*, nuclei in the endosarc, from which the vacuolated ectosarc is clearly distinguishable. In the centre of the pseudopodia the axial thread is visible.

(*pseudopodia*); and these serve not only as a means of movement but also for the reception of nourishment. The pseudopodia may, how-

* Dujardin, "Observations sur les Rhizopodes" (*Comptes rendus*, 1835). Ehrenberg, "Über noch jetzt zahlreich lebende Thierarten der Kreidebildung und den Organismus der Polythalamien" (*Abhandlung der Akad. zu Berlin*, 1839). Max Sigm. Schultze, "Über den Organismus der Polythalamien" (Leipzig, 1854). Joh. Müller, "Über die Thalassicolen, Polycystinen und Acanthometren" (1858). E. Haeckel, "Die Radiolarien" (Eine Monographie. Berlin, 1862).

ever, be broad, lobed, or finger-like processes by means of which a quick and flowing motion can be imparted to the body mass. A tougher, clear homogeneous external layer (*Exoplasm*) is usually to be distinguished as the peripheral boundary from a more fluid and more granular internal mass (*Endoplasm*). During motion the former is projected in processes into which the granules of the latter stream more or less quickly.

In the stiffer pseudopodia streams of granules are observable, slow but regular, passing from the base to the extremity and *vice versa*. The explanation of these movements is to be sought in the contractility of the surrounding portions of sarcode (fig. 120).

A pulsating space, the contractile vacuole, is not unfrequently to be found in the sarcode, e.g., *Diffugia*, *Actinophrys*, *Arcella* (fig. 121). Nuclei are also usually present in the sarcode, by which the morphological value of the Rhizopod body as cell or as cell aggregate is

placed beyond all doubt. There are also forms in the protoplasm of which no trace of a cell nucleus has been found. In such either the protoplasm of the nucleus is not yet differentiated as a separate structure (the Monera of E. Haeckel), or we have to do with a transient, non-nucleated stage in the life-history.

The sarcode usually secretes silicious or calcareous structures, either as fine spicula and hollow spines which are directed from the centre to the periphery in regular order and number, or as lattice-work chambers (*Radiolaria*), which often bear points and spines, or finally

FIG. 121.—*Amœba* (*Dactylosphæra*) *poly-podia* (after Fr. E. Schultze). *N*, Nucleus. *Pv*, pulsating vacuole.

as single and many chambered shells with finely perforated walls (*Foraminifera*) and one larger opening. Through this last (fig. 123), as well as through the countless pores of the small shells (fig. 122), the slender threads of sarcode pass out to the exterior as pseudopodia, changing without intermission in form, size, and number, and often joining themselves together in delicate networks (figs. 122, 123).

The pseudopodia, by their slow, creeping movements, afford a means of locomotion, while they also serve for the taking up of nourishment

by surrounding and transporting into the interior of the body small vegetable organisms as *Bacillaria*. Among the shell-bearing forms, the reception and digestion of food takes place outside the shell in the peripheral threads and networks of sarcode; for each spot on the surface can for the time being assume the functions of mouth, and

✓ FIG. 122.—*Rotalia venata* (after M. Schultze), with a Diatom taken in the network of Pseudopodia.

also of anus, by rejecting the undigested remnants. The Rhizopoda live for the most part in the sea, and contribute by the accumulation of their shells to the formation of the sea sand, and even to the deposition of thick strata. An innumerable quantity of fossil forms from various and very ancient formations are known.

Order 1.—FORAMINIFERA.*

Rhizopoda, either naked or with a shell, the shell almost invariably calcareous and usually pierced with fine pores for the exit of the pseudopodia.

Only in rare cases, for instance *Nonionina* and *Polymorphina*, is the shell substance of a silicious nature; in all other forms it is

✓ FIG. 123.—*Miliola tenera*, with network of pseudopodia (after M. Schultze).

membranous or consists of a calcareous deposit in a basis of organic matter. The shell is either a simple chamber, usually provided with a large opening, or is many chambered, that is, is composed of numerous chambers arranged upon one another according to definite laws. The spaces of these chambers communicate by means of narrow

* Besides D'Orbigny, Max Schultze, l. c., compare W. C. Williamson, "On the recent Foraminifera of Great Britain," London, 1858. Carpenter, "Introduction to the Study of the Foraminifera," London, 1862. Reuss, "Entwurf einer system. Zusammenstellung der Foraminiferen," Wien, 1861.

passages and large openings in the partition walls. In like manner those portions of the living sarcode body which are enclosed in the individual chambers are in direct communication with one another by means of processes which pass through the passages and openings in the septa, and connect one portion with another. The quality of the body-substance, the mode of movement and nourishment, agree closely with those which have been depicted as characteristic of the order. Our knowledge of the mode of reproduction is imperfect. Amongst the forms without a shell, fission has been observed as well as fusion, which may perhaps be referred to a species of sexual reproduction (*conjugation*). The reproduction of shell-bearing Foraminifera such as *Miliola* and *Rotalia* has also been observed. The former produces from the protoplasm of its body single chambered, the latter three-chambered, young. Probably this mode of reproduction is preceded by an increase in the number of nuclei, and the animal divides into as many portions as there are nuclei, each of which becomes a young Foraminifer, and contains but one nucleus.

In spite of their small size, the shells of our simple organisms may lay claim to no small consequence, since they not only accumulate in enormous quantity in the sea sand (M. Schultze calculated their number for an ounce of sea sand from Molo di Gaëta at about one and a half millions), but are also found as fossils in different formations (the cretaceous and tertiary), and have yielded an essential material to the construction of rocks. Silicious nodules of *Polythalamia* are even found in Silurian deposits. The most remarkable, on account of their considerable size, are the *Nummulites* (fig. 124) in the thick formation of the so-called Nummulite limestone (Pyrenees). A coarse chalk of the Paris basin, which makes an excellent building stone, contains the *Triloculina trigonula* (*Miliolite chalk*).

The greater number of Foraminifera are marine, and move by creeping on the bottom of the sea, but *Globigerina* and *Orbulina* have been met with on the surface. The bottom of the sea at very considerable depths is also covered with a rich abundance of forms, especially with *Globigerina*, the remains of the shells of which give rise to an enduring deposit.

1. Sub-order: **Lobosa** (*Amœbiformes*).—Amœba-like fresh-water Rhizopoda, usually with pulsating vacuole, sometimes naked, sometimes with a single-chambered firm shell. The sarcode body consists as a rule of a tougher exoplasm and a fluid granular endoplasm. The pseudopodia are lobed or finger-shaped processes of considerable

size, occasionally tougher slender processes without granule streams (figs. 125 and 126).

Amœba princeps Ehrbg., *A. terricola* Greef., *Petalopus difflugiens* Clap. Lachm. Here should also be placed the famous *Bathybius Haeckeli* Huxl., which is found in the deep sea mud of the Atlantic Ocean, if it is indeed a living organism (and not simply a deposit of Gypsum).

Arcella vulgaris Ehrbg., *Difflugia proteiformis* Ehrbg., *Euglypha globosa* Cart. have shells and tough, pointed, dichotomously branching pseudopodia (fig. 125).

FIG. 124. — Nummulitic Limestone, with horizontal section of *N. distans* (after Zittell).

FIG. 126. — *Difflugia oblonga* (after Stein).

✓ FIG. 125. — *Euglypha globosa* (after Hertwig und Lessee).

✓ FIG. 127. — *Acervulina globosa* (after M. Schultze).

2. Sub-order: **Reticularia** (*Thalamophora*). Principally marine Rhizopods with extremely slender anastomosing pseudopodia, with granule streams in the latter, rarely naked (*Protogenes*, *Lieberkühnia*), usually with membranous or calcareous shell, which is single-chambered (*Monothalamia*) or many-chambered (*Polythalamia*) (fig. 127).

1. *Imperforata*. With membranous or calcareous shell, which is without fine pores, but possesses, in one place, an opening, either simple or sieve-like, through which the pseudopodia project. To these belong the *Gromiæ*, with a membranous chitinous shell: *Gromia oviformis* Duj., and *Miliolidæ*, with a porcellaneous shell: *Cornuspira planorbis* M. Sch., *Miliola cyclostoma* M. Sch., from the Miliolite chalk.

2. *Perforata*. The shell, which is usually calcareous, is invariably pierced with innumerable fine pores as well as by one larger opening, and has complicated passages in the partition walls of its chambers.

The *Lagenidæ* have a hard shell, with a large opening surrounded by a toothed lip: *Lagena vulgaris* Williamson.

The *Globigerinidæ* on the contrary have a hyaline shell pierced by large pores, and a simple slit-like opening: *Orbulina universa* D'Orb., *Globigerina bulloides* D'Orb., *Rotalia* D'Orb., *Textularia* D'Orb.

The greatest size is attained by the *Nummulinidæ*, which possess a firm shell and an internal skeleton, which last is pierced by a complicated canal system: *Polystomella* Lam., *Nummulina* D'Orb.

FIG. 123.—Young *Actinosphaerium*, still with a single nucleus (after F. E. Schultze). N, Nucleus.

Order 2.—HELIOZOA.*

Fresh-water Rhizopods usually with pulsating vacuole, and one or more nuclei. A radial silicious skeleton sometimes present.

The sarcode body sends out in all directions tough radiating pseudopodia (fig. 128). When a skeleton is secreted, it consists either of radially arranged silicious spines (*Acanthocystis*) or of latticed silicious shells (*Clathrulina*), and so closely resembles the skeleton of the Radiolaria that the Heliozoa have been actually described as *fresh-water Radiolaria*.

They differ from the Radiolaria in the absence of the complicated

* L. Cienkowski, "Ueber *Clathrulina*." *Archiv. für mikrosk. Anatomie*, Tom III., 1867. R. Greeff, "Ueber Radiolarien und radiolarienähnliche Rhizopoden des süßsen Wassers." Tom V. & XI. R. Hertwig und Lesser, "Über Rhizopoden und denselben nahe stehende Organismen." Suppl. Tom X., 1874. Also Archer and F. E. Schultze, etc.

differentiations of the sarcode, particularly of the central capsule. One or more nuclei may be present in the central mass. An important distinguishing mark is afforded by the presence of the pulsating vacuoles, which have not been observed in any marine Radiolarian.

The reproduction very frequently takes place by fission, occasionally

FIG. 123.—*Thalassicolla pelagica*, with central capsule and single large nucleus, also numerous alveoli in the protoplasm (after E. Haeckel).

after previous conjugation of one or more individuals, also during encystment. Multiplication by spores has also been observed (*Clathrulina*).

In the *Actinophryidæ* there is no skeleton secreted: *Actinosphærium Eichhornii* Ehrbg. The central matter contains numerous nuclei. *Actinophrys sol* Ehrbg. of small size, with a single central nucleus.

In the *Acanthocystidæ* slender silicious spikes are found: *Acanthocystis spinifera* Greeff. with silicious spikes and needles.

In *Clathrulina* there is a latticed silicious shell, and the body has a stalk *Clathrulina elegans* Cienk.

Order 3.—RADIOLARIA.*

Marine Rhizopoda with complicated differentiation of the sarcode body, with central capsule and radial silicious skeleton.

The sarcode body contains a membranous porous capsule (the *central capsule*), in which is contained a tough slimy protoplasm with vacuoles and granules (*intracapsular sarcode*), fat and oil globules, and albuminous bodies, and more rarely crystals and concretions. The intracapsular mass contains also a single large nucleus or several small nuclei. The sarcode which surrounds the capsule and which emits on all sides simple or anastomosing pseudopodia, contains numerous yellow cells, sometimes pigment masses; and in some cases delicate transparent vesicles, or alveoli, are found in the peripheral layer between the radiating pseudopodia (*Thalassicola pelagica*, fig. 129).

Many Radiolaria form colonies, and are composed of numerous individuals. In such colonies the alveoli are placed in the common protoplasm, which contains in itself, not as in the monozoic Radiolaria a single central capsule, but a number of capsules. Only a few

FIG. 130.—*Acanthometra Mülleri* (after E. Haeckel).

species remain naked and without firm deposits; as a rule, the soft body possesses a silicious skeleton, which either lies entirely outside the central capsule (*Ectolithia*) or is partially within it (*Entolithia*). In the most simple cases the skeleton consists of small, simple, or toothed silicious needles (spicula) united together, which sometimes give rise to a fine sponge work round the periphery of the protoplasm, e.g., *Physematium*. In a higher grade we find stronger hollow silicious spicules, which radiate from the middle point of the body to the periphery in regular number and order, e.g., *Acanthometra*

* Joh. Müller, "Ueber die Thalassicollen, Polycystinen und Acanthometren," *Abh. der Berl. Akad.* 1858. E. Haeckel, "Die Radiolarien," Eine Monographie Berlin, 1862.

(fig. 130). A fine peripheral framework of spicules may be added to these. In other cases simple or compound lattice-works, and pierced shells of various external form (like helmets, bird-cages, shells, etc.) are found, and on the periphery of these, spicules and needles, and even external concentric shells of similar shape may be formed, e.g., *Polycystina* (figs. 131 and 132).

Up to the present time but little has been made out about the reproduction of these animals. Besides fission (*Polycyttaria*), the formation of spores has been observed. These are formed from the contents of the central capsule, and, after the bursting of the latter, become free-swimming mastigopods. Radiolaria are inhabitants of

the sea, and swim at the surface, but are also able to sink to deeper levels.

Fossil remains of Radiolaria have been made known in great numbers by Ehrenberg, e.g. from the chalky marl and polishing slate found at certain parts of the coast of the Mediterranean (Caltanissetta in Sicily, Zante and Ægina in Greece), and in particular from the rocks of Barbados and Nikobar, where the Radiolaria have given rise to widely

✓ FIG. 131.—*Heliosphæra echinoides* (after E. Haeckel).

extended rock formations. Samples of sand also from very considerable depths have shown themselves rich in Radiolarian shells.

I. *Radiolaria monozoa*. Radiolaria which remain solitary.

1. Fam. **Thalassicollidæ**. Skeleton absent or consisting of single spicules not joined together. *Thalassicolla* (without skeleton) *nucleata* Huxl., *Physematium Müller*i Schn.

2. Fam. **Polycystinidæ**. The skeleton consists of a simple or divided latticed shell, the long axis of which is bounded by two poles of different structure. *Heliosphæra*. *Eucyrtidium galea* E. Haeck.

3. Fam. **Acanthometridæ**. The skeleton consists of several radial spicules which pass through the central capsule and unite in its centre, without forming

a latticed shell. The extra-capsular cells [yellow bodies] are wanting. *Acanthometra pellucida* Joh. Müll.

II. *Polycyttaria*. Radiolaria which form colonies with several central capsules. Amongst the Sphærozoa a skeleton is wanting or consists of single pieces not joined together. *Collozoum inerme* E. Haeck. *Sphærozoum punctatum* Joh. Müll. In *Collosphæra* the skeleton consists of simple latticed spheres, each of which encloses a central capsule, *Collosphæra Hurleyi* Joh. Müll.

FIG. 132.—*Eucyrtidium cranoides* (after E. Haeckel).

CLASS II.—INFUSORIA.*

Protozoa with a definite form and provided with an external membrane, bearing either flagella or cilia. Mouth and anus usually, contractile vacuole and one or more nuclei always present.

Infusoria were discovered towards the end of the 17th century

* Ehrenberg, "Die Infusionsthierchen als vollkommene Organismen," 1838. Balbiani, "Études sur la Reproduction des Protozoaires," *Journ. de la Phys.*, Tom. III. Balbiani, "Recherches sur les phénomènes sexuels des Infusoires,"

in a vessel of stagnant water by A. von Leeuwenhoek, who made use of a magnifying glass for the examination of small organisms. The name Infusoria, which was at first used to denote all animalculæ which appear in infusions and are only visible with the aid of a microscope, was first brought into use by Ledermüller and Wrisberg in the last century. Later on the Danish naturalist O. Fr. Müller made valuable additions to our knowledge of Infusoria. He observed their conjugation and their reproduction by fission and gemmation, and wrote the first systematic work on the subject. O. Fr. Müller included a much larger number of forms than we do now-a-days, for he placed among the Infusoria all invertebrate water animalculæ without jointed organs of locomotion and of microscopical size.

The knowledge of Infusoria received a new impulse from the comprehensive researches of Ehrenberg. The principal work of this investigator, "Die Infusionsthierchen als vollkommene Organismen," discovered a kingdom of organisms hardly thought of. These were observed and portrayed under the highest microscopic powers. Many of Ehrenberg's drawings may even yet be taken as patterns, and are hardly surpassed by later representations, but the significance of the facts observed has been essentially corrected by more recent investigations. Ehrenberg also conceded too great an extent to the group of Infusoria, including not only the lowest plants such as *Diatomaceæ*, *Desmidiaceæ*, under the name of *Polygastrica anentera*, but also the much more highly organised *Rotifera*. As he chose the organization of the last-named for the basis of his explanations, he was led into numerous errors. Ehrenberg ascribed to the Infusoria mouth and anus, stomach and intestines, testis and ovary, kidneys, sense-organs, and a vascular system, without being able to give reliable proofs of the nature of these organs. There very soon came a reaction in the way of regarding the Infusorian structure; for the discoverer of the *Rhizopoda*, Dujardin, as well as von Siebold and Kölliker (the latter taking into consideration the so-called *Nucleus* and *Nucleolus*), referred the Infusorian body to the simple cell. In the subsequent works of Stein, Claparède, Lachmann, and Balbiani numerous differentiations were certainly shown to exist, which, however, can all be referred to differentiation of the body of the cell. This view is supported by

Journ. de la Phys., Tom. IV. Claparède und Lachmann, "Études sur les Infusoires et les Rhizopodes," 2 vol. Genève, 1858—1861. E. Haeckel, "Zur Morphologie der Infusorien" *Jen Zeitschrift*, Tom. VII., 1873. O. Bütschli, "Studien über die ersten Entwicklungsvorgänge des Eizelle, die Zelltheilung und die Conjugation des Infusorien," Frankfurt, 1876.

the more recent work of Bütschli, who has shown that the reproduction of these animals is essentially similar to that of the cell.

The outer boundary of the body is usually formed by a cuticle, a delicate, transparent membrane, the surface of which is beset with vibratile and moving appendages of various kinds arranged in regular order. In the smallest Infusoria, the *Flagellata*, we find only one or two long whip-like cilia; while the more highly differentiated *Ciliata* are usually richly provided with cilia. According to the varying thickness of the external membrane, which cannot in all cases be isolated, and according to the different condition of the peripheral parenchyma of the body, we get forms which change their shape, forms which have a fixed shape and armoured forms. If the simply organized Flagellata, which present numerous affinities and transitional forms to the Algæ and Fungi, are not entirely removed from the region of the Infusoria, the two principal groups to be distinguished are the *Ciliata* and *Flagellata*.

Order 1.—FLAGELLATA.*

Infusoria of small size, characterised by possessing one or more long whip-like cilia, usually placed at one end of the oval body. A row of cilia sometimes and a nucleus always present.

The Flagellata are Infusoria the locomotive organs of which consist of one or more whip-like cilia, rarely with an accessory row of cilia. They pass through an inactive stage, and in their development as well as in their mode of nourishment are allied to certain Fungi.

The reasons for regarding the Flagellata as Protozoa are—the perfect contractility of the body, which is not surpassed by Myxomycetes in the mastigopod stage; also the contractility of the cilia, the apparently purposed and voluntary movements, the occurrence of *contractile vacuoles*, and, as has been established in many cases, the reception of solid substances into the body through an opening at the base of the flagellum. Nevertheless these phenomena are by no means a test of animal organization.

The *Monadinae* are a large group of Flagellata, found for the most part in putrefying infusions, and are hard to distinguish from the monads usually regarded as fungi. They reproduce themselves by

* Besides Ehrenberg, Claparède, and Lachmann, loc. cit., compare Stein, "Organismus der Infusionsthier," Tom. III., 1878. Bütschli, "Beiträge zur Kenntniss der Flagellaten," *Zeitschr. für Wiss. Zool.*, Tom. XXX. Dallinger and Drysdale, "Researches on the Life-history of the Monads," *Monthly Microscop. Journal*, Tom. X.—XIII.

transverse fission, and also by spore formation in an encysted condition; the latter method seems in many forms to be preceded by conjugation. The best known species are *Cercomonas* Duj. and *Trichomonas* Donné, of which the first is characterised by the possession of a caudal filament, while *Trichomonas* has an undulating row of cilia close to the flagella, which are usually two in number (fig. 133). They live principally in the intestines of Vertebrates, but are also found in Invertebrates. *Cercomonas intestinalis* Lambl. and *Trichomonas vaginalis* Donné, are found in Man.

The *Monads*,* which cannot be sharply separated from the *Monadinae*, are simple cells free from chlorophyll, the swarm spores of which usually pass into an amœboid stage, and after receiving nourishment enter upon a motionless stage characterised by the possession of a firm cell-membrane. A number of them (*Monas*, *Pseudospora*, *Colpodella*), the so-called *Zoospores*, are mastigopods resembling the

FIG. 133.—a, *Cercomonas intestinalis*.
b, *Trichomonas vaginalis* (after R. Louckart).

mastigopods (swarm spores) of Myxomycetes, and, with the exception of *Colpodella*, grow up to creeping Amœbæ which protrude pointed pseudopodia. In this stage they may also be simply regarded as small plasmodia, especially when, as in *Monas amyli*, several mastigopods fuse together to form the amœba. They then take—in *Colpodella* without first entering the amœba stage—a globular form, their surface develops a membrane, and in this cyst they break up by division of protoplasm into a number of segments which pass out as swarm spores and repeat the course of development (*Colpodella pugnax* to *Chlamydomonas*, *Pseudospora volvocis*).

Other Monads, the so-called *Tetraplasta* (*Vampyrella*, *Nuclearia*), do not pass through the mastigopod (swarm spore) stage. Their protoplasm during the inactive encysted stage gives rise by division into two or four, to the same number of Actinophrys-like Amœbæ, of which some, like *Colpodella*, suck their nourishment from alga cells (*Spirogyra*, *Oedogonia* Diatomacea, etc.), and some envelope extraneous bodies.

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In mode of nourishment and locomotion the monads are allied to the Rhizopods, but also to lower fungus forms like *Chytridium*.

* L. Cienkowski, "Beiträge zur Kenntniss der Monaden," *Archiv für Microsk. Anatomie*, Tom. I., 1865. L. Cienkowski, "Über Palmellaceen und einige Flagellaten," Tom. VI., 1870.

In their whole developmental cycle they agree very closely with unicellular algæ and fungi; still the analogy to the developmental processes of many Infusoria, *Amphileptus*, is not to be passed over. *Spumella vulgaris* (termo Ehrbg.) of Cienkowski shows a somewhat different development and cyst formation; it receives solid food (by aid of the food vacuoles) and is fixed by a fibre, as also *Chromulina nebulosa* Cnk., and *Ochracea* Ehrbg.

A second group nearly allied to the Algæ (*Protococcaceæ*) is that of the *Volvocinidæ*. These organisms consist of colonies of cells united by a common gelatinous substance, and the following characteristics indicate their close relationship to the Algæ:—(1) in the inactive stage they possess a cellulose membrane; (2) they exhale oxygen; (3) they possess an abundance of chlorophyll and of vegetable red or brown coloured oils.

✓ FIG. 134.—*Euglena viridis*. *a* and *b*, free swimming, in different states of contraction. *c*, *d*, *e*, encysted and in process of division.

During the motile stage they possess the power of reproduction, since the individual cells give rise to daughter colonies inside the mother colony. A sexual reproduction (conjugation) has also been shown. Certain of the mother cells increase in size and divide into numerous microgonidia corresponding to spermatozoa; others grow to large ovicells, which are impregnated by the former, and then surround themselves with a capsule, and sink to the ground as large star-shaped cells. They also reproduce themselves during their period of inactivity by fission within the cellulose capsule, while at the same time a change of colour takes place. Amongst the best known of the Volvocina are *Volvox globator*, *Gonium pectorale*, *Staphanosphæra pluvialis*.

The *Astasiadæ* are contractile unicellular *Flagellata*, which are allied to the *Volvocinidæ* in their life phenomena, but they take up

solid nutriment. The best known genus is *Euglena*, which, according to Stein, has a mouth and gullet.

In their inactive stage they secrete a capsule and divide up into parts which pass out as mastigopods. *Euglena viridis* (fig. 134), *E. sanguinolenta*. Another genus, also with a mouth, is *Astasia* Ehrbg. *A. trichophora* Ehrbg., with rounded posterior end, a very long flagellum, and an abruptly terminated anterior end.

The genera *Salpingoeca* and *Codosiga* described by Clark were included by Bütschli under the name *Cylicomastiges*, on the ground that they possess a well-marked collar surrounding the basis of the flagellum, and corresponding to the collar on the entoderm cells of the Sponges (hence Clark regarded the Sponges as most nearly related to the Flagellata); *Codosiga Botrytis* Ehrbg, forming colonies, possessing food vacuoles which contain the solid bodies taken up as nutriment, with nucleus and contractile vacuole.

Salpingoeca Clarkii Bütsch. (the individuals of this species possess a shell).

Another group, the *Cilioflagellata*,* is characterised by the possession of a row of cilia, situated in a furrow of the hard cuticular exoskeleton (fig. 135), in addition to the flagellum. The *Peridiniæ*, some of which are of peculiar appearance,

with large horned processes of the shell, belong to the group, and are allied, so far as their development is known, most nearly to the *Euglenæ*. The mouth lies in a depression; there is sometimes a kind of gullet, at the end of which the nourishing materials pass into a vacuole. In addition to the locomotive and armoured forms, there are also some without shell or organs of locomotion; and again there are encysted stages in the interior of which a number of small young forms are said to take their origin (*Ceratium cornutum* Perhgw., *Peridinium tabulatum* Ehrbg).

Finally *Noctiluca* † is included in this group. It is an inhabitant

FIG. 135.—*Ceratium tripos* (after Nitzsch).

* R. S. Bergh, "Der Organismus der Cilioflagellaten," *Morph. Jahrb.* Tom. VII.

L. Cienkowski, "Ueber *Noctiluca miliaris*," *Archiv. für microsk. Anatomie*, 1871 and 1872.

of the sea, and possesses a peach shaped body which is surrounded by a cuticular envelope, and bears a tentacle-like appendage. A furrow-like invagination is situate at the base of this appendage, at one end of which is the mouth close to a tooth-like prominence and a slender vibratile flagellum. The soft body consists of a central mass of contractile protoplasm, connected by fine and anastomosing threads with a layer of the same substance which lines the cuticular envelope of the body. In the central protoplasm lies a clear body, the nucleus; and the spaces between the radiating processes, which exhibit the phenomena of granule currents, are filled with fluid. The contractile substance extends into the appendage, and there assumes a cross-striped appearance (fig. 136).

FIG. 136.—*Noctiluca miliaris* (partly after Cienkowski). *N*, Nucleus. *a*, Single animal. *b*, conjugation of two individuals. *c* and *d*, swarm spores.

The reproduction takes place by means of fission (Brightwell), preceded by division of the nucleus; or by spore formation (Zoospores). In the latter case, the flagellum is absorbed or thrown off, and the Noctiluca assumes a spheroidal shape. After the disappearance of the nucleus, the sarcode contents accumulate on the inner side of one region of the cuticle, divide into from two to four masses which are not sharply separated from one another, and the cuticular envelope is thrust out into a corresponding number of protuberances. These buds increase and form numerous wart-like prominences, the future spores. They arise, therefore, at the expense of the protoplasmic contents of the disc, which is gradually exhausted in their for-

mation. The buds separate themselves from the membrane and become free as small spores, with nucleus and cylindrical appendage, to assume the *Noctiluca* form under circumstances which have as yet not been closely observed. According to Cienkowski, conjugation may take place between normal forms as well as between encysted forms.

The *Noctiluca* owe their name to their power of producing light, —a power which they share with numerous sea animals, such as *Medusæ*, *Pyrosoma*, etc. The light proceeds from the peripheral layer of protoplasm. Under certain conditions they rise from the deep to the surface of the sea in such enormous numbers as to cause wide tracts of the sea to give out a reddish light. It is after sunset, and especially in the evening, when the sky is overcast, that we get the beautiful phenomenon of the phosphorescent sea.

The species distributed in the North Sea and in the Atlantic Ocean is *Noctiluca miliaris*. Nearly allied is the Mediterranean *Leptodiscus medusoides* R. Hertwig.

FIG. 137.—*Stylonychia mytilus* (after Stein), (seen from ventral side). *Wz*, Adoral zone of cilia; *C*, contractile vacuole; *N*, nucleus; *N'*, paranucleus; *A*, anus.

Order 2.—CILIATA.*

Ciliated Infusoria with mouth and anus, sarcode body of complicated structure (with endoplasm and exoplasm), with nucleus and paranucleus (nucleolus).

The locomotive cuticular appendages that we most frequently meet with are slender cilia, which often cover the whole surface of the body in close rows, and give it a striped appearance. The cilia are usually stronger in the region of the mouth, and are here grouped so as to form an *adoral zone* of large cilia, which, during swimming, causes a whirlpool, and conducts the matter which serves as nourishment into the mouth (fig. 137). This adoral zone is more highly developed in fixed Infusoria such as the *bell animalcule*, the surface of which has no uniform coating of cilia. In these animals there are

* Besides Ehrenberg, Claparède, Lachmann, Bütschli, l. c., compare especially Fr. Stein, "Der Organismus der Infusionsthier," I. and II., Leipzig, 1859 and 1867.

one or more rings of large cilia round the edge of a raised lid-like flap which is capable of being shut down. There is also an inferior row of cilia upon this flap running to the mouth. The free-swimming Infusoria often possess in addition to these delicate cilia and zones of cilia, thicker hairs and stiff bristles, and more or less bent hooks, which are employed in locomotion and for attachment.

Certain fixed Infusoria as *Stentor* (fig. 138) and *Cothurnia* secrete external coverings or shells, into which they retract themselves. Nourishment is taken in in a few cases by endosmosis through the whole surface of the body, e.g., the parasitic *Opalina*. The *Acineta* feed themselves by sucking the body of their prey. They are without a mouth, and are incapable of taking in solid food. But they possess a number of long, narrow, contractile tentacles, which radiate from the surface of their bodies, and have the form of delicate tubes, presenting a structureless external wall and a semi-fluid granular axis. The *Acineta* applies one or more of these organs to the body of an extraneous organism, when the substance of the latter travels down the interior of the granular axis of the tentacle into the body of the *Acineta* (fig. 139).

By far the greatest number of Infusoria possess an oral aperture, usually near the anterior pole of the body, and a second aperture which acts as anus, and which can be seen in a definite part of the body as a slit during the exit of the excreta.

The body parenchyma, which is bounded by the external membrane, is divided into a viscid exoplasm and a more fluid endoplasm, into

FIG. 138.—*Stentor Ræclii* Ehrbg. (after Stein). O, oral aperture with gullet; PV, pulsating vacuole; N, nucleus.

FIG. 139.—*Acineta ferrugineum* Ehrbg., which is sucking the body of a small Infusorian (*Enchelys*) (after Lachmann). T, sucking tentacle; V, vacuole; N, nucleus.

which a slender œsophagus, rarely supported by firm rods (*Chilodon*, *Nassula*), often projects (fig. 140). Through this the food stuff passes into the endoplasm, in which it gives rise to food vacuoles. The latter undergo a slow rotating movement round the body in the endoplasm, which is caused by the contractility of the sarcode. During this process the food is digested, and finally the solid, useless remainder is ejected through the anal aperture. A digestive canal, bounded by distinct walls, exists no more than do the numerous stomachs which Ehrenberg, who was deceived by the food vacuoles, ascribed to his *Infusoria polygastrica*. In all cases where a digestive canal has been described, we have to do with peculiar strings and trabeculae of the internal parenchyma which enclose spaces filled with a clear fluid.

FIG. 140.—*Chilodon cucullus* (after Stein), with gullet resembling a fish-basket. *N*, nucleus with nucleolus; excreta are passing out of the anus.

The more viscid exoplasm is pre-eminently to be regarded as the motor and sensory layer of the body. In it we find differentiations resembling muscles (*Stentor*, the stalk of *Vorticella*). Sometimes small rod-shaped bodies are present (e.g., *Bursaria leucas*, *Nassula*), which are comparable to the thread cells of *Turbellaria* and *Cœlenterata*. The contractile vacuoles appear as further differentiations of the external layer, structures which to the number of one or more are found in quite definite portions of the body. They are clear, mostly spherical spaces filled with a fluid; they diminish suddenly and then vanish, but gradually reappear and increase to their original size. These pulsating vacuoles are usually connected with one or more vessel-

like lacunæ, which swell considerably during the contraction of the vacuole. These structures have been compared to the water vascular system of *Rotifera* and *Turbellaria*, and have been explained as excretory—an interpretation which has in its favour the fact that the contractile vacuoles in certain cases open to the exterior through a fine pore at the surface, through which granules pass to the exterior.

The *nucleus* and *nucleolus* lie in the exoplasm of the infusorian body. The *nucleus*, which ten years ago was compared to the nucleus of the simple cell, is a structure of variable shape but with a definite position in the body. One, or more than one, may be present. It is sometimes round or oval, sometimes elongated, being drawn out

to the shape of a horse-shoe or a band, and may be broken up into a number of fragments. It contains a granular viscid substance, is bounded by a delicate membrane, and, according to the erroneous views of Stein and Balbiani, gives rise to ova or to germinal spores. The *nucleolus* or paranucleus also varies in form, position, and number in different species. It is always much smaller than the nucleus, and is strongly refractile; it usually lies close to the nucleus, or even sunk in a cavity of the latter. Both play an important part in the reproduction of the Infusoria.

The most usual method of reproduction in the Infusoria is by fission. When the forms reproduced remain together and connected with the parent, a colony of Infusoria is formed, *e.g.*, the stocks of *Epistylis* and *Carchesium*. Fission usually takes place by a transverse division (at right angles to the long axis), as in the *Oxytrichidæ*,

FIG. 141.—*a*, *Aspidisca lynceaster* (after Stein). *b*, *Aspidisca polystyla*, during fission (after Stein).

FIG. 142.—*Podophrya gemmipara* (after R. Hertwig). *a*, with extended suction-tubes and prehensile tentacles, with two contractile vacuoles. *b*, the same with ripe buds, in which processes of the branched nucleus *N* enter. *c*, free young form.

Stentoridæ, etc., and, obeying definite laws, follows conjugation and division on the one hand of the nuclei, and on the other of the nucleoli (fig. 141). Less frequently (*Vorticella*) the fission takes place through the long axis (fig. 143, *a*, *b*), and far more rarely in a diagonal direction. The asexual reproduction is often preceded by encystment, which appears to be of great importance for the

preservation of the Infusoria from desiccation. The animal retracts its cilia, contracts its body to a globular mass, and then secretes a transparent cyst, which hardens and protects the animal, thus enabling it to survive in damp air. In the water, the contents of the cyst divide into a number of parts, which attain freedom by the bursting of the cyst, each one becoming a young animal.

Moreover, many Infusoria (*Acinetæ*) produce with participation of the nucleus a number of buds asexually, which separate themselves from the walls of the parent body (fig. 142). The broods of *Sphærophrya* make their way into the interior of other Infusoria,

as *Paramæcium* and *Stylonychia*, nourish themselves at the cost of the enlarged nucleus, and form embryos by fission. These embryos swarm out, and were for a long time taken by Stein for the embryo broods of *Stylonychia* (fig. 144, *b*).

The process of conjugation observed by Leeuwenhoek and O. Fr. Müller is very general, and is connected with changes of the nucleus and nucleolus. These changes, which gave rise to the erroneous interpretation of the

FIG. 143.—*Vorticella microstoma* (after Stein). *a*, In process of fission; *N*, nucleus; the mouth apparatus in each portion is formed afresh, *oe*, gullet. *b*, Fission is completed, the smaller product is set free after the formation of a posterior ring of cilia; *w*, adoral zone of cilia. *c*, *Vorticella* in process of bud-like conjugation; *K*, the bud-like individuals attached.

two structures as ovary and testis, are in reality simply preparatory to a process of regeneration of the nucleus by parts of the paranucleus, a process comparable to the phenomena of the fertilization of the ovum in sexual reproduction.

The conjugation of two Infusoria occurs in very different ways, and leads to a more or less complete fusion, which, after regeneration of the nucleus, is followed by an increase in the frequency of fission. *Paramæcium*, *Stentor*, *Spirostoma*, during conjugation, become con-

nected by their ventral surfaces; other Infusoria with a flat body like *Oxytrichina*, *Chilodon*, by their sides; while *Enchelys*, *Halteria*, *Coleps*, join together the anterior extremities of their bodies, giving the appearance of transverse fission. A lateral conjugation also takes place not unfrequently in *Vorticella*, *Trichodina*, etc., between individuals of unequal size, the smaller one having the appearance of a bud (bud-like conjugation) (fig. 143, c).

The alterations which the *nucleus* and *paranucleus* undergo during and after conjugation have been especially worked out in *Paramœcium* and *Stylonychia* (fig. 144 a, 145). When several nuclei are present they

FIG. 144.—a, *Stylonychia mytilus*, in process of conjugation. The nucleus is depicted during division (Balbiani's so-called ova); the nucleoli have divided into four spheres (supposed spermcapsules). b, *Stylonychia* filled with parasitic *Sphaerophrya* (after Balbiani).

FIG. 145.—*Stylonychia mytilus* in process of conjugation, slightly magnified, (treated with acetic acid), (after Bütschli). a, Stage of conjugation with two nucleoli (paranuclei); Nb, the four pieces into which the nucleus has divided in each individual. b, Stage of conjugation with four nucleoli, of these N' becomes the nucleus, and n' the two nucleoli; Nb, the four remaining pieces of the old nucleus. c, *Stylonychia* on the sixth day after conjugation with nucleus and two nucleoli.

fuse together to form a single oval body (Balbiani), the substance of which takes a finely fibrous structure previous to further fission,

like the substance of a true cell nucleus, when undergoing division.

✓ FIG. 146. — *Paramæcium Bursaria* about one hour after conjugation (after Bütschli). *n*, nucleolus; *N*, nucleus; *PV*, contractile vacuole. Two of the nucleoli have become clear spheres.

The paranucleus too increases in size and becomes striated, and divides into a number of bodies by a single or repeated division. Some of these bodies produced by the division of the nucleus and paranucleus disappear or are cast out, and others are employed in the formation of the new nucleus and paranucleus. The processes of regeneration are for the most part not completed until the conjugating animals have separated. Conjugation is probably followed by a repeated division (fig. 146).

The mode of life of the Infusoria, which principally inhabit fresh water, is very various. Most of them lead an independent life, and take up larger or smaller bodies, even Rotifera, as nourishment. Some, as *Amphileptus*, select fixed Infusoria, as *Epistylis* and

Carchesium, for their prey, and swallow them down as far as the origin of the stalk; they then, while fixed on the stalk, secrete a capsule, and divide up into two or more individuals, which pass out. Certain Infusoria, as the mouthless *Opalina*, and many *Bursariæ*, are parasitic in the intestine and bladder of Vertebrates. To these belongs the *Balantidium coli* from the large intestine of Man (fig. 147).

FIG. 147. — *Balantidium coli* with two pulsating vacuoles (after Stein). Under the nucleus lies a starch-granule that has been eaten, a ball of excrement is passing out of the anus at the posterior end.

1. Sub-order: **Holotricha**. — Body uniformly covered with cilia, which are arranged in longitudinal rows, and are shorter than the body. Longer cilia are sometimes found in the region of the mouth, but these do not form an adoral zone.

Besides the parasitic *Opalinæ* (*Opalinæ ranarum*), without mouth or anus, the following families belong to this group:—

Fam. Trachelidæ. Body of changeable shape prolonged into an anterior neck-like process. Mouth ventral, without longer cilia. *Trachelius ovum* Ehrbg., *Amphileptus fascicola* Ehrbg.

Fam. Colpodidæ. Form of body definite. Mouth ventral, in a depression,

always furnished with long cilia or undulating membranes. *Paramœcium Aurelia* Fr. Müller, *P. Bursaria* Focke, *Colpoda cucullus* Ehrbg., *Glaucoma scintillans* Ehrbg.

2. Sub-order: **Heterotricha**.—Body uniformly covered with fine cilia, which are arranged in longitudinal rows, with a distinct adoral zone of cilia.

Fam. **Bursariidæ**. The adoral zone of cilia is on the edge usually of the left half of the body. *Bursaria truncatella* O. Fr. Mull., *Balantidium coli* Malmst., parasitic in the colon of man; *Spirostomum ambiguum* Ehrbg.

Fam. **Stentoridæ**. At the anterior end of the body is a peristomial space with a funnel-shaped depression, without any distinct gullet. *Stentor polymorphus*, O. Fr. Müll., *St. cæruleus* Ehrbg.

3. Sub-order: **Hypotricha**.—Body with sharply defined dorsal and ventral surface. The convex dorsal surface is usually naked, the ventral covered with cilia and beset with styles and processes, mouth on the ventral surface.

Fam. **Oxytrichidæ**. Body elongated to an oval. On the left half of the ventral surface is a peristomial region, with an adoral zone of cilia. The ventral surface is beset at either edge by a marginal row of cilia, and also with bristles and hooks. *Stylonychia pustulata* Ehrbg., with eight anterior styles, five ventral, and five anal cilia. *Oxytricha gibba* O. Fr. Müller.

Fam. **Chilodontidæ**. Body usually armoured, with gullet in the form of a fish-basket. *Chilodon cucullus* Ehrbg.

4. Sub-order: **Peritricha**.—Infusoria with cylindrical or bell-shaped partially ciliated body. The cilia are placed on an adoral ciliated disc, and frequently on a ring-like zone.

Fam. **Vorticellidæ**. Peritricha with adoral spiral of cilia, without a shell, attached by a stalk, usually forms colonies. *Vorticella microstoma* Ehrbg., *Epistylis plicatilis* Ehrbg., *Zoothamnium arbuscula* Ehrbg., *Carchesium polypinum* Ehrbg.

Fam. **Trichodinidæ**. Peritricha with adoral spiral of cilia, and circle of cilia as well as an apparatus for attachment at the posterior end. *Trichodina pediculus* Ehrbg.

Fam. **Halteriidæ**. Near the adoral spiral of cilia is an equatorial zone of longer cilia. *Halteria volvox* Clap. Lachm.

5. Sub-order: **Suctorina**.—Body usually without cilia, with knobbed tentacle-like processes which serve as sucking tubes.

Fam. **Acinetidæ**. *Acineta mystacina* Ehrbg., *Podophrya cyclopum* Clap. Lachm., *Sphærophrya* Clap. Lachm.

As an appendix to the Protozoa we will now proceed to consider the *Schizomycetidæ*, which approach more nearly to the Fungi, and the *Gregarinidæ*.

1. The *Schizomycetæ** (Bacteria) are small globular or rod-shaped bodies which are found in decaying matter, and are especially numerous on the surface of putrefying fluids, where they give rise to a slimy film (fig. 148). They are most nearly allied to the fungus of yeast, with which they also agree in their manner of nourishment, in that they make use of ammonia and organic compounds containing carbon. Like the yeast fungus they excite and maintain the fermentation or, as may happen, putrefaction of organic matter by withdrawing its oxygen or by attracting oxygen from the air (reduction or oxydation ferments). But they are clearly separated from the fungi by their development, for *they increase by dividing into two halves*, while the yeast fungus (*Saccharomyces*, *Hormiscium*) forms buds which separate off as spores. The transverse division takes place, after the cell has become elongated, by a constriction of the protoplasm and by the secretion of a cross partition wall. The daughter-cells either divide at once, or remain united and produce chains of Bacteria (filiform Bacteria) by a fresh fission. Sometimes the successive generations of cells remain connected by a gelatinous substance, and so produce irregular shaped gelatinous masses (*zoogloea*). Sometimes they become free and are dispersed in swarms. They may also settle on the bottom in the form of a

FIG. 148.—Schizomycetes (after F. Cohn). *a*, Micrococcus. *b*, Bacterium termo, bacteria of putrefying fluids, both in the motile and zoogloea form.

granular precipitate, as soon as the nourishment in the fluid is exhausted. The greater number have a motile and a motionless stage; in the first they rotate themselves about their long axis, but are also able to bend and extend, but never to serpentine. Their activity seems to be connected with the presence of oxygen.

Owing to the absence of sexual reproduction, the division of Bacteria into genera and species is beset with such difficulty that we must content ourselves with establishing, in an artificial fashion, form species and physiological species and varieties without always being able to demonstrate their independence. F. Cohn distinguishes four groups:—(1) Globular Bacteria, *Micrococcus* (*Monas* and *Mycoderma*); (2) Rod Bacteria (*Bacterium*); (3) Filiform Bacteria (*Bacillus* and *Vibrio*); (4) Spiral Bacteria (*Spirillum* and *Spirochaeta*).

The Globular Bacteria are the smallest forms, and only exhibit molecular movements. They cause various forms of decomposition, but not putrefaction.

* F. Cohn, "Beiträge zur Biologie der Pflanzen." Heft 2 and 3, 1872 and 1875. "Untersuchungen über Bakterien," 1, 2, and 3 (*Bacterium termo*). Compare further the works of Eberth and Klebs.

They can only be divided, according to their various methods of development, into chromogenous (pigment), zymogenous (fermentation), and pathogenous (contagion) divisions. The first appear in coloured gelatinous masses and vegetate in the Zooglocaform, *e.g.*, *M. prodigiosus* Ehrbg. in potatoes, etc., To the Zymogenous belong *M. ureæ*, urine ferment; to the Pathogenous *M. vaccinæ*, the Pox Bacteria, *M. septicus* of pyæmia, *M. diphthericus* of diphtheritis.

The Rod Bacteria form small chains or threads, and exhibit spontaneous motions, especially in the presence of abundant nourishment and oxygen. Here belongs *Bacterium termo* Ehrbg. distributed in all animal and vegetable infusions and the necessary ferment in putrefaction, just as yeast is in alcohol fermentation; also *B. Lineola* Ehrbg. of considerable size, which exists in spring water and in standing water, in which there are no products of putrefaction, and, as well as the former, has a zoogloca jelly. Another Bacterium form acts as ferment of lactic acid, according to Hoffmann.

Of the Filiform Bacteria the motile *Bacillus (vibrio) subtilis* Ehrbg. occasions butyric acid fermentation, but is also found in infusions together with *B. termo*. Very nearly allied and hardly to be distinguished is the motionless *Bacillus anthracis* of inflammation of the spleen. *Vibrio rugula* and *serpens* are characterised by constant undulations of the chain. Finally these lead to the spiral forms of which *Spirochæta* resembles a long and flexible but closely wound, and *Spirillum*, a thick, short, and coarse screw. *Spirillum tenax*, *undula*, *volutans*, the last with a flagellum at each end.

2. The *Gregarinidæ** are unicellular organisms which live as parasites in the intestine, and in the internal organs of the lower animals. The body is frequently elongated like that of a worm, and consists of a granular viscid central mass surrounded by a delicate external membrane (sometimes with a subcuticular layer of muscle stripes). The nucleus, a round or oval clear body, is embedded in

FIG. 140.—*Gregarina* (after Stein and Kölliker). *a*, *Stylorhynchus oligacanthus* out of the intestine of *Callopteryx*. *b*, *Gregarina (Clepsidrina) polymorpha* from intestine of the meal beetle, during conjugation. *c*, The same in process of encystment. *d*, Encysted *Gregarina*. *e*, Stage of formation of *Pseudonavicellæ*. *f*, *Pseudonavicellacyst* with ripe *Pseudonavicellæ*.

* N. Lieberkühn, "Evolution des Grégarines," *Mém. cour. de l'Acad. de Belg.* 1855. N. Lieberkühn, "Beitrag zur Kenntniss der Gregarinen." *Arch. für Anat. und Physiol.*, 1865. E van Beneden, "Recherches sur l'évolution des Grégarines." *Bulletin de l'Acad. roy. de Belgique*, 2 Ser. xxxi., 1871. Aimé Schneider, "Contributions à l'histoire des Grégarines des Invertébrés de Paris et de Roscoff." *Arch. de Zool. Experiment.*, Tom IV., 1875.

the central mass. The structure of the body may be complicated by the presence of a partition wall which parts off the anterior end from the main mass of the body. The anterior portion of the body gets in this way the appearance of a head, upon which there may be formed here and there prominences in the form of hooks and processes for the purpose of attachment. Nourishment is effected by endosmosis, through the external walls. Motion is confined to slow gliding forward of the feebly contractile body.

In their full-grown state the Gregarina are frequently seen fastened to one another, two or more together. This connected state precedes reproduction (fig. 149). The two individuals lying with their long axes in the same straight line contract and surround themselves with a common cyst, and after undergoing

FIG. 150.—Rainey's corpuscles from the flesh of a pig. *a*, An animal inside a muscle fibre. *b*, Posterior end of the same, strongly magnified; *C*, cuticular layer; *B*, spores.

a process resembling segmentation, divide into a number of small spore-like balls, which become spindle-shaped bodies (pseudonavicellæ). The cyst secreted round the conjugating individuals, or, as is often the case, round a single individual, becomes a pseudonavicella cyst, and by its bursting the spindle-shaped bodies reach the exterior. The contents of each Pseudonavicella sometimes gives rise to a small amœboid body, as may be inferred from Lieberkühn's observations on the *Psorosperms* of the pike. In other cases (*Monocystis*, *Gonospora*, etc.) sickle-shaped bodies arise in the spores, which, without passing through an amœboid stage, give rise to young Gregarines. *Monocystis agilis* from the testis of the earth-worm. *Gregarina* L. Duf. (*Clepsidrina* Hammersch.) Body with flat partition wall and wart-like head at anterior end. In the young stage the anterior end of *Gr. blattarum* v. Sieb. is fixed in the cells of the intestinal epithelium of *Blatta*. *Gr. polymorpha* Hammersch. in the meal-worm.

[The Gregarines are found mainly in Invertebrata. They may be divided

into two main groups, the *Polycystidea* and the *Monocystidea*. In the former, which are found for the most part in Arthropods, there is a partition dividing the body into two parts; in the latter, which are found chiefly in Vermes, there is no such partition.]

The structures long known as *Psorosperms* from the liver of the rabbit, the slime of the intestine, the gills of fishes, and the muscles of many Mammalia, etc., present a great resemblance to the Pseudonavicellæ; but we are not yet fully enlightened as to their nature. The case is the same with the structures known as Rainey's or Mischer's corpuscles from the muscles of, *e.g.*, the pig; and

the parasitic animals from various wood-lice and Crustacea, which were assigned by Cienkowski to the fungi, under the name of *Amœbidium parasiticum*, remind us by their reproduction no less of the Gregarinæ and their cysts.

The *Coccidia* which we meet with in the cells of the epithelium of the intestine as well as in the bile-ducts of Mammalia should also be regarded as *Gregarinæ* (fig. 151). They transform themselves into egg-shaped zoospores by the formation of a capsule and the production of several

FIG. 151.—*Coccidium oviforme* from the liver of the rabbit, magnified 550 diam. (after R. Leuckart). c, d, Stages of spore formation which have only been observed outside the cells.

spores from their granular contents. In *Coccidium oviforme* from the liver of man and of the rabbit there are only four spores formed, which become sickle-shaped rods.

CHAPTER VII.

CÆLEENTERATA (ZOOPHYTES).*

Radially symmetrical animals with a body composed of cells. They have a body-cavity which serves alike for circulation and digestion (gastrovascular space).

Amongst the *Cæleenterata* we meet for the first time with organs and tissues composed of cells. In addition to the external and internal epithelium, cuticular, calcareous, and silicious structures, as well as muscles, nerves, and sense-organs are very generally present. On the other hand, the internal surface of the body is not differentiated into organs of circulation and digestion distinct from each other. The vegetative processes are performed by the internal surface of the gastric cavity, the gastrovascular space, of which the central part functions as stomach and intestine, the peripheral as vascular system.

R. Leuckart was the first to recognise the importance of these characters, and made use of them to separate the *Polyyps* and the *Medusæ* from the *Echinoderms*, thus resolving Cuvier's type of *Radiata* into the types of *Cæleenterata* and *Echinodermata*.

It is only in more recent years that Naturalists have been convinced of the close relationship between the *Porifera* and the *Polyyps*

* R. Leuckart, "Ueber die Morphologie und Verwandtschaftsverhältnisse niederer Thiere," Braunschweig, 1848.

and *Medusæ*, and have included the former in the group of the *Cœlenterata*. The *Porifera* were for a long time taken for plants, and more recently for Protozoon-stocks. While, however, the *Polyps* and *Medusæ* are distinguished as *Cnidaria* and are characterised by the possession of nematocysts and by the higher differentiation of their tissues, the *Porifera* or *Spongiaria* present more simple forms of tissue in the spongy structure of their body, and are without nematocysts. The entire structure of the body may, generally speaking, be described as radial, although the radial symmetry does not appear in most sponges, and among the *Cnidaria* transitions towards lateral

FIG. 152.—Young *Sycon* (after Fr. E. Schulze). O, Osculum or exhalant pore; P, pore in the wall.

symmetry are apparent. Similar organs are usually repeated round the body axis four or six times or in multiples of these numbers.

Four distinct types of body form are met with in the group *Cœlenterata*, viz., that of the *Sponge*; of the *Polyp*; of the *Medusa*; and of the *Ctenophora*.

The Sponge type.—The simplest form of

Sponge is represented by a fixed cylindrical tube, with an exhalant opening, the *Osculum*, at the free end (fig. 152). The contractile wall is supported by skeletal spicules, and is pierced by numerous inhalant pores, through which water and small food particles pass into the ciliated internal space. By the fusion of separate individuals, and by reproduction by gemmation, the latter being the more frequent mode, widely different Sponge stocks with complicated canal systems are formed. The polyzoid nature of these is made apparent by the presence of many oscula.

The Polyp type.—The Polyp has the form of a cylindrical or club-shaped tube, of which the posterior end is fixed and the opposed

free pole pierced by an oral opening situated on a flat or conical prominence, the oral cone. The mouth is surrounded by one or more circles of tentacles, and leads into a simple cylindrical body cavity (*Hydroidpolyps*), or through an œsophageal tube into a complicated gastrovascular cavity (*Anthozoa*, fig. 153). The disappearance of the tentacles gives rise to the so-called *polypoid* form, which consists of a simple hollow tube furnished with a mouth.

The Medusa type.—The free-swimming Medusa consists of a flattened disc or arched bell of gelatinous or cartilaginous consistence, from the under surface of which hangs a central stalk, the *manubrium*, bearing at its free

FIG. 153.—*Sagartia nivea* (after Gosse).

frequently prolonged in the neighbourhood of the mouth into numerous lobes and tentacles, while from the edge of the disc arise a varying number of thread-like tentacles. The central cavity of the body, into which the hollow manubrium leads, is called the gastric cavity, and from it peripheral pouches or radial canals, the so-called vessels, run to the edge of the disc, where, as a rule, they are connected by a circular vessel.

The movements of the Medusa are effected by the alternate contraction and dilatation of the muscular under surface of the bell, *i.e.* of the subumbrella.

Rudimentary Medusæ, in which the manubrium and marginal tentacles are absent, are found. They are called Medusoids, and do not acquire individual independence, but remain attached to the body of the Medusa or Polyp from which they are budded.

FIG. 154.—Medusa of the *Podocoryne carnea* with four tentacles at the edge of the disc, ovaries and manubrium, immediately after separation from the stock.

The Medusæ and Polyps, in spite of the important differences between them, are but modifications of the same plan of structure. A Medusa may be compared to a free, flattened Polyp, possessing a large gastric cavity and a muscular and enlarged oral disc.

The Ctenophor type has fundamentally the form of a sphere,

beset with eight meridional rows of vibratile plates, which, working like oars, serve for locomotion (fig. 155).

The body parenchyma in the Sponges consists principally of amœba-like cells, which frequently bear flagella, but which never produce stinging threads. In the *Cnidaria* (Polyps and Medusæ),

in certain cells the peculiar structures known as *thread cells* (fig. 156) are developed. They consist of small capsules filled with fluid, and containing a sharp-pointed, spirally coiled thread; they are developed in cells which may be called *cnidoblasts*. Under certain mechanical conditions, *e.g.* under influence of the pressure produced by contact with a foreign body, these capsules burst, and the thread is suddenly protruded, and either fastens on to the cause of disturbance or pierces it, carrying into it a part of the fluid contents of the capsule. In

FIG. 156. — Nematocysts and cnidoblasts of *Siphonophora*. *a* and *b*, with the cnidocil of the cell. *c* to *e*, Nematocysts with evaginated thread.

FIG. 155. — *Cydippe* (*Hormiphora*) *plumosa* (after Chun). *O*, mouth.

many parts of the body, and especially on the tentacles, which serve for the capture of prey, these small microscopic weapons are collected in masses, and are often united in a peculiar arrangement to form batteries of thread cells.

The tissues (which are composed of cells) are generally arranged in two or three layers, of which the external layer is known as *ectoderm* and forms the outer skin, while the internal layer, *the endoderm*, lines the gastric cavity.

Between the two there is developed a delicate homogeneous supporting membrane or a stronger layer of connective tissue, in which the skeletal elements are developed. This intermediate layer is known as the *mesoderm*. The skeletal formations present great variations in structure and arrangement.

Muscles are formed in the deeper part of the ectoderm as cell-processes (the so-called neuromuscular fibres), but often penetrate within the mesoblast as independent cell structures. Sense epithelium, nerve fibrillæ, and ganglion cells also appear as differentiations of the ectoderm. The endoderm cells, on the other hand, often bear cilia, and are principally concerned in the processes of digestion and secretion.

A sexual reproduction by fission and gemmation is prevalent in these animals, constituted, as they are, on the whole of homogeneous tissues. If the individual forms so produced remain united, they give rise to the colonies which are so widely distributed amongst the Polyps and Sponges, and which, by the continual multiplication of their individuals, may in course of time attain a very considerable size. But we also meet everywhere with the sexual reproduction, in that ova or spermatozoa are produced in the tissues, usually in the region of the gastrovascular cavity, in a definite portion of the body. As a rule, the ova come in contact with the spermatozoa away from the place where they are produced; either within the body cavity or outside the parent body, in the sea-water. In a few cases only do both the sexual elements originate in the body of the same individual, as, for example, in many of the *Spongiaria*, some *Anthozoa*, and in the hermaphrodite *Ctenophora*. As a rule, in the colonies of *Anthozoa* the monœcious arrangement of sexes obtains, the individuals of the same stock being partly male, partly female. Some are diœcious, e.g. *Veretillum*, *Diphyes*, *Apolemia*.

The development of the *Celenterata* for the most part consists of a metamorphosis. The just hatched young differ from the sexual animal in the form and structure of the body, and pass through larval stages. The greater number of them leave the egg as ciliated larvæ, which resemble somewhat an Infusorian in external appearance. They acquire a mouth, body cavity, and organs for obtaining food, either during their existence as free larvæ, or after

attachment to solid surrounding objects in the sea. If the young forms, which differ from the sexual animal, gain the power of reproducing by budding, the development leads to various forms of alternation of generation.

SUB-GROUPS.—I. SPONGIARIA *=PORIFERA.

The body has a spongy consistence and is composed of masses of cells capable of amœboid movements and supported by a solid, calcareous, silicious, or horny skeleton. There are external pores, an internal canal system, and one or many exhalent openings (ostula).

The sponges are at present universally regarded as *Cœlenterata*, and in this group they are distinguished from the *Cnidaria* (Polyps and Medusæ). They are composed of a contractile tissue, which is usually supported by a framework composed of spicules and fibres; the whole being arranged in such a manner that there exists on the external wall of the body larger and smaller openings; and in the interior a system of canals and spaces in which a continuous stream of water is maintained by the vibratile motion of cilia.

FIG. 157. — Amœba-like cell of Spongilla.

Amœba-like cells, net-like membranes of sarcodæ, flagellated cells, spindle cells, ova, spermatozoa, and tissues derived as excretions from cells are present as the histological elements of the Sponge body. The chief mass of the contractile parenchyma is composed of the amœba like cells. These are granular cells, which, like Amœbæ, have no external membrane, can protrude and retract processes, and

take into their interior foreign substances (fig. 157).

The framework or skeleton, which we find wanting only in the soft

* Literature: Nardo G. D., "System der Schwämme," *Isis*, 1833 and 1834. Grant, "Observations and Experiments on the Struct. and Funct. of Sponges," *Edin. Phil. Journal*, 1825—1827. Bowerbank, "On the Anatomy and Physiology of the Spongiadæ," *Philos. Trans.*, 1858 and 1862. Lieberkühn, "Beiträge zur Entwicklungsgeschichte der Spongillen," *Müller's Archiv*, 1856. Lieberkühn, "Zur Anatomie der Spongien," *Müller's Archiv*, 1857, 1859, 1863, 1865, 1867. O. Schmidt, "Die Spongien des adriatischen Meeres," Leipzig, W. Engelmann, 1862, as well as Supplement. Leipzig, W. Engelmann, 1864, 1866, 1868. E. Haeckel, "Die Kalkschwämme," 3 Bde, Berlin. 1872. Fr. E. Schulze, "Untersuchungen über den Bau und die Entwicklung der Spongien," *Zeitschrift, für wiss. Zool.*, 1876—1880.

gelatinous Sponges or *Myxospongia*, is composed of horny fibres or silicious or calcareous spicules.

The horny fibres form, without exception, anastomosing networks of varying degrees of thickness, and present a lamellated structure (fig. 158), which indicates that they are formed of a number of layers. They are formed by excretion as hardening portions of sarcode. The calcareous needles (fig. 159) are simple or three- and four-rayed spicules, and take their origin, as do the silicious structures, in the interior of cells. The silicious spicules present, however, an extraordinary variety of form: some of them constitute a connected framework of silicious fibres, and others are free silicious bodies with simple or branched central canals (fig. 160). The latter are found in the form of needles, spindles, cylinders, hooks, anchors, wheels, and crosses, and arise in nucleated cells, probably as deposits round a hardening of organic matter (central fibre).

FIG. 158.—Piece of network of horny fibres from *Euspongia equina*.

In order to understand the morphology of the *Spongiaria* we must begin by examining the structure of a young Sponge, which proceeds from the fixed larva. The young Sponge, after the formation of a ciliated gastric cavity and an exhalent opening or osculum, has the form of a simple hollow tube, the walls of which are pierced by pores for the passage of small food particles suspended in the water (fig. 152).

FIG. 159.—Calcareous Spicules of *Sycon*.

In this stage we can distinguish three layers — (1) an entoderm, formed of elongated flagellated cells; (2) a mesoderm, the skeletogenous cell layer, the structure of which recalls connective tissue; and (3) an ectoderm, which forms the outer layer of the Sponge, and consists of a flat epithelium. The cylindrical cells of the endoderm possess at their free ends surrounding the flagellum a delicate

hyaline marginal membrane, which, derived from a prolongation of the hyaline plasma, projects as a hollow cylinder resembling the protoplasmic collar of certain *Flagellata** (*Cylicomastiges*). [This

FIG. 160.—Siliceous bodies from different silicious Sponges. *a*, Silex needle from *Spongilla*, inside the cell. *b*, Amphidisc of a gemmule of *Spongilla*. *c*, Anchor from *Ancorina*. *d*, Hook from *Esperia*. *e*, Star from *Chondrilla*. *f*, Anchor from *Euplectella aspergillum*. *g*, *h*, needle rays from the same. *i*, Six-rayed needle from the same, with central canal.

structure is commonly known as the collar, and the cells as the collared cells.]

FIG. 161.—Portion of the external layer of *Spongilla* with the pores, *P* (after Luberkuhn).

The thick layer in which the skeletal spicules are produced consists of a hyaline matrix, in which irregularly branched or spindle-shaped amœboid cells are embedded, and may be regarded, like the gelatinous substance of the *Acalepha*, as mesoderm, while the external, clearly defined, flat epithelium (also in the *Asconia*, *Leucosolenia*) is to be considered as ectoderm.

The pores or inhalent openings so characteristic of the Sponge body are in reality only intercellular spaces, and are able to close themselves, vanish and be replaced by new pores, which arise by the separation of one cell from another (fig. 161).

* Upon this ground Clark declared the Sponges to be nearly allied to the *Flagellata*, and regarded them as great colonies of the latter.

Amongst the calcareous Sponges, the simple Sponge with inhalent pores and terminal osculum (*Olynthus*-form) is represented by the stock-forming *Leucosolenia* (*Grantia*), which is composed of numerous hollow cylinders. The structure of this sponge has been described by Lieberkühn.

In the *Syconidæ* the body cavity has a more complicated form. The central space opens into secondary peripheral spaces or radial tubes, which are lined by ciliated cells, and open externally through the inhalent pores (fig. 162).

In other calcareous Sponges (*Leuconidæ*) the radial canals have the form of irregular parietal canals, giving off branches to the periphery and possessing dilated, ciliated chambers. This form of internal canal system is also found in most of the stock-forming, silicious Sponges (fig. 163).

Sponge forms may become more complicated by the formation of stocks; the originally simple Sponge, which has developed from a single ciliated larva, gives rise by budding and incomplete fission to a polyzoid sponge body; or several

originally separate individuals, each of which has origi-

nated from a single larva, fuse together to form a compound sponge stock. Both these methods of growth are repeated in a similar manner in the formation of the stocks of Polyps (fig. 164). In the same way that the fan-like nets of the Fan Coral (*Rhipidogorgia flabellum*) are formed by the repeated fusion of its

branches, the gastrovascular cavities of which anastomose, so also in the case of the branching sponges, as a result of the same process, reticulate, or coiled or even massive stocks are formed (fig. 165).

FIG. 162.—Longitudinal section through *Sycon raphanus*, slightly magnified. *O*, Osculum with collar of spicules; *Rt*, radial tubes which open into the central cavity.

FIG. 163.—Section of *Corticium candelabrum* (after Fr. E. Schulze). *Gk*, Ciliated chamber of the parietal canal.

In this case the canal system, in which the modifications before described for each individual Sponge are repeated, becomes more complex, partly through the formation of anastomoses, and partly because irregular gaps and winding passages make their appearance between the fused branches of the stock and form spaces which lead into the ciliated cavities.

Reproduction takes place mainly asexually by fission and the production of germs or *gemmules*, but also by the formation of ova and sperm capsules. The gemmules are in the fresh-water *Spongilla* masses of cells which are surrounded by a firm shell composed of silicious structures (*amphidiscs*), and, like encysted Protozoa, pass through a long period of rest and inactivity. After the expiration of the cold and sterile season of the year, the contents pass out of the opening of the capsule and generally surround the latter, and with increasing growth become differentiated into amœboid cells and all the essential parts of a new small sponge body. Multiplication by means of gemmules is also common among the marine Sponges. The gemmules take their origin under certain conditions as small globules surrounded by a membrane. The contents are essentially formed of sponge cells and spicules, and, after a longer or shorter period of inactivity, reach the exterior by the rupture of the membrane.

Sexual reproduction was first demonstrated with certainty by Lieberkühn for *Spongilla*, but more recently has been shown to exist in almost every group of Sponges. In most cases the ova and spermatozoa seem to reach maturity at different times in the same Sponge.

The spermatozoa are needle-shaped, and lie in small spaces lined with cells. The ova, like the mother cells of the spermatozoa, are modified cells of the parenchyma, and are derived from cells of the same tissue layer (mesoderm) in which the needles and skeletal structures take their origin. The ova are naked amœboid cells, and pass into the canal system, while in the viviparous *Sycons* they

FIG. 164.—*Axinella polypoides*
(after O. Schmidt).

remain in the mesoderm, and there undergo their development. It is only later that the ciliated embryos or larvæ fall into the canal system, pass out, and attach themselves, to develop into a young sponge.

The embryonic development among the calcareous sponges is most accurately known for the

FIG. 165.—*Euspongia officinalis adriatica*, with a number of oscula, O (after Fr. E. Schulze).

Syconida from the investigations of Fr. Schulze and Barrois.

FIG. 166.—Development of *Sycon raphanus* (after Fr. E. Schulze). *a*, Ripe ovum. *b*, Stage with four segmentation cells. *c*, Stage of segmentation with sixteen cells. *d*, Blastosphere with large dark granular cells at the open pole. *e*, Free-swimming larva, one-half of the body (entodermal) being formed of long ciliated cells, the other (ectodermal) of large granular cells.

After the completion of the tolerably regular segmentation (fig. 166, *a—c*), *Sycon* (*Sycandra*) *raphanus* passes through a blastosphere stage, during which the greater half of the ovum consists of clear cylindrical cells, and the smaller half at the still open pole of large dark granular cells (fig. 166, *d*). The cylindrical cells of the larger half develop cilia, and the embryo passes out of the body cavity and becomes a free-swimming larva, which attaches itself and alters its shape in such a manner that the dark cells grow over the ciliated portion of the globe, which is meanwhile invaginating. The ecto-

FIG. 167.—Young *Sycon* (after Fr. E. Schulze). O, Osculum or exhalant aperture; P, pores of the wall.

derm and mesoderm are derived from the dark granular cells, and the ciliated cells give rise to the entoderm of the gastric cavity. Later on the body of the sponge becomes cylindrical, the osculum makes its appearance, and calcareous needles appear in the wall, which becomes pierced by pores (fig. 167).

With the exception of *Spongilla*, the sponges are marine, and are met with under very different con-

ditions, and covering a wide area of distribution. The horny sponges live in shallow seas, as also the *Myxospongiae* and *Chalinae*, or siliciceratous Sponges; while the *Hexactinellidae* inhabit very considerable depths. Petrified remains of sponges are also found preserved in various formations, for instance in the chalk; and these remains differ much from the greater number of those living. On the other hand, the hyaline sponges of the deep sea agree so fully with the ancient forms that they seem to be the direct descendants of the latter. Finally, many of the principal groups extend back into the palæozoic age, in which *Lithistidae* and *Hexactinellidae* especially are met with in the most ancient Silurian

strata. Hence palæontology affords us no facts for determining the phylogenetic development of the *Porifera*.

CLASS I.—SPONGIA.

(With the characteristics of the Group).

Order 1.—MYXOSPONGIA (gelatinous sponges). Soft, fleshy sponges, without any skeleton, with a hyaline gelatinous mesoderm, often containing fibrous cords. The ectoderm cells are fairly elongated, and bear flagella.

Fam. *Halisarcidæ*. *Halisarca* Duj. *H. lobularis* O. S., colour dark violet; encrusts stones; Sebenico. *H. Dujardinii* Johnst., forms a white encrustment on the *Laminaria* of the North Sea.

Order 2.—CERAOSPONGIA (horny sponges). For the most part branched or massive sponge stocks, with a framework of horny fibres, in which grains of silex and sand are present as foreign bodies.

Fam. *Spongiadæ*. *Euspongia* O. S., with very elastic fibrous framework, of equal strength throughout, mostly capable of being used for bath and washing sponges. *E. adriatica* O. S., *equina* O. S., *zimocca* O. S., in the Greek Archipelago, *molissima* O. S., Levantine sponge, cup-shaped. *Spongelia elegans* Nardo.

Order 3.—HALICHONDRIÆ (siliciceratous sponges). Sponges of very various shapes, with usually uniaxal silicious needles, simple silicious spicula, which are connected by delicate or firmer plasmatic structures, disposed in networks or enclosed in sponge fibres. Of the numerous families the following may be mentioned:—

Fam. *Chondrosidæ*. (*Gumminæ*), Coriaceous sponges. *Chondrosia reniformis* Nardo.

Fam. *Suberitidæ*. Sponges of massive form, with knobbed silex spicules, which, as a rule, are arranged in network. *Suberites* Nardo. *S. domuncula* Nardo, Adriatic, Mediterranean.

Fam. *Spongillidæ*. Massive or branched with simple spicules, connected by investments of sarcodæ. *Spongilla fluviatilis* Lk., *Sp. lacustris* Lk.

Order 4.—HYALOSPONGIA. Sponges with a firm, often hyaline lattice-work of silex spicules, which present the most perfect form of six-rayed spicules (*Hexactinellidæ*), and may be cemented together by a stratified silicious substance.

Fam. *Hexactinellidæ* (hyaline sponges). With connected silicious framework and network of stratified silicious fibres, which join the six-rayed silicious bodies, frequently with isolated spicules and tufts of silex hairs, which serve to attach the sponge. They live for the most part at considerable depths, and are allied to the fossil *Ventriculitidæ*. *Dactylocalyx* Bbk. *Euplectella* Owen,

E. aspergillum Owen, Philippines. In the body cavity of the glassy sponge are found *Aega spongiphila*, and a small *Palæmon*. *Hyalonema Sieboldii* Gray, Japan. *H. boreale* Lovén, North Sea.

Order 5.—**CALCISPONGIÆ**, Calcareous sponges. Usually colourless, sometimes red-coloured sponges and sponge stocks, the skeletons of which consist of calcareous spicules. These are either simple needles (as they first appear in the embryonic form) or three or four-armed cross spicules. Very often, however, we meet with two or all three forms of spicules in the same sponge.

Fam. Asconidæ (*Leucosolenidæ*, Ascons). Calcareous sponges, the walls of which are pierced by simple canals. *Grantia* Lk. (*Leucosolenia* Bbk.), these are divided by E. Haeckel into seven genera, *Ascyssa*, *Ascetta*, *Ascilla*, *Ascortis*, *Asculmis*, *Ascaltis*, *Ascandra*, according to the form of the calcareous needles or spicula. *Gr. botryoides* Lk. (*Ascandra complicata* E. Haeck), Heligoland, nearly allied to *Gr. Lieberkühnii* O. S. from the Mediterranean and Adriatic.

Fam. Leuconidæ (*Grantiidæ*, Leucons), calcareous sponges, with thick wall, which is pierced by branched channels. *Leuconia* Grt., divided by E. Haeckel into seven genera, according to the form of the calcareous spicules—*Leucyssa*, *Leucetta*, *Leucilla*, *Leucortis*, *Leuculmis*, *Leucaltis*, *Leucandra*. L. (*Leucetta*) *primigenia* E. Haeck.

Fam. Sycondiæ (Sycons). Mostly solitary calcareous sponges, with thick walls, which are pierced by straight radial tubes. The latter project on the surface as conical prominences of the wall. *Sycon* Risso, divided by E. Haeckel into seven genera—*Sycyssa*, *Sycetta*, *Sycilla*, *Sycortis*, *Syculmis*, *Sycaltis*, *Sycandra*.

SUB-GROUP II.—CNIDARIA (CŒLENTERATA, s. str.)

Cœlenterata, with consistent tissues not pierced by a system of pores; the osculum is replaced by a mouth; with thread cells in the epithelial tissues.

The Cnidaria represent the Cœlenterata in a more restricted sense; and in their structure the radial symmetry appears more strongly marked. In them the amœboid cell, as an independent tissue unit, loses its importance for the functions of locomotion and nourishment, although the entoderm cells often possess the power of absorbing solid particles, after the manner of the amœbæ. The gastrovascular apparatus, on the contrary, functions distinctly as a digestive and circulatory body cavity. Pore systems in the skin are not required for the introduction of nourishment, since the mouth, which corresponds to the osculum, provides for the reception of food. Nematocysts are very commonly found as productions of the epithelial cells,

principally of the ectoderm, but also of the entoderm. Each *cnidoblast*, from the contents of which a nematocyst is developed, possesses a fine superficial plasmatic process (*cnidocil*), which is probably very sensitive to mechanical stimuli, and occasions the bursting of the capsule.

Very frequently the cnidoblasts are found thickly grouped together at certain places, and form wart-like swellings or batteries (fig. 168). The differentiation of tissues and organs also appears to have reached a higher stage in the *Cnidaria*, in comparison with the *Porifera*, in which cnidoblasts have not hitherto been discovered.

Sense cells, in particular, are found in the ectoderm, and these are not seldom grouped together as specific sense organs. Nerve cells and fibres are also present; the latter often

form a deeper layer of fibrous tracts beneath the superficial layer of the ectoderm, with which they stand in connection through pro-

cesses of the sense cells. Amongst many Medusæ (*Craspedota* and *Charybdea*) we find a single or double nerve ring near the edge of the disc, while in the Polyps (*Actinia*), the nerve fibres have a more irregular distribution (fig. 169).

FIG. 168.—Group of nematocysts at the end of the tentacle of a *Scyphistoma*

FIG. 169.—Longitudinal section through the nerve ring of *Charybdea*. Sz, Sense cells in the ectoderm; Gz, ganglion cells; Nf, nerve fibres; Stl, supporting lamella; E, entoderm cells.

CLASS I.—ANTHOZOA* = ACTINOZOA (*Coral polyps*).

Polyps with œsophageal tube and mesenteric folds, with internal generative organs (no medusoid sexual generation), usually with solid mesodermal calcareous skeleton.

The polyps of the Actinozoa are distinguished from the polyps

* Ehrenberg, "Beiträge zur physiologischen Kenntniss der Korallenthier im Allgemeinen und besonders des rothen Meeres." Ehrenberg, "Über die Natur und Bildung der Korallenbänke," *Abh. der Berl. Akad.*, 1832. Ch. Darwin,

of the Hydromedusæ by their larger size and the more complicated structure of their gastrovascular cavity (fig. 43). The latter is not a simple cavity in the body, but is divided by numerous vertical partitions, the *mesenteric folds*, into a system of vertical pouches which communicate with one another at the bottom of the gastric cavity. In addition a system of capillary passages is also frequently present in the body wall. At their upper extremity the pouches are continuous with the canals leading into the hollow tentacles, since the edges of the mesenteries bounding them unite with the wall of the oral tube which hangs from the mouth. An opening may however persist in each mesentery underneath the oral disc, putting the neighbouring chambers in communication. The oral tube has the significance of an œsophagus, and possesses at its internal end, where the peripheral chambers open into the central cavity, an opening capable of being closed, by means of which its cavity stands in communication with the gastrovascular system. The mouth is used not only for the reception of food, but also for the rejection of excreta. The secretions of the coiled and twisted filaments (mesenteric filaments) at the edge of the mesenteries must be regarded as aiding in digestion (fig. 43).

The body of the polyp consists of an external coating of cells, an internal layer lining the gastric cavity, and an interposed connective tissue layer of very various thickness and structure (mesoderm). The latter appears rarely as gelatinous tissue, and more frequently as a tough homogeneous connective tissue containing spindle and star-shaped cells (*Aleyonidæ*, *Gorgonidæ*). This tissue may also assume the form of fibrous connective tissue, and become the seat of calcareous deposits. Muscle fibres, which take their origin from the entoderm cells, may also appear in the mesoderm; while the newly discovered ectodermal sense epithelium and nerve fibrillæ keep their superficial position in the region of the oral disc and on the tentacles. The generative products arise on the mesenteries near the mesenteric filaments as band-shaped or folded thickenings, and, according to Hertwig, are products of the entoderm. The sexes are for the most part separate, although hermaphrodite individuals

"The Structure and Distribution of Coral Reefs," London, 1842. J. D. Dana, "United States Expl. Expedition, Zoophytes," Philadelphia, 1846. M. Edwards et J. Haime, "Histoire naturelle des Corailliaires," 3 Tom, Paris, 1857—1860. Lacaze Duthiers, "Histoire naturelle du Corail," Paris, 1864. Gosse, "Actinologia britannica," London, 1860. Kölliker, "Anatomisch-systematische Beschreibung der Aleyonarien," 1872. Moseley, "The Structure and Relations of the Aleyonarian *Heliopora cœrulea*, etc," *Philosoph. Transactions of the Roy. Soc.*, 1876.

are met with. In rare cases all the individuals are hermaphrodite, e.g., *Cerianthus*.

The embryos produced from the fertilised ovum, which undergo a complete segmentation, are frequently born alive as ciliated larvæ, and possess an internal gastric cavity, and an oral aperture situated at the pole, which is directed backwards during movement. They then fix themselves by the pole opposed to the oral aperture and protrude in the region of the mouth first two, then four, eight, twelve, etc., tentacles; in the *Octactinia* eight tentacles at once.

In the *Polyactinia*, the tentacles and mesenteric pouches of which are arranged in multiples of six, it was till recently erroneously believed with M. Edwards that six primary mesenteries were first developed, then six secondary between them; then twelve were formed, then twenty-four, etc., so that mesenteries of equal size were of equal age and belonged to a cycle formed at one time. Lacaze Duthiers however produced proofs that the increase of mesenteries and of tentacles follows an entirely different law of growth, and that these structures in the first phases of development show a bilateral symmetry; and it is only later that the six radial symmetry appears by the equalization of the alternating elements of unequal age. A remnant of the primitive bilateral symmetry is moreover often preserved in the elongated mouth slit, which falls in the plane of the two primary tentacles.

Amongst the *Polyactinia* the very young larvæ of the *Actinia* (*A. mesembryanthemum*, *Sagartia*, *Bunodes*) have been most accurately investigated. They are small ciliated planulæ, one pole of which is somewhat drawn out and bears a tuft of longer cilia. The opposite end of the body is flattened and pierced with a mouth. This leads by a short œsophageal tube, which arises by invagination, into the narrow gastric cavity. The first differentiation consists in the appearance of two folds placed opposite each other, which divide the gastric cavity into two unequal chambers. The mouth is drawn out in the form of a longitudinal slit symmetrical with and at right angles to these primary mesenteric folds; so that by means of them the position of the median plane can be determined. Two new folds soon arise in the larger chamber, which we will call the anterior; these lie opposite to one another and symmetrically with the median plane; so that four chambers are now present, an anterior, a posterior, and two smaller lateral ones. A third pair of folds are then developed in the posterior space, and a fourth pair follow quickly in the lateral chambers: the fourth pair are slightly smaller

than the preceding ones. After an interval four new folds appear, one on each side of the two primary mesenteries (fig. 170). The twelve gastrovascular chambers thus formed gradually become equal in size, and can be separated into two unpaired chambers situated in the median plane, and into five pairs placed symmetrically on either side of it.

FIG. 170.—From the history of the development of *Actinia mesembryanthemum* (after Lacaze Duthiers). *a*, Larva with eight mesenteries and two coiled bands; *O*, mouth. *b*, Slightly more advanced larva with the commencement of eight tentacles. *c*, *d*, Young *Actinia* with twenty-four tentacles, two longitudinal sections at right angles to one another. *e*, Mouth and tentacles seen from the oral surface.

The tentacles begin to develop before the appearance of the fifth and sixth pairs of mesenteries. They appear at the oral end of the gastrovascular chambers, and the tentacle of the anterior unpaired

chamber* appears first, surpassing in size those which follow it. The opposite (posterior) unpaired tentacle and the other paired tentacles then make their first appearance as small wart-like prominences. When the twelve tentacles have been formed, they become alternately equalised, so that six larger tentacles, amongst which are reckoned the unpaired tentacles of the long axis, alternate with the same number of smaller ones, and we have two circles of six tentacles of the first and the same number of the second order.

The asexual reproduction by gemmation and fission is of great significance. Buds can be formed in various positions, even at the oral end, in which case a strobila-like form appears. In *Blastotrochus* the buds appear at right angles to the axis of the parent animal (fig. 171).

FIG. 171.—*Blastotrochus nutrita* (after C. Semper). LK, Lateral bud.

If the individuals so produced remain connected with one another, a polyp-stock is formed, which may attain very various forms and great size. As a rule the individuals are imbedded in a common body mass, the *cænenchym*, and their gastric cavities communicate more or less directly, so that the juices acquired in the individual polyps penetrate into the collective stock. This stock affords us an excellent example of an animal community built up out of similar members. The formation of the generative products alone is distributed, as a rule, to different individuals, which, however, unite in discharging all animal and vegetative functions together (fig. 172).

The skeletal formations of the polyps are specially worthy of remark (*polyparia*). In almost every case, with the exception of *Aetinia*, there is a deposit of solid calcareous matter in the mesoderm, and

* Like the first tentacle of the young *Scyphistoma* polyp among the *Hydro-Medusæ*.

according to the density of this deposit, there is produced a leathery, chalky, or even stony framework.

If isolated needles or toothed rods (fig. 173) of calcareous substance are distributed beneath the epidermis and the cœnenchyma, the polyp-stock has a fleshy, leathery nature (*Alcyonaria*); but if, on the contrary, the calcareous structures are fused together or are cemented together in a larger mass, a solid, more or less firm, often stony calcareous skeleton is developed (*Madreporaria*). In the individual

animals the formation of this sub-epidermic skeleton begins on the foot surface, and advances thence in such a manner that near the calcareous foot-plate there is formed in the under part of the polyp body a more or less cup-shaped theca, from which numerous perpendicular plates, the *septa*, radiate inwards. In the cup-shaped calcareous framework of the individual polyp, the structure of the gastrovascular cavity is repeated, with the exception that the calcareous septa correspond to the interspaces of the mesenteries (fig. 174). The number of the septa increases as does that of the mesenteries and tentacles with the age of the polyp according to the same laws. At the same time a great number of systematically important

FIG. 173.—Calcareous bodies (*Sclerodermites*) of *Alcyonaria* (after Kölliker). *a*, of *Plexaurella*. *b*, of *Gorgonia*. *c*, of *Alcyonium*.

modifications of the skeleton are effected by further differentiation. A column-like, calcareous mass sometimes arises in the axis of the cup (*columella*), and in its neighbourhood a circle of calcareous rods (*pali*), which are separate from the septa (fig. 175). There may further be formed between the lateral surfaces of the septa processes of calcareous substance as interseptal rods or horizontal shelves (*dissepimenta*); also on the outer side of the wall of the theca ribs (*costæ*) projecting beyond its external surface, and similar dissepiments may be produced between these.

The important diversities of form in the polyp stocks are not only occasioned by the differences of structure of the skeleton of the

FIG. 174.—Vertical section through a polyp of *Astroides calycularis* (after Lacaze Duthiers). The mouth opening and oesophageal tube are seen as well as the mesenteries fastened to the same; also the calcareous septa between the mesenteries, and the columella of the skeleton, *Sk*.

FIG. 175.—Vertical section through the cup of *Cyathina Cyathus* (after Milne Edwards). *S*, Septa; *P*, pali; *C*, columella.

polyp, but are also the resultant of varying methods of growth by gemmation and imper-

FIG. 176.—*Madrepora verrucosa* after Ed. H.

fect fission. According to the method, numerous modifications of branched stocks are distinguished, e.g., *Madrepores* (fig. 176), *Oculinidæ* (fig. 177), and the lamellar and massive stocks as *Astræa* (fig. 178) and the *Mæandrinidæ* (fig. 179).

The *Anthozoa* are all inhabitants of the sea,

FIG. 177.—Branch of *Oculina speciosa* (after Ed. H.).

and live mostly in the warmer zones, but certain types of the fleshy

Octactinia and *Actinia* are distributed in all latitudes. The polyps which build banks and reefs are confined to a zone extending about 28 degrees on either side of the equator, and only here and there extend beyond these bounds. They live for the most part near the coast, and produce there in course of time rocky masses of colossal extent by the accumulations of their stony calcareous frameworks.

FIG. 178.—*Astraea* (*Goniastraea*) *pectinata* Ehrbg. (after Klunzinger).

These masses may form *coral reefs* (*atolls*, *barrier reefs*, *fringing reefs*), which are perilous to shipping, and may also become the foundations of islands. In both cases a gradual alteration of level, the raising of the bottom of the sea, assists the work of the coral animals. The presence of the coral banks in the deep sea is, on the other hand, due to a continual sinking of the sea-bottom

The part which the *Anthozoa* take in the alteration of the earth's surface is considerable. In the present time they protect the coast

FIG. 179.—*Meandrina* (*Caeloria*) *arabica* Klz. (after Klunzinger).

from the consequences of the breaking of the waves and assist in the formation of islands and rocks by producing immense masses of calcareous matter. In earlier geological epochs they have played a still more important part judging from the great thickness of

the coral formations of the Palæozoic period and of the Jurassic formation.

Order 1.—RUGOSA = TETRACORALLA.

Palæozoic Corals with numerous symmetrically arranged septa, grouped in multiples of four.

To these belong the families of the *Cyathophyllidæ*, *Stauridæ*, etc.

Order 2.—ALCYONARIA = OCTACTINIA.

Polyps and polyp stocks with eight plumed tentacles and the same number of uncalcified mesenteric folds.

The calcareous secretions of the so-called cutis lead to the formation of fleshy polyparia or of friable crusts surrounding an axial skeleton, which is sometimes horny, sometimes calcareous and stony, or of rigid calcareous tubes (*Tubipora*). In all cases definite calcareous bodies, the sclerodermites, form the foundation of the skeleton. The embryos are mostly born as ciliated larvæ, without mesenteries or tentacles. The separation of the sexes in different individuals is the rule (fig. 172).

1. Fam. *Alcyonidæ*. Fixed polyp stocks without axial skeleton, usually with a fleshy, leathery polyparium, with only a slight deposition of calcareous matter in the cutis. The colonies arise either through lateral gemmation, when they form lobed and ramified masses, *e.g.* *Alcyonium palmatum*, Pall., *digitatum* L., or the individual animals are connected by basal buds and root-like processes, *e.g.*, *Cornularia crassa* Edw.

2. Fam. *Pennatulidæ* (Sea feathers). Polyp stocks, the naked free basis of which is embedded in sand and mud, usually with horny, easily bent axial skeleton. There are small sterile polyps as well as the sexual animals. The presence of an opening in the stem for the ejection and reception of water is worthy of remark. The animals sometimes are placed on the side twigs of the stem, and the polyparium is feather-like, *e.g.*, *Pennatula rubra* Ellis; sometimes they are distributed on all sides of the simple stem, *e.g.*, the dioecious *Veretillum cynomorium* Pall. In other cases the polyparium appears flat and shaped like a kidney, with a bulbous root without an axis, *Renilla violacea* Quoy. Gaim., or a kind of umbel is formed by the aggregation of the polyps at the upper end of a long stem, *Umbellula Thomsonii* Köll.

3. Fam. *Gorgonidæ*. The fixed colonies possess a horny or calcareous tree-like branched axial skeleton, which is surrounded by a friable crust, or by a softer parenchyma containing calcareous particles. The body cavities of the individual animals communicate by branched vessel-like tubes which contain the common nutritive fluid. The axis is either horny, flexible, and unjointed, as, *e.g.*, *Gorgonia verrucosa* Pall., (*Rhipidogorgia*) *flabellum* L., or composed of alternating horny and calcareous segments, as, *e.g.*, *Isis hippuris* Lam., *Melithæa ochracea* Lam., or stony and formed of calcareous matter. The red coral, *Corallium rubrum* Lam., falls under the last head, and yields the coral stone which is used in jewellery. This species is found in the Mediterranean, on the rocky coasts of Algiers and Tunis, and there forms an important object of industry.

4. Fam. *Tubiporidæ*, organ coral. The polyparia resembling the pipes of an organ. The animals are placed in parallel calcareous tubes connected by horizontal plates. *Tubipora Hemprichii* Ehrbg.

Order 3.—ZOANTHARIA = HEXACTINIA.

Polyps and polyp stocks, whose tentacles usually alternate in several circles, and are either six or some multiple of six in number.

The body is seldom quite soft, or with a leathery framework; as a rule it has a calcareous stony polyparium with radial striations. Separated sexes are the rule, but hermaphrodite polyps (*Actinia*) are not seldom to be met with. The polyps very generally retain their embryos for a long time, so that they are born eight or twelve rayed, with rudimentary tentacles. Many give rise to coral reefs and islands (figs. 175—179).

1. ANTIPATHARIA. Mostly with only six tentacles, and horny skeletal axis.

Fam. **Antipathidæ**. Polyp stocks with soft non-calcareous body, but with simple or branched axial skeleton. Only six tentacles surround the mouth, *e.g.*, *Antipathes* Pall.

2. ACTINIARIA, with no hard structure.

Fam. **Actinidæ**, with soft body; sometimes single animals with several alternating circles of tentacles, *Actinia* L.; sometimes connected in stolons and aggregated to form stocks, *Zoanthus* Cuv. The former are able, by means of their contractile foot, to leave their place of attachment and to move freely. Many reach a relatively considerable size, and possess beautiful colours. Under the name of sea anemones they are the ornaments of salt water aquaria. *Actinia mesembryanthemum* L. The skin sometimes secretes a glutinous mass filled with nematocysts or a kind of membrane, *Cerianthus* Delle Ch.

3. MADREPORARIA with continuous hard calcareous skeleton.

(a) *Aporosa*.

Fam. **Turbinolidæ**. Mostly single polyps with compact calcareous framework, imperforate thecæ, and well developed septa, the spaces between which are open to the bottom. *Turbinolia* Lam., *Flabellum* Less., *Caryophyllia* Lam., *C. cyathus* Lam., *Blastotrochus* Ed. H.

Fam. **Oculinidæ**. Polyp stocks with hard usually branched polyparium, with coenenchyma rich in calcareous matter, and but few septa in the cup of the individual. *Oculina virginea* Less., Indian Ocean. *Amphihelia oculata* L. white corals of the Mediterranean.

Fam. **Astræidæ**, Star corals. Mostly massive polyp stocks with fused thecæ, and without coenenchyma. The septa have sometimes cutting edges, sometimes toothed edges. The interseptal spaces are filled with horizontal partition walls. *Eusmilia* Edw. The single animals are produced by fission and remain connected only at their bases. They produce a cespituous polyparium, the septal edges of the cup being cutting. *Galaxea* Oken. The single cups arise by gemmation, are free at the upper edge; the septa have cutting edges. *Astræa* Lam., single cups fused throughout the entire wall. The septal edges of the cup are jagged. *Mæandrina* Lam., the neighbouring cups fused to form long valleys. *M. Crassa* Edw. H.

Fam. **Fungidæ**. Mushroom corals. Usually with large flat single cups, sometimes polyp stocks; without thecæ, with numerous strongly developed septa, toothed and connected by synapticulæ. *Fungia discus* Dana., *Halomitra* Dana., *Lophoseris* Edw. H.

(b) *Perforata*.

Fam. **Madreporidæ**, Madrepores. Polyps and polyp stocks with porous coenenchyma and perforated thecæ. Gastric cavity open at the bottom and communicating with the central canal in the axis of the branched polyparium.

Septa but slightly developed. *Madrepora cervicornis* Lam., *Dendrophyllia ramea* Edw., Mediterranean, *Astroides ealycularis* Pall.

CLASS II.—POLYPOMEDUSÆ.* [HYDROZOA.]

Polyps without œsophageal tube, with simple gastrovascular cavity. The generative elements are developed in medusoid forms which may be either free-swimming, or permanently attached to hydroid forms.

This class includes the small polyps and polyp stocks, and the *Medusæ* which form the sexual generation. The *Polypomedusæ* have always a simpler structure than the *Anthozoa* to which they are also usually inferior in size. They lack œsophagus, septa, and gastrovascular pouches. Only the polyps of the asexual generation of the *Scyphomedusæ* [*Acraspeda*], known as *Scyphistoma*, possess a remnant of the gastric folds as four gastric ridges from which filaments are developed. The polyp stocks develop in rare cases (*Milleporidæ*) a compact calcareous framework comparable to the polyparium. When skeletal formations are present they consist as a rule of more or less horny secretions of the ectoderm, which as delicate

FIG. 180 a.—Branch of an *Obelia*-stock (*O. ge'atinosa*). *O*, Mouth of a nutritive polyp with extended tentacles. *M*, Medusa buds on the body of a proliferous polyp (blastostyle); *Th*, bell-shaped cup (theca) of a nutritive polyp.

tubes surround the stem and its ramifications, and sometimes form small cup-like structures surrounding the polyp, and known as

* Escholtz, "System der Acalephen," Berlin, 1829. Th. Huxley, "Memoir on the Anatomy and Affinities of the Medusæ," *Phil. Trans.*, London, 1849.

hydrothecæ (fig. 180 *a*). A more or less stiff mesoderm lamella is also developed in the interior of the body wall, between the ectoderm and the endoderm. This serves to support the soft parts of the animal, and, in the *Medusæ*, is in part represented by the gelatinous connective tissue of the disc.

The *Medusa* (fig. 180 *b*) is without doubt morphologically higher than the *Polyp*, since it represents the mature sexual individual, while the *Polyp* performs the nutritive and vegetative functions.

The *Medusa*, in correspondence with its power of free locomotion, possesses an ectodermal nervous system and sense organs. The nervous system consists of nerve fibres and ganglion cells, and is usually specially concentrated round the edge of the disc, where it

forms a double ring of fibres running parallel to the circular vessel.

The sense organs are the so-called marginal bodies.

The generative products of the *Medusæ* either have their origin in the ectoderm, in which case they may be developed on the under surface of the disc (sub-umbrella) in the ectoderm immediately underlying the radial canals (*Eucopidæ*), or in the ectoderm of the

FIG. 180 *b*.—Free *Medusa* of *Obelia gelatinosa*, as yet without generative organs; *g*, auditory vesicles.

manubrium (*Oceanidæ*); or they may arise from the endoderm of the under surface of the umbrella (*Scyphomedusæ*).

Both *Polyps* and *Medusæ* frequently remain at a lower grade of morphological differentiation, the former becoming polypoid appendages, the latter medusoid buds enclosing the generative products. In either case they are situated on the stem or on some part of the *Polyp*. The individuality of such appendages appears limited; the medusoid or polypoid animal sinks, physiologically speaking, to the value of a portion of the body or of an organ, while the entire stock

approaches more nearly to a single organism. The more completely polymorphism and division of labour are impressed upon the polypoid and medusoid appendages, so much higher becomes the unity of the whole which is morphologically a colony of animals. In these cases it is often difficult to distinguish between budding and simple growth.

For a long time it was considered as a remarkable circumstance, hardly admitting of a satisfactory explanation, that organisms which differed so widely as Polyps and Medusæ—they had, indeed, been systematically separated as different classes—should only form different stages in the life-history of a single cycle of development and thus be united in the closest genetic connection. The theory of "Alternation of Generations" contained only a description of the matter, and offered no explanation. The discovery of the mode of origin of the Medusa as a bud on the body of the Polyp first clearly demonstrated the direct relation of the two forms, for it proved that *the Medusa is a flattened, disc-shaped Polyp with a shallow but wide gastric cavity, the peripheral part of which has, by the fusion of its upper and lower walls along four, six, or eight radiating areas, become divided into the vascular pouches (gastric pouches), or, as they are called, radial canals, which correspond to the gastrovascular pouches of the Anthozoa.* The differences consist, in connection with the discoidal form, mainly in the position of the gastric tube as an external appendage, the manubrium, and in the great reduction in height of the radially extended septa (mesenteries), which are traversed by a layer of endoderm cells, the vascular or endoderm lamella. This layer is derived from the fusion mentioned above of the aboral with the oral layer of the endoderm of the peripheral part of the gastro-vascular cavity. At the same time the oral disc becomes enlarged and concave to form the cavity of the bell, the ectodermal lining of which gives rise to the muscles of the subumbrella. The supporting substance of the arched (after it is freed from its attachment) aboral surface of the disc becomes very much thickened and gives rise to the gelatinous substance (mesodermic), which sometimes contains cells; while that of the oral surface keeps the character of a thin but firm lamella, and serves as a support for the muscles on the under surface of the disc. The tentacles accordingly arise near the edge of the disc, and become the marginal tentacles of the *Medusa*. In addition to these, four simple or branched oral appendages appear as outgrowths from the manubrium.

In addition to the sexual reproduction, asexual multiplication is

widely distributed, especially amongst the polypoid forms, in which it leads to the formation of polymorphous animal stocks. The two forms of reproduction alternate for the most part in regular order, so as to produce different generations. There are, however, *Medusæ* (*Aeginopsis*, *Pelagia*) which proceed without alternation of generations and develop directly from the ovum by continuous development with metamorphosis; but, as a general rule, the egg of the *Medusa* (phanero-codonic gonophore) or the medusoid generative bud (adelo-codonic gonophore) produces a Polyp, and this Polyp either at once, by transverse fission (*Scyphomedusæ*), or later, after a longer period of growth, in which a sessile or free-swimming polyp stock is produced, gives rise to a generation of free-swimming *Medusæ*, or of medusoid buds which never become separate from the polyp stock. The Hydromedusæ feed entirely on animal substances, and for the most part are inhabitants of the warmer seas. The free-moving *Medusæ* and *Siphonophora* are phosphorescent.

Order 1.—HYDROMEDUSÆ.*

Colonial forms, the individual Polyps of which are without œsophageal tube or mesenteric folds. The sexual generation has the form either of small free-swimming Medusæ provided with a velum (Craspedote Medusæ) or of medusoid generative buds (rudimentary Medusæ) which remain attached to the hydroid colony.

The Polyps and polypoid forms are the asexual individuals. They form small moss- or tree-like stocks which are frequently surrounded by chitinous or horny tubes (cuticular skeleton). These exoskeletal structures may become extended into cup-like hydrothecæ surrounding the individual Polyps. The stem and ramified branches [cœnosark] contain a central canal which communicates with the gastric space of each individual Polyp and polypoid appendage and contains the common nourishing fluid.

The Polyps have no œsophageal tube, and the ciliated gastric cavity is undivided by mesenteries. As a rule, the ectoderm and entoderm remain simple, and are only separated by a thin interposed supporting lamella which does not contain cells. The presence of elongated muscle fibres as processes of the ectodermal epithelial cells is very general (*Hydra*, *Podocoryne*). These muscles may, however,

* L. Agassiz, "Contributions to the Natural History of the United States of America," vol. ii.—iv., 1860—1862. G. J. Allman, "A Monograph of the Gymnoblatic or Tubularian Hydroids," vol. i. and ii., London, 1871 and 1872. N. Kleinberg, "Hydra," Leipzig, 1872. O. and R. Hertwig, "Das Nervensystem und die Sinnesorgane der Medusen," Leipzig, 1878.

be separated as an independent layer of nucleated fibre cells below the epithelium.

The Polyps are not invariably alike, proliferous Polyps (or Blastostyles) being frequently found as well as the nutritive ones. The proliferous Polyps develop generative buds on their walls. The sterile Polyps may differ from one another in the number of tentacles and in their entire form, so that different kinds of individuals may be found on a single stock. Thus we find the polymorphism of the *Siphonophora* foreshadowed amongst the *Hydroidea* (*Podocoryne*, *Plumularia*).

The generative products are only exceptionally developed in the Polyp body itself, in which case they are produced in the ectoderm (*Hydra*). This exception is probably to be looked upon as an extreme case of degeneration of a medusoid bud. As a rule the generative products are developed in special medusoid buds [gonophores] formed from both cell-layers.

In the most simple cases the budding individuals of the sexual generation contain a diverticulum of the gastric cavity of the

FIG. 181.—*Podocoryne carnea* (after C. Grobben). P, Polyp; M, Medusa bud on the proliferating polyp; S, spiral-zooid; Sk, skeleton Polyp (compare the free Medusa, fig. 154).

polyp-shaped parent or of the axial cavity of the hydroid stock. The generative products become accumulated around this diverticulum (*Hydractinia echinata*, *Clava squamata*). In a more advanced stage we find a mantle-like envelope enclosing the bud, and constituting the rudiment of the umbrella, with a continuous vascular lamella or with more or less developed radial vessels (*Tubularia coronata*, *Eudendrium ramosum*, Van Ben.) Finally, at the highest stage, the buds develop into small Medusæ (*Campanularia gelatinosa* van Ben., *Sarsia tubulosa*), which become free, and sooner or later,

often only after a long period of free life, in which they become much larger and undergo a metamorphosis, reach sexual maturity.

The Medusæ belonging to the order Hydromedusæ are, with but few exceptions, distinguished from the *Acalephæ* (Scyphomedusæ) by their smaller size—although certain forms, for example *Aequorea*, may attain such a size as to have a diameter of more than a foot—and by their simpler organization. The number of their radial vessels is smaller (4, 6, or 8), their sense organs (marginal bodies) are not covered by folds of membrane (hence *Gymnophthalmata* Forbes), and they have a muscular velum (hence *Craspedota* Gegenbaur) (fig. 182). The generative products are always formed from the ectoderm, and originate on the walls of the radial canals or of the manubrium, but

never, as in the *Acalepha*, in diverticula of the gastric cavity.

The hyaline gelatinous substance of our Medusæ is, as a rule, structureless, and contains no cellular elements; there may, however, be fibres running perpendicularly through it (*Liriope*). These fibres are probably derived from cell processes of the ectoderm and entoderm, and have arisen contemporaneously with the gelatinous disc, which is itself to be looked upon as an excretion product of the adjoining

FIG. 182.—*Phialidium variabile* represented from the underside of the umbrella. *V*, Velum; *O*, mouth; *Ov*, ovary; *Ob*, auditory vesicle; *Rf*, tentacles on the margin of the disc; *Rw*, marginal swellings.

ectoderm and entoderm epithelium.

The nerve-ring is placed at the edge of the disc at the point of insertion of the velum. It is covered by a sense epithelium composed of small cells bearing sense hairs, and has the form of a double fibrous cord containing ganglion cells. The larger upper nerve-ring runs above the velum, while the weaker nerve-ring, on the other hand, is placed below it. The lower nerve-ring is composed of larger fibres and larger ganglion cells; bundles of fibrillæ pass off from it to supply the muscles of the velum and subumbrella, where they form a sub-epithelial plexus interspersed with ganglion cells, between

the muscular epithelium and the fibrous layer. The ganglion cells in the upper nerve-ring are smaller, and the fibrillæ given off from it pass to the tentacles. The fibrillæ of the sense nerves may be derived from both rings. The *marginal bodies* have long been recognised as sense organs, and are either eye spots (ocelli) or auditory vesicles; hence the *Hydromedusæ* may be divided into two groups, the Ocellata or Vesiculata.

In the *Vesiculata* the auditory vesicles are situated at the edge of the under side of the umbrella, and contain one or more concretions (otoliths) which are formed in the interior of cells. Peculiar sense cells surround each vesicle-like cell containing a concretion. The curved hairs of these sense cells (auditory hairs) are in contact with the concretion vesicle. A nerve fibrilla enters the basis of the auditory cells (fig. 183).

FIG. 183.—Sense organ on the nerve-ring and circular vessel of *Octorchis* (after O. and R. Hertwig). *Rb*, Sense organ; *O*, *O'*, two otoliths; *Hh*, auditory cilia; *Hz*, auditory cells; *Nv*, upper nerve-ring; *Rg*, circular vessel. (Type of the auditory organ of the *Vesiculata*.)

The auditory organs of the *Trachymedusæ* are placed above the velum, and are in connection with the upper nerve ring; they have the form of

FIG. 184.—Auditory vesicle of *Geryonia* (*Carmarina*), seen from the surface (after O. and R. Hertwig). *N* and *N'*, The auditory nerves; *Ot*, otolith; *Hz*, auditory cells; *Hh*, auditory cilia (type of the auditory organ of the *Trachymedusæ*).

small projecting tentacles furnished with otoliths and auditory hairs. The tentacle may either project freely on the surface (*Trachynema*), or, as in *Geryonia*, it may be placed in a vesicle (fig. 184) which lies in the gelatinous substance of the disc and close to the edge of the latter.

Separate sexes are almost invariably the rule, but it is rare to find that the colonies are dioecious, *i.e.*, that male and female medusoids are developed in different colonies (*Tubularia*). Gemmation has occasionally been observed among the *Medusæ* (*Sarsia prolifera*) and division (*Stomobrachium mirabile*). The larvæ of *Cunina*, which are parasitic on the *Geryoniidæ*, may also there give rise to a cluster of buds.

The development of the ovum, which is, as a rule, naked (*i.e.*, without a vitelline membrane), has hitherto only been completely followed out in a few cases. In every case the segmentation seems to be complete, and leads to the formation of a segmentation cavity and a single-layered blastoderm [a single-layered blastosphere]. The latter gives rise to a second endodermal layer of cells, which lines the segmentation cavity. The segmentation cavity thus becomes converted into the gastric cavity of the future polyp. The spherical or oval larva now either attaches itself and gives rise by budding to a small hydroid stock, or swims freely and develops directly into a small Medusa (*Trachymedusæ*).

The *Medusa*, after becoming free, usually undergoes a more or less fundamental change of form, which concerns not only the alteration caused by the enlargement of the umbrella and manubrium, but also the increase, according to definite laws, of the marginal tentacles, sense organs (*Tima*), and the radial canals (*Aequorea*). We must remark, however, that the sexually complete Medusæ exhibit very considerable variations in size, number of sense organs and tentacles (*Phyalidium variabile*, *Clythia volubilis*).

The difficulty of systematic arrangement is augmented by the fact that closely allied Polyp stocks can produce different sexual forms. Thus, for example, *Monocaulus* gives rise to sessile generative buds and *Corymorpha* to free Medusæ (*Steenstrupia*). Medusæ of identical structure also, which one would place in the same genus, may form the sexual generations of hydroid stocks belonging to different families (*isogonism*). There are also cases in which we find Medusæ of closely allied genera, some developed from hydroid stocks by an alternation of generations, and others developed directly. Hence it appears just as little satisfactory to found a classification entirely upon the sexual generations as to pay attention to the asexual generation alone.

(1) Sub-order: *Eleutheroblasteæ*. Simple hydroid Polyps without medusoid buds; both generative products are developed in the body-wall of the Polyp.

Fam. **Hydroidæ**. *Hydra*, the fresh-water polyp. *H. viridis* L., *H. fusca* L., remarkable for great powers of reproduction.

(2) Sub-order: *Hydrocoralliaæ*. Coral-like hydroid stocks with calcareous coenenchyma and tubular hydrothecæ opening to the exterior by pores. Some of these contain the larger nutritive animals, while others contain animals without a mouth and beset with tentacles.

The latter are arranged usually in the form of a circle round each of the nutritive animals. The polyparia are found in the fossil state

Fam. *Milleporidæ*. *Millepora* L. *M. alcicornis* L.

Fam. *Stylasteridæ*.

(3) Sub-order: *Tubulariæ* (Ocellata). Polyp stocks which are either naked or clothed by a chitinous periderm without cup-shaped hydrothecæ surrounding the polyp head. The generative buds arise on the body of the Polyp or on the stock. The *Medusæ* which are set free belong to the genera *Oceania*, *Sarsia*, etc., and have ocelli.

Fam. *Clavidæ*. Polyp stocks with a chitinous periderm. Polyp club-shaped, with scattered, simple, filiform tentacles. The generative buds arise on the Polyp body and for the most part remain sessile. *Cordylophora* Allm. The stock is branched; there are stolons which grow over external objects. Oval gonophores covered by the perisarc. The animals are dioecious. In fresh water—*C. lacustris* Allm. *albicola* Kirchp., Elbe, Schleswig. The following are marine genera—*Clava* O. Fr. Müller. Allied are the *Eudendridæ* with *Eudendrium ramosum* L.

Fam. *Hydractinidæ*. Polyp stocks with flat extended coenenchyma and firm encrusted skeletal excretions. The Polyps are club-shaped, with a circle of simple tentacles. In addition to the latter there are large tentacle-shaped Polypoids (Spiralzooids). *Hydractinia* van. Ben. The medusoid buds sessile on the proliferous animals, which are without tentacles. *H. echinata* Flem. *Podocoryne* Sars. (fig. 181). The generative buds are freed as *Oceanidæ*. *P. carnea* Sars.

Fam. *Tubularidæ*. Polyp stocks clothed with a chitinous periderm. The polyps possess a circle of filiform tentacles on the proboscis inside the external circle of tentacles. The generative buds arise between the two circles of tentacles. *Tubularia* L. The hydroid stocks form creeping root-like branches at the bottom, from which arise simple or branched twigs with the terminal polyp heads; the generative buds are sessile. *T. (Thamnocnidia* Ag.) *coronata* Abilg. dioecious. *Corymorpha* Sars. The stalk of the solitary polyp is clothed with a gelatinous periderm, attaches itself by root-like processes, and contains radial canals which lead into the wide digestive cavity of the Polyp-head. The freed *Medusa* is bell-shaped, with one marginal tentacle, and bulbous swellings at the end of the other radial canals. *C. nutans* Sars., *C. nana* Alder.

(4) Sub-order: *Campanulariæ* (Vesiculata). The chitinous skeletal tubes widen out round the Polyp-head to form cup-like hydrothecæ. The Polyp-head, the oral cone (proboscis), and tentacles can be in most cases completely retracted into these hydrothecæ.

The generative buds arise almost regularly on the walls of the proliferous individuals, which have neither mouth nor tentacles. The buds are sometimes sessile, and sometimes become separated off

as small vesiculate *Medusæ*, with generative organs on the radial canals (*Eucopidæ*, *Geryonopsidæ*, *Aequoridæ*).

Fam. Plumularidæ. The hydrothecæ of the branched hydroid-stocks are arranged in single rows; those of the nutritive Polyp have small accessory calyces filled with nematocysts (nematocalyces). *Plumularia cristata* Lam., *Antennularia antennina* Lam.

Fam. Sertularidæ. Branched Polyp stocks, the Polyps of which project in flask-shaped hydrothecæ on opposite sides of the stem. *Dynamena pumila* L., *Sertularia abietina*, *cupressina* L.

Fam. Campanularidæ—Eucopidæ. The cup-shaped hydrothecæ are placed at the end of ringed stalks. The Polyps possess a circle of tentacles below their conical proboscis. *Campanularia* Lam. The proliferous individuals are situated on the branches and give rise to free *Medusæ*, bell-shaped, with a short manubrium with four lips, four radial canals, the same number of marginal tentacles, and eight inter-radial marginal vesicles. After separation the inter-radial tentacles are formed. *C. (Clythia) Johnstoni* = *volubilis* Johnst., probably with *Eucepe variabilis* Cls. *Obelia* Pér. Les., is distinguished from *Campanularia* by its *Medusæ*. These are flat, disc-shaped *Medusæ* with numerous marginal tentacles, but with eight inter-radial vesicles. *O. dichotoma* L. = (*Campanularia gelatinosa* van Ben.), *C. geniculata* L., *Laomedea* Lamx. The generative buds remain sessile in the hydrotheca of the proliferous polyps. *L. caliculata* Hincks.

Fam. Aequoridæ. *Medusæ* with numerous radial vessels and marginal tentacles. *Aequorea* Forsk. The *Geryonopsidæ* are allied here. *Octorchis* E. Hæeck. *Tima*.

(5) Sub-order: *Trachymedusæ*. *Medusæ* with firm, gelatinous umbrella, supported by cartilaginous ridges with stiff tentacles filled with solid rows of cells; these may be confined to the young stage (larvæ of *Geryonidæ*). Development by metamorphosis without hydroid asexual individual.

Fam. Trachynemidæ, with stiff marginal tentacles, which are scarcely capable of motion. The genital organs are developed on vesicle-like swellings of the eight radial canals. *Trachynema ciliatum* Ggbr. *Rhopalonema velatum* Ggbr., Messina.

Fam. Aeginidæ. The hard cartilaginous umbrella has a flat, discoid shape. The extended digestive cavity has pouch-like enlargements in place of the radial vessels. The circular vessel is usually reduced to a row of cells. *Cunina albescens* Ggbr., Naples. *Aegineta flavescens* Ggbr.

Fam. Geryonidæ. Umbrella with cartilaginous mantle ridges and four or six hollow tube-shaped marginal tentacles. The manubrium is long, cylindrical, or conical, with a proboscis-like oral portion, and four or six canals which lead into the radial canal. The generative organs lie on the radial canals; eight or twelve marginal vesicles. *Liriope* Less., with four radial canals, four or eight tentacles and eight vesicles. *L. tetraphylla* Cham., Indian Ocean. *Geryonia* Pér. Les., with six radial canals without lingual cone. *G. umbella* E. Hæeck, *Carmarina* E. Hæeck., with six radial canals and a lingual cone, E. Hæeck. *C. hastata*, Nice.

Order 2.—SIPHONOPHORA.*

Free-swimming polymorphous hydroid-stocks with contractile stem, with polypoid nutritive individuals and medusoid buds, usually also with nectocalyces, hydrophyllia and dactylozooids.

Morphologically the *Siphonophora* are directly allied to the hydroid-stocks; but they possess to a much greater extent than the latter the characters of individuals, in consequence of the highly developed polymorphism of their polypoid and medusoid appendages. The functions of the latter seem so intimately connected and are so essential for the preserva-

FIG. 185.—Diagram of a colony of *Physophorida*. *St*, Stem; *Ek*, ectoderm; *En*, entoderm; *Pn*, Pneumatophor; *Sk*, nectocalyx being budded off; *S*, nectocalyx; *D*, hydrophyllium; *G*, gonophore; *T*, dactylozooid; *Sf*, tentacle; *P*, polyp; *O*, mouth of the latter; *Nk*, battery of nematocysts.

* Besides Klliker, C. Vogt, Huxley and others, compare C. Gegenbaur, "Beobachtungen ber Siphonophoren," *Zeitschrift fr wiss. Zool.*, 1853. C.

nophora physiologically as an organism and its appendages as organs. In this connection we may mention that the sexual medusoid generation is so little independent that it only exceptionally (*Veilellidæ*) reaches the morphological grade of the free-swimming Medusa.

In place of the attached and ramified hydroid-stocks we find in

FIG. 186.—A portion of the stem and appendages of *Halistemma tergestinum*. *St*, Stem; *D*, hydrophyllium; *T*, dactylozoid; *Sf*, tentacle of the latter; *Wg*, female, *Mg*, male, gonophores.

the *Siphonophora* a free-swimming contractile unbranched stem (hydrosoma), which is rarely provided with simple lateral branches. The upper end of the hydrosoma is frequently dilated to the form of a flask (pneumatophore), and contains an air chamber [pneumatocyst] (fig. 185). In every case there is a central space in the axis of the stem in which the nutritive fluids are kept in constant motion by the contractility of the walls and by the movements of the cilia. The air sac or pneumatocyst at the apex of the hydrosoma is connected to the chamber which contains it by radial septa, and in many cases attains a considerable size (*Physalia*). It functions as a hydrostatic apparatus, and in those forms, which have a long spiral hydrosoma (*Physophoridae*), serves to keep the body in an upright position. In some cases the gaseous contents can escape freely by one or more openings.

The appendages which are attached to the spirally twisted bilaterally symmetrical stem and whose cavities communicate with that of the stem are of at least two kinds

—(1) The polypoid nutritive animals with their tentacles; (2) the medusoid sexual buds. The nutritive Polyps (hydranths) are simple tubes provided with a mouth, and never

Gegenbaur, "Neue Beiträge zur Kenntniss der Siphonophoren," *Nova Acta.*, Tom. XXVII., 1859. R. Leuckart, "Zoologische Untersuchungen," I., Giessen, 1853. R. Leuckart, "Zur näheren Kenntniss der Siphonophoren von Nizza," *Archiv. für Naturgesch.*, 1854. C. Claus, "Ueber *Halistemma tergestinum* n. s. nebst Bemerkungen über den feineren Bau der Physophoriden," *Arbeiten aus dem Zoologischen Institut der Univ. Wien, etc.*, Tom. I., 1878. E. Metschnikoff, "Studien über die Entwicklung der Medusen und Siphonophoren," *Zeitsch. für wiss. Zool.*, Tom. XXIV., 1874.

possess a circle of tentacles. They always, however, have a long tentacle arising from their base. This tentacle can be extended to a considerable length, and be retracted into a spiral coil. It rarely has a simple form, but, as a rule, it bears a number of unbranched lateral twigs, which are also very contractile. These tentacles are invariably beset with a great number of nematocysts, which in many places are closely packed and have a regular arrangement. These aggregations of thread-cells are especially found on the lateral branches of the tentacles, and give rise to large, brightly-coloured swellings, the batteries of nematocysts. The batteries show considerable variations

FIG. 187.—Group of buds of a *Physophora* at the bottom of the pneumatophore. *C*, Central cavity; *Sk*, nectocalyx bud with the ectodermal ingrowth.

FIG. 188.—Development of *Agalmopsis Sarsii* (after Metschnikoff). *a*, Ciliated larva. *b*, Stage with developing hydrophyllium (*D*). *c*, Stage with cap-shaped hydrophyllium (*D*) and developing pneumatophore (*Lf*). *d*, Stage with three hydrophyllia, (*D*, *D'*, *D''*), polyp (*P*), and tentacle.

in form in the various species, genera, and families, and such variations afford valuable characters for systematic lacssification.

The second form of appendage, the *gonophores*, usually possess a bell-shaped mantle containing circular and radial vessels, and surrounding the central stalk or clapper (manubrium), which is filled with ova or spermatozoa. They usually arise in clusters at the base of the tentacles, more rarely from the nutritive Polyps themselves (e.g. in *Velella*). The male and female generative products always arise separately in differently shaped buds, but are usually found closely

FIG. 189.—Small larval stock of *Agalmopsis* after the type of *Athorybia*. *Lf*, Pneumatophore; *D*, hydrophyllium; *Nk*, groups of nematocysts; *P*, polyp.

approximated on the same stock (fig. 186). There are, however, also dioecious *Siphonophora*, or if the medusoid buds or gonophores be regarded as generative organs, *Siphonophora* of distinct sexes, e.g., *Apolemia uvaria* and *Diphyes acuminata*. The ripe sexual *Medusoids* frequently become separated from the stock, i.e. after the development of the generative products, and only rarely become liberated as small *Medusæ* (*Chrysomitra* in the *Velellidæ*), which produce generative products during their free life.

Besides the constant nutritive Polyps and medusoid gonophores, there are inconstant appendages, which are also modified Polypoids or Medusoids. These are the mouthless worm-like *dactylozoids* (fig. 186), which, like the Polyps, are provided with a tentacle, which is, however,

shorter and simpler, and has no lateral branches or aggregations of nematocysts; also the leaf-shaped hard cartilaginous *hydrophyllia*, which serve to protect the polyps, dactylozoids, and gonophores; and finally the appendages known as *nectocalyces*, which are placed beneath the pneumatophore. The nectocalyces have a structure similar to that of the *Medusæ*, though their bilateral symmetry is apparent;

they are, however, without manubrium, mouth, tentacles, and sense organs.

The deeply concave sub-umbrella surface of the nectocalyx is largely developed and has a very powerful muscular covering in relation to its exclusively locomotive function. All the appendages are developed as buds formed of ectoderm and endoderm, and containing a central cavity which communicates with the central space of the stem. In the nectocalyces and gonophores an ectodermal ingrowth gives rise to the covering of the sub-umbrella and to the generative products respectively (fig. 187).

The ova, of which there is often only one in each female gonophore, are large, and have no vitelline membrane, and, after impregnation, undergo a complete and regular segmentation.

A nectocalyx (*Diphyes*) is the first structure formed in the free-swimming larva, or the upper part of the body of the larva gives rise to a cap-shaped protective cover or hydrophyllium as well as a pneumatophore, and the under part

becomes the primary nutritive polyp (*Agalmopsis*, fig. 183). Since new buds give rise to leaf-shaped hydrophyllia, a small stock with

FIG. 190.—*Physophora hydrostatica*. Pn, Pneumatophore; S, nectocalyces arranged in double rows on the swimming column; T, dactylozoid; P, polyp (nutritive individual) with tentacles, Sf; Nk, groups of nematocysts on the latter; G, clusters of generative buds.

FIG. 191.—*Halistemma tergustinum*. Pn, pneumatophore; S, Nectocalyx; P, polyp; D, hydrophyllium; Nk, groups of nematocysts.

provisional appendages is formed which allows us to regard the development of the *Siphonophora* as a metamorphosis (fig. 188 and 189).

The crown of hydrophyllia, which is completed by the addition of fresh hydrophyllia after the appearance of a tentacle with provisional groups of nematocysts, persists only in *Athorybia*, where a swimming column with nectocalyces is never formed.

In *Agalmopsis* and *Physophora* the primary hydrophyllia of the larva fall off as the stem becomes larger, and are replaced by nectocalyces.

(1) Sub-order: *Physophoridae*. Stem short, extended in the form of a sac (fig. 190), or elongated spirally (fig. 191), with a pneumatophore, usually nectocalyces, which are arranged in two or more rows on a swimming column below the pneumatophore. Hydrophyllia and dactylozooids are usually present, and alternate with the polyps and gonophores in regular order. The body of the larva usually develops

first a polyp with pneumatophore and tentacle beneath an apical hydrophyllium. The female gonophore has only one egg.

Fam. **Athorybiadæ**. With a bunch of hydrophyllia in place of the swimming column; resembling a persistent larval stage. *Athorybia rosacea* Esch., Mediterranean.

Fam. **Physophoridæ**. s. str. Stem short and enlarged to a spiral sac beneath the swimming column with its double row of nectocalyces. No hydrophyllia but instead two outer bunches of dactylozooids with gonoblastidia, nutritive polyps and tentacles lying beneath them. *Physophora* Forsk., *Ph. hydrostatica* Forsk., Mediterranean (fig. 190).

Fam. **Agalmidæ**. Stem unusually elongated and spirally twisted. Swimming column with two or more rows of nectocalyces. There are both hydrophyllia and tentacles. *Forskalia contorta* M. Edw., *Halistemma*. Dactylozooids and hydrophyllia directly connected with the stem. In the ciliated larva a pneumatophore is first developed at the upper pole. *H. rubrum* Vogt, Mediterranean. *H. tergestinum* Cls. (fig. 191). *Agalmopsis Sarsii* Köll., *Apolemia uvaria* Less., Mediterranean. Dioecious.

(2) Sub-order: *Physalidæ*.—Stem dilated to form a large chamber, the pneumatophore lying almost horizontally, containing a very large pneumatocyst opening to the exterior. Nectocalyces and hydrophyllia absent. On the ventral line of the sac are situated large and small nutritive polyps with strong and long tentacles. There are also clusters of gonophores attached to the tentacle-like polyps. The female buds seem to become free-swimming *Medusæ*.

Fam. **Physalidæ**. With the characteristics of the group *Physalia* Lam., *P. caravella* Esch. (*Arcthusa Til.*), *pelagica*, *utriculus* Esch., Atlantic Ocean.

(3) Sub-order: *Calycophoridæ*. Stem long and without pneumatophore. Swimming column with double row of nectocalyces (*Hippopodidæ*) or with two large opposed nectocalyces, more rarely with only one nectocalyx. There are no dactylozooids. The appendages arise in groups arranged regularly, and can be retracted into a cavity of the nectocalyx (fig. 192). Each group of individuals consists of a small nutritive polyp, a tentacle with naked kidney-shaped groups of nematocysts, and gonophores.

FIG. 192.—*Diphyes acuminata*, magnified about 8 times. *Sb*, Fluid reservoir in the upper nectocalyx (somatocyst).

To these is usually added a funnel or umbrella-shaped hydrophyl-ium (fig. 192). These groups of individuals may in some Diphyids become free, and assume a separate existence as *Eudoxia* (fig. 193). The gonophores contain numerous ova in the manubrium, which often projects as a cone from the aperture of the bell. In the larva the upper nectocalyx is the first formed.

Fam. **Hippopodidæ**. The swimming column has two rows of nectocalyces, and is situate on an upper lateral branch of the stem. The male and female gonophores are grouped in clusters and are situate at the base of the nutritive polyp. *Gleba Hippopus* Forsk., Mediterranean.

Fam. **Diphyidæ**. With two very large nectocalyces at the upper end of the stem and opposite to each other. *Diphyes acuminata* Lkt., dioecious; with *Eudoxia campanulata*. *Abyla pentagona* Esch., with *Eudoxia cuboides*, Mediterranean. *Sphæronectes* Huxl. = *Monophyes* Cls., *Sp. gracilis* Cls. with *Diplophysa inermis*, Mediterranean.

FIG. 193.—Part of a *Diphyid* (after R. Leuckart). *D*, Hydrophyl-ium; *GS*, genital nectocalyx; *P*, polyp with tentacles. The individual groups separate as *Eudoxia*.

(4) Sub-order: *Discoideæ*. Stem compressed to a flat disc, with a system of canal-like spaces (central cavity). Above lies the pneumatocyst in the form of a disc-shaped reservoir of cartilaginous consistence composed of concentric canals opening to the exterior. The polypoid and medusoid appendages are situate on the under side of the disc. In the centre is a large nutritive Polyp, around which are a number of smaller ones. To the base of these small Polyps are attached the gonophores. The dactylozooids are not far from the edge of the disc. The gonophores are set free as small *Medusæ* (*Chrysomitra*), which do not produce the generative material till long after separation.

Fam. **Veilellidæ**. *Veilella spirans* Esch., Mediter-ranean. *Porpita mediterranea* Esch.

Order 3.—SCYPHOMEDUSÆ = ACALEPHA.*

Medusæ of considerable size, with gastric filaments. The edge of the umbrella lobed. The sense organs covered. The embryonic stages are not hydroid stocks but Scyphistoma and Strobila forms.

The *Medusæ* of this order are distinguished from those of the hydroid group by their considerable size and the great thickness of

* Besides the works of Brandt, L. Agassiz, Huxley, Eysenhardt, compare v. Siebold, "Beiträge zur Naturgeschichte der wirbellosen Thiere," 1839. M.

their umbrella, the gelatinous connective tissue of which is richly developed and contains a quantity of strong fibrillæ and a network of elastic fibres, which structures confer upon it a greater firmness and rigidity.

Another characteristic of the group is derived from the structure of the edge of the umbrella. This is divided by a regular number

FIG. 194.—*Aurelia aurita*, from the oral surface. *MA*, The four oral tentacles with the mouth in the centre; *Gk*, generative organs; *GH*, aperture of sub-genital pit; *Rk*, sense organ (marginal body); *RG*, radial vessel; *T*, tentacle at edge of the disc.

of indentations usually into eight groups of lobes between which the sense organs are contained in special pits (fig. 194).

The marginal lobes of the Acalephæ, like the continuous velum of the *Hydromedusæ*, appear to be secondary formations at the edge of the disc. In the young stage known as *Ephyra*, which is common at least to all the *Discophora*, they are present as eight pairs of

Sars, "Ueber die Entwicklung der *Medusa aurita* und *Cyanea capillata*," *Archiv. für Naturgesch.* 1841. H. J. Clark, "Prodromus of the History, etc., of the Order *Lucernaria*," *Journ. of Bost. Soc. of Nat. Hist.* 1863. C. Claus, "Studien über Polypen und Quallen der Adria," *Denkschriften der k. Akademie der Wissensch. Wien*, 1877. C. Claus, "Untersuchungen über *Charybdea marsupialis*," *Arbeiten aus dem Zool. Institut, Wien*, 1878. Also E. Haeckel, l. c.

relatively long tongue-like processes, and grow out from the disc-like segments of the *Strobila* as marginal cones. An undivided marginal membrane (the *velarium*), differing from the velum of the *Craspedota* [in containing prolongations of the canals of the gastro-vascular system], is present in the *Charybdeidae* alone.

The *Acalepha* differ from the *Hydromedusæ* in possessing, as a rule, large oral tentacles at the free end of the wide manubrium. These may be regarded as being derived from an unequal growth of the edges of the mouth. They grow as four arm-like processes of the manubrium from the angles of the mouth, and are placed radially,

FIG. 195.—Diagrammatic longitudinal section through a *Rhizostoma*. *U*, Umbrella; *M*, gastric cavity; *S*, sub-umbrella; *G*, genital band; *Sh*, sub-genital pit; *F*, filament; *SM*, muscle system of the sub-umbrella; *Rgf*, radial vessels; *Rk*, sense organs; *Rg*, olfactory pits; *Al*, ocular lobe; *Sk*, shoulder tufts; *Dk*, dorsal tufts; *Vk*, ventral tufts of the eight arms; *Z*, terminal parts of the arms.

i.e. they alternate with the genital organs and gastric filaments. In some cases the arms become forked at an early period, and four pairs of arms are formed, the lobed tufted edges of which may again divide and sub-divide into many branches. In this case, the margins of the mouth and the opposed surfaces of each pair of arms fuse in early life in such a way that the original central mouth becomes obliterated, and in its place there are developed a number of small tufted orifices on the peripheral parts of the arms, through which nutriment is taken in (*Rhizostomidae*, fig. 195).

The form of the gastrovascular apparatus exhibits considerable differences, which in the *Discophora* may be considered as modifications of the *Ephyra* type. The flat disc of the *Ephyra*, which is split into eight pairs of lobes, contains a central gastric cavity into which the canal of the short, wide, four-cornered manubrium leads. From this central cavity there diverge eight canal-like peripheral diverticula (radial pouches), between which there are formed sooner or later in the vascular lamella the same number of short intermediate canals (intermediate pouches). The radial and intermediate canals sometimes become enlarged, as in *Pelagia* and

FIG. 196. Section through the olfactory pit, the sense-organ (marginal body) and its nerve centre, of *Aurelia aurita*. R, Olfactory pit; L, lobe of the umbrella covering the sense organ; P, eye spot; Ot, otolith of the auditory sac; Z, cells after solution of the otoliths; En, entoderm; Ec, ectoderm with the underlying layer of nerve fibrillæ, F.

Chrysaora, so as to form unusually broad gastric pouches separated by thin septa and without any communication with each other at the periphery. Sometimes, however, they become transformed into narrow vessels, between which, in the broad intervening septa, there is secondarily developed during the subsequent growth by a separation of the two layers of the vascular-lamella, a rich network of anastomosing canals, and near the edge of the disc a circular canal (*Aurelia*, *Rhizostoma*).

The gastrovascular apparatus of the cup- or bell-shaped *Calycozoa* and *Charybdeidae* differs from the types above described, and resembles that of the more primitive *Scyphistoma* stage, in that the gastric cavity presents only four peripheral vascular pouches, which are very wide, and separated by extremely thin septa.

The worm-like movable tentacles of the gastric cavity, the gastric filaments, which are not found in any *Hydromedusæ* afford an important distinctive mark. They correspond to the so-called mesenteric filaments of the *Anthozoa*, and afford the same aid to digestion through the secretion of their glandular entodermal covering. In every case they are attached to the sub-umbrella wall of the stomach, and fall in the four radii of the generative organs (radii of the second order), which alternate with the radii of the angles of the mouth, or radii of the first order. They usually follow the inner edge of the generative organs in a simple or convoluted curved line.

The existence of the nervous system of the *Acalepha* has only recently been demonstrated with certainty. It has been proved that the centres of the nervous system are contained in the ectoderm of the stalk and base of the marginal bodies, and consist of a considerable layer of nerve fibrillæ deep in the ciliated ectodermal epithelium, the nerve cells of which are elongated in the form of a rod, and bend round at their basal extremities to be continued directly into the nerve fibrillæ (fig. 196). There is in addition a widely distributed and important peripheral nerve plexus in the muscles of the sub-umbrella.

Up to the present time no investigations have completely elucidated the manner in which this nerve plexus is related to the nerve centres of the marginal bodies, and how the latter are connected with one another. The existence of a nerve ring on the sub-umbrella surface has been proved only for the *Charybdeidae*, in which the edge of the disc is not notched (fig. 169). The antimeres of the *Acalepha* show in all cases a great degree of individuality, and, when cut off, are able to live for a considerable time.

The marginal bodies, as well as the pit-like depressions on the dorsal side of the excavations in which the marginal bodies are placed (olfactory pits), must be considered as sense-organs.

The marginal bodies are morphologically the remnants of reduced tentacles. They may be seen on the under side of the umbrella in the stage of the *Ephyra*, and are overgrown by portions of the edge of the umbrella (*Steganophthalmata*). [They contain a central canal lined by endoderm and continuous with the gastro-vascular system of the disc, fig. 196]. They appear in all cases to unite the functions

of ocular and auditory apparatus. The auditory function is provided for by a large sac containing crystals, which originates from the cells of the entoderm; while the eye consists of a mass of pigment lying on the dorsal or ventral face, and nearer the end of the stalk. In some exceptional cases (*Nausithoë*) it is provided with a refractile cuticular lens. But it is in the *Charybdeidæ* that the sense body reaches the highest development; for in them, in addition to the terminal sac of otoliths, there is also present, in the wall of the dilated vascular space of the papilla, an extremely complicated visual organ, formed of four small paired and two large unpaired eyes, in which lens, vitreous body, and retina can be distinguished.

The four generative organs of the *Acalepha* can be easily distinguished in consequence of their size and their bright colouring. In some cases, at any rate in the *Discophora*, they protrude as folded bands into special cavities in the umbrella, the so-called sub-genital pits (hence the term *Phanerocarpæ* Esch.) In all cases these bands lie on the lower (sub-umbrella) wall of the digestive cavity (figs. 194, 195), from which they originate as leaf-like prominences. The upper surface is covered with gastric epithelium; the under, which is turned towards the sub-umbrella, with germinal epithelium, the elements of which, in the process of development, pass into the gelatinous substance of the band.

The formation of the cavities in the sub-umbrella of the *Discophora* is due to a local growth of the gelatinous substance of the sub-umbrella; in some cases, however, they may be completely absent (*Discomedusa*, *Nausithoë*). The mature generative products are dehiscenced into the gastric cavity, and pass out through the mouth; but in many cases the ova undergo their embryonic development either in the ovary (*Chrysaora*) or in the oral tentacles (*Aurelia*). Separate sexes are the rule. Male and female individuals, however, apart from the colour of their generative organs, have only slight sexual differences, as, for instance, the form and length of the tentacles (*Aurelia*). *Chrysaora* is hermaphrodite.

In the *Discophora* the development is generally accompanied by an alternation of generations; the asexual generations being represented by the *Scyphistoma* and *Strobila*; but in exceptional cases it is direct (*Pelagia*). In all cases a complete segmentation leads to the formation of a ciliated larva, the so-called *planula*, which attaches itself by the pole which is directed forwards in swimming. This pole is, however, opposite to the gastrula mouth, which in the meantime becomes closed, while round the mouth, which is

formed as a perforation at the free end, the tentacles appear. As in the embryo *Actinia*, two opposite tentacles first make their appearance; not, however, simultaneously, the one appearing after the other, so that the young larva about to develop into the *Scyphistoma* presents a bilaterally symmetrical structure. Subsequently the second pair appear in a plane at right angles to the plane of the first tentacles. These four tentacles mark the radii of the first order. Then alternating with these, but in a less regular succession, the third and fourth pairs appear; and soon after in the plane of these latter four longitudinal folds of the gastric cavity are developed (radii of the second order or of the gastric filaments and genital organs).

The eight-armed *Scyphistoma* soon produces eight fresh tentacles, which succeed one another in irregular succession, and alternate with the tentacles already present. Their position determines the intermediate radii of the future young *Discophor* or *Ephyra*. After the formation of the circle of tentacles and the secretion of a clear basal periderm (*Chrysaora*), the *Scyphistoma* is capable of reproduction by fission and gemmation. At first the *Scyphistoma* appears to multiply only by budding; the second mode of reproduction, the process of strobilization, begins later. This consists essentially in the fission and division of the anterior half of the body into a number of segments, thus changing the *Scyphistoma* to a *Strobila*. The separation of the segments progresses continuously from the anterior end to the base of the *Strobila*, so that after the disappearance of the tentacles, first the terminal segment, then the second, and so forth, attain independent existence. Each segment becomes an *Ephyra*, developing eight pairs of elongated marginal lobes, with a marginal body in the notch which separates the two lobes of the same pair. It is these marginal lobes which give to the edge of the umbrella of the *Ephyra* its characteristic appearance. The young *Ephyra* gradually acquires the special peculiarities of form and organization of the sexually mature animal (*vide* figs. 113 *a—h*).

The number of nematocysts accumulated on the upper surface of the disc and on the tentacles of many *Medusæ* enable them to cause a perceptible stinging sensation on contact. Many, *e.g.* *Pelagia*, are phosphorescent. According to Panceri, this phenomena originates in the fat-like contents of certain epithelial cells on the surface.

In spite of the delicacy of their tissues, certain large *Medusæ* have left impressions in the lithographic slate of Sohlenhofen (*Medusites circularis*, etc.)

(1) Sub-order: **Calycozoa** (Cylicoza).

Cup-shaped Acalepha attached by their aboral pole. They have four wide vascular pouches separated by narrow walls, and eight arm-like processes beset with tentacles on the edge of the umbrella.

The *Calycozoa* are best considered in their relation to the *Scyphistoma*. They may be looked upon as *Scyphistoma* deprived of their tentacles, which indeed are only transitory structures, and elongated so as to assume the form of a cup, and changed in several particulars which are characteristic of the medusa stage. The four septa arise by the fusion of the four gastric folds with the wide oral disc, which becomes drawn in and concave like a sub-umbrella. These four septa separate the same number of gas-

FIG. 197.—*a*, A *Calycozoon* (*Lucernaria*) from the oral surface magnified about 8 diameters. *S*, Septa of the four gastric pouches; *L*, longitudinal muscle fibres with the genital band; *Rt*, marginal tentacles. *b*, The *Calycozoon* seen from the side; *G*, Genital organs; *Gw*, gastric fold in the stalk; at the base is the foot gland.

trovascular pouches; while the margin of the cup is drawn out into eight arm-like processes, from which groups of short, knobbed tentacles arise (fig. 197).

The genital organs extend on the oral wall of the umbrella into the arms as eight band-shaped, plicated ridges. They run along in pairs at the lower part of each septum in the gastric cavity. The ovum, according to Fol, undergoes a complete segmentation, which results in a single-layered blastosphere. This becomes an oval, two-layered larva, which becomes ciliated, swims freely about, and finally attaches itself. The further development probably takes place directly without alternation of generations.

Fam. *Lucernariæ*. *Lucernaria* O. Fr. Müller, Calycozoa with four radial chambers; without genital pouches, and without the accessory chambers of the digestive cavity alternating with these. *L. quadricornis* O. Fr. Müller, *campanulata* Lmx. *Craterolophus* Clark, with genital pouches and four chambers of the gastric cavity alternating with them. *Cr. Leuckarti* Tschb. = *helgolandica* Lkt., Heligoland.

The *Lucernaria* are without exception marine animals, and are remarkable for their great reproductive power. According to A. Meyer, if the stalk be cut off, the cup reproduces a new one, and injured individuals, and even excised pieces, can become perfect animals.

(2) Sub-order: **Marsupialida** (*Lobophora*).

Tetra-radiate Acalepha having a four-sided pouch-like form. The velum has a smooth margin, and contains vessels [prolongations of the gastro-vascular system]. On the margin of the disc there are four vertically placed lobe-like appendages. There are four covered sense organs, and the same number of vascular pouches separated by narrow partition walls.

The *Charybdeæ* are distinguished by the deep bell shape of their body, and were formerly reckoned as "Craspedota" among the *Hydro-medusæ*, with which they certainly have some characteristics in common. Amongst these characteristics the most striking is the possession of a smooth-edged velum, which, however, contains vessels.

On the other hand, the presence of the gastric filaments and of the large sense organs enclosed in

FIG. 193.—*Charybdea marsupialis*, natural size. *T*, Tentacles; *Rh*, marginal bodies (sense organs); *Ov*, ovaries.

niches points to a relationship with the *Acalepha*; and this view is supported by the character of their whole structure, in which the peculiarities of the *Lucernariæ* are perceptible, though greatly

modified. As in *Lucernaridæ*, the vascular spaces are wide pouches divided from each other by four narrow septa (figs. 198, 199).

The nervous system is allied to that of the *Hydromedusæ* by the presence of a sharply defined nerve-ring. This nerve-ring is placed on the sub-umbrella side of the bell, and, since at the bases of the four sense organs it lies further from the margin than it does at the corners of the bell, it has a sharply marked, zig-zag course. The nerve fibrillæ given off from it mostly supply the muscular system of the sub-umbrella, and there give rise to numerous reticula of fibrillæ connected with large ganglion cells. Large bundles of fibrillæ comparable to nerves have only been found in the four radii of the marginal bodies. The latter attain a high degree of development, since the knob-like swelling in which they terminate possesses, in addition to the lithocyst, a complicated visual apparatus consisting of two large unpaired median eyes and four small paired lateral eyes.

The generative organs have a very peculiar form. They are separated from the gastric filaments and as thin, rather broad plates attached in pairs to the four partition walls, reach the whole length of the vascular pouches. Unfortunately nothing is as yet known of the development.

Fam. **Charybdeidæ**. *Charybdea marsupialis* Pér. Les. (*Marsupialis Planci* Les.) Mediterranean.

(3) Sub-order: **Discophora** (*Acrospeda*), *Ephyra-medusæ*.

Disc-shaped Acalepha, the margin of whose disc is divided into eight lobes. They have at least eight sub-marginal sense organs contained in niches, and with the same number of ocular lobes. As a rule there are four great cavities in the umbrella for the generative organs.

The *Discophora*, which are generally known simply as *Acalepha*, can at once be distinguished from the *Calycozoa* and the *Charybdeidæ* by the disc-shaped lobed umbrella and usually by the large size of the oral tentacles. The lobes of the umbrella, however much they may differ in detail, can always be reduced to the eight pairs of lobes of the *Ephyra*, which, as the common starting-point of the *Discophora*, presents most clearly the eight-rayed symmetry char-

FIG. 199.—The apical half of a *Charybdea* divided transversely, seen from the sub-umbrella side. The four oral arms are visible. Ov, Ovaries on the four septa, S; Ost, ostia of the gastric pouches; Gf, gastric filaments.

acteristic of the group. The striped muscles of the sub-umbrella are strongly developed to correspond with the great size of the body ; and beneath them the supporting lamella is usually thrown into a number of closely aggregated circular folds, thus causing a considerable increase in the surface on which the muscular epithelium with its circularly arranged fibres are placed.

The generative organs have the form of horse-shoe shaped frills which project into four widely open cavities in the sub-umbrella, the *sub-genital pits*. These cavities are not developed in some exceptional cases (*Nausithoë*, *Discomedusa*). The germinal epithelium,

FIG. 200.—*Aurelia aurita*, seen from the oral surface. *MA*, The four oral arms with the mouth in the centre; *Gk*, The genital frills; *GH*, Openings of the sub-genital cavities; *Rk*, Marginal bodies; *RG*, Radial vessels; *T*, Tentacles on the margin of the disc.

which is always embedded in the gelatinous substance, is covered with an endodermal layer, and is probably itself an endodermal product (fig. 200). Development takes place by alternation of generations. In rare cases (*Pelagia*) the development is simplified, and the larva passes directly into the *Ephyra*, missing out the attached Scyphistoma and the Strobila stage (*Krohn*).

1. *Semæostomeæ*. Discophora with large central mouth surrounded by four large often multi-lobed oral arms. The form of the

umbrella edge, the number of lobes and marginal tentacles present great variations.

Fam. **Ephyropsidæ**. *Ephryopsis*, Ggbr. (*Nausithoe* Köll). Disc small and like that of *Ephyra*, with simple gastric sacs, without oral arms, but with eight marginal tentacles. The genital organs (in four pairs) do not lie in umbrella cavities. *E. pelagica* Köll., Mediterranean and Adriatic.

Fam. **Pelagidæ**. *Pelagia* Pér. Les. With wide gastric pouches and eight long marginal tentacles in the interradii. No alternation of generations. *P. noctiluca* Pér. Les., Mediterranean. *Chrysaora* Pér. Les., with twenty-four long marginal tentacles. The radial and intermediate gastric pouches are perceptibly different. *Chr. hyoscella* Esch. Hermaphrodite, North Sea and Adriatic.

Fam. **Cyaneidæ**. *Cyanea* Pér. Les. The tentacles are united in bundles on the under surface of the deeply lobed thick disc. There are sixteen (eight radial and eight intermediate) more or less wide gastric pouches, which break up near the end of the marginal lobes into small ramified vessels. *C. capillata* Esch.

Fam. **Aurelidæ**. *Discomedusa* Cls. With large oral arms, with branched vessels and 24 marginal tentacles. Subgenital pits present. *D. lobata* Cls., Adriatic. *Aurelia* Pér. Les., with branched radial vessels and edge of disc fringed with small tentacles. *A. aurita* L. (*Medusa aurita* L.), Baltic, North Sea, Adriatic, etc. *A. flavidula* Ag., coast of North America.

2. **Rhizostomeæ**. No central mouth, funnel-shaped slits in the eight oral arms and eight, rarely twelve, marginal bodies on the lobed margin of the disc. There are no marginal tentacles. The central mouth, which is at first present, becomes closed during the larval development by the fusion of the edges of the lips. Funnel-like splits are formed on the folded edges of the four pairs of arms, the so-called suctorial mouths, by means of which microscopic bodies are received into the canal system of the oral arms (fig. 195).

Rhizostoma Cuv. The arms end in simple tubular prolongations, and bear accessory tufts at their bases. *Rh. Cuvieri* Pér. Les., *Cephea* Pér. Les. The branched oral arms have groups of nematocysts and long filaments between the terminal tufts. *Cephea* Pér. Les. (*Cassiopsea*) *borbonica* Delle Ch., Mediterranean and Adriatic.

CLASS III.—CTENOPHORA.*

Medusæ of spherical or cylindrical, rarely band-shaped form; with eight meridional rows of vibratile plates formed of fused cilia. They

* C. Gegenbaur, "Studien über Organisation und Systematik der Ctenophoren," *Archiv. für Naturgesch.*, 1856. L. Agassiz, "Contributions to the Natural History of the United States of America," vol. iii., Boston, 1860. A. Kowalevski, "Entwicklungsgeschichte der Rippenquallen," Petersburg, 1866. H. Fol, "Ein Beitrag zur Anatomie und Entwicklungsgeschichte einiger Rippenquallen," Inaugural dissertation, Jena, 1869. A. Agassiz, "Embryology of the Ctenophoræ," Cambridge, U.S., 1874. C. Chun, "Die Ctenophoren des Golfes von Neapel," Leipzig, 1880.

possess an œsophageal tube and a gastro-vascular canal system. Two lateral tentacles, which can be retracted into pouches, are often present.

The *Ctenophora* possess a shape which can in all cases be reduced to a sphere. They are radially symmetrical free-swimming *Cœlenterata* of gelatinous consistence. The body is often bilaterally compressed, so that it is possible to

FIG. 201.—*Cydippe*, seen from the apical pole. *S*, Sagittal plane; *T*, transverse plane; *R*, swimming plates; *Gf*, gastro-vascular system.

to distinguish two planes passing through the long axis at right angles to one another; these are the sagittal plane and

the transverse plane, and are analogous to the median (longitudinal vertical), and lateral (longitudinal horizontal) planes of bilaterally symmetrical animals (fig. 201). The arrangement of the internal organs bears a relation to these two planes. All parts of the body which occur in pairs, as the two tentacles, the gastric canals, the hepatic bands of the stomach, and the vessels which give origin to the eight lateral canals, all lie in the transverse plane, while the sagittal plane coincides with the longer axis of the œsophageal (gastric) tube (whence also called the gastric plane), the two so-called polar fields, and the terminal vessels of the infundibulum.

The infundibulum is so compressed that its longest diameter falls in the lateral plane, which on this account is sometimes called the infundibular plane. Since these two planes divide the body into halves, which correspond with one another, and since there is no division into dorsal and ventral surfaces, the arrangement of the body may be said to be bi-radially symmetrical, but cannot be called

FIG. 202.—*Cydippe (Hormiphora) plumosa* (after Chun). *O*, Mouth.

bilaterally symmetrical, although each half possesses this property. The body is divided by these two perpendicular planes into four similar quadrants.

Locomotion is principally effected by the regular vibration of the hyaline swimming plates, which are disposed over the surface of the body in eight meridional rows, in such a way that each quadrant possesses two rows of plates, a transverse and a sagittal (fig. 202). Locomotion is also assisted by the contractility of the muscle fibres of the gelatinous tissue; this contractility in the band-shaped *Cestidae* causes an undulating motion of the whole body.

The mouth, which is sometimes surrounded by umbrella-shaped lobed processes of the gelatinous tissue, leads into a wide (*Beroë*) or narrow œsophageal tube, which in the latter case soon becomes flattened and broad. The œsophageal tube is furnished with two hepatic bands, and communicates posteriorly, by an opening capable of being closed by muscles, with the gastric cavity, or, as it is commonly called, the *infundibulum*. The long œsophageal tube projects and opens freely into the infundibulum, and is completely surrounded by the gelatinous substance, as far as the level of the two longitudinal vessels which accompany the two lateral surfaces in the transverse plane.

FIG. 203.—Aboral end of *Callianira bialata* (after R. Hertwig). *x*, The two polar spaces; *w*, the beginning of the eight rows of swimming plates, between which the otolith vesicle and the herve plate are seen.

The infundibulum, which is in all cases compressed in a direction at right angles to the œsophageal tube, gives off eight vessels to the swimming-plates. These vessels have a bi-radial symmetry. It also gives off two vessels, which are dilated into two terminal sacs; the latter surround the sense-organ at the aboral pole, which is known as the otolith vesicle, and each of them opens to the exterior by an orifice which is placed in a diagonal plane and is capable of being closed. Two tentacular vessels may arise from the bottom of the infundibulum. The internal surface both of the œsophageal tube and of the infundibulum and its vessels seem to be completely clothed with cilia.

Up to the present time, the nervous system of the *Ctenophora* (fig. 203) is but imperfectly known. There is no doubt that the large vesicle found at the aboral pole, with its clear fluid and vibratile otoliths, is a sense-organ; it is also exceedingly probable, taking into consideration the organization of the *Acalepha*, that the central nervous system of the *Ctenophora* is contained in the thickened base of the vesicle, the *Otolith plate*, especially as the latter is also closely united with a second sense-organ, the sagittal *polar areas*, which have already been described by Fol as olfactory organs, and is also directly connected with the swimming plates by eight ciliated grooves.

True nematocysts are but seldom found in the ectoderm of the *Ctenophora*, but they are represented by peculiar *fixing* or *prehensile cells*, the base of which is prolonged into a spirally coiled thread, while the projecting and convex free end (fig. 204) is of a glutinous consistence, and becomes readily attached to any object which touches it.

FIG. 204. — Smooth muscle fibres, prehensile cells (*kf*), and tactile cells (*b*), from the lateral filaments of the tentacle of *Euplocamus stationis* (after R. Hertwig). *kf'*, Prolongation of the contractile thread of a prehensile cell.

The *Ctenophora* are hermaphrodite. Both kinds of generative products arise on the wall of the vessels of the swimming plates or of blind sac-like diverticula of the same. Sometimes their production is localised (*Cestum*); sometimes they originate along the whole length of the canals, one side of the latter being beset with egg-follicles, the other with sperm-sacs (*Beröe*). The germ layers, which arise from the ectoderm, are covered by entodermal epithelium, and are separated from one another by a projecting fold.

Ova and spermatozoa pass into the gastro-vascular cavity, and are ejected through the apertures of the same.

The fertilized ovum, which is enclosed by a loosely fitting membrane, consists, as in the case of many *Medusæ*, of a thin outer layer of finely granular protoplasm (exoplasm) and a central food yolk (endoplasm), containing vacuoles. The segmentation, which is complete, leads to the formation of two, four, eight segmentation spheres, each of which, like the original ovum, consists of a central mass, surrounded by a thin layer of finely granular protoplasm. In

the stage with four segments, the segments are so disposed that two perpendicular planes placed between them would correspond to the two principal planes of the fully developed animal. Each of the four spheres gives rise to one of the four quadrants of the adult animal (Fol.) The whole mass of the finely granular exoplasm now becomes collected at the upper end of the segmentation spheres, where it is separated off and gives rise to eight new small spheres. These, by continued division, break up into a great number of small nucleated cells, which increase rapidly and grow round the eight large segmentation spheres or the cells produced from them.

The young *Ctenophora* sooner or later leave the egg membranes, and at this period differ more or less from the sexually mature animal in the simpler and usually more spherical form of the body, in the small size of the tentacles and swimming plates, and in the difference in the relative size of the œsophageal tube, infundibulum, and vascular canals. The differences are most striking in the lobed *Ctenophora* (with the exception of *Cestum*), the embryos of which have a great similarity to the young of *Cydidippe*, and have no traces of bi-radial structure. It is only after a longer period of larval life that the completely mature form is attained by the unequal growth of the swimming plates and their canals, the outgrowth of the tentacle-like processes, and the formation of two lobe-like projections round the mouth from those halves of the body which correspond to the longer rows of swimming plates. The phenomenon remarked by Chun is worthy of notice, that the young of *Eucharis*, while still in the larval stage, become sexually mature during the hot period of the year.

The *Ctenophora* live in the warmer seas, and, under favourable conditions, often appear in great quantities at the surface. They feed on marine animals of various size, which they capture with their tentacles. Many, as the *Beroidæ*, which do not possess tentacles, are compensated for this deficiency by the possession of an unusually large mouth (fig. 205), by means of which they are able

FIG. 205. — *Beroides oratus*. *Ot*, Lithocyst, at its sides are the small tentacles of the polar areas; *Tr*, infundibulum.

to receive relatively large bodies, even fishes, into the wide œsophageal tube, and to digest them. Although the average size is small, some of them, as *Cestum*, *Eucharis*, reach the length of a foot.

Fam. **Cydippidæ**. Body slightly compressed, spherical or cylindrical, with extremely regular development of the swimming plates. Their structure is therefore apparently octoradial. They possess two tentacles; the vessels of the stomach and swimming plates end blindly. *Cydippe hormiphora* Ggbr. = *Hormiphora plumosa* Ag., Mediterranean. *Eschscholtzia cordata* Köll., Mediterranean.

Fam. **Cestidæ**. Body elongated to the form of a band in the direction of the sagittal plane. Two tentacles. *Vexillum parallelum* Fol., Canary Isles. *Cestum Veneris* Less., Venus' Girdle, Mediterranean.

Fam. **Lobatæ**. The laterally compressed body possesses two umbrella-like lobes near the mouth, and has relatively small tentacles. *Eurhamphaea vexilligera* Ggbr., Mediterranean and Atlantic Ocean. *Chiaja papillosa*, M. Edw. (*Alcinœ papillosa* Delle Ch. = *Neapolitana* Less.), Mediterranean.

Fam. **Beroidæ**. Characterised by the laterally compressed body with fringe-like appendages on the periphery of the polar spaces; without tentacles. *Berœ Forskalii* M. Edw. (*albescens* and *rufescens* Forsk.), *Idyiopsis Clarki* Ag., *Pandora Flemmingii*, Esch.

CHAPTER VIII.

ECHINODERMATA.*

Animals with a radial, usually pentamerous arrangement. They possess a skin bearing spicules and indurated by calcareous deposits, a digestive canal, a water-vascular apparatus, and a true vascular system.

The radial arrangement of the Echinoderms was for a long time held to be a character of typical value, and was the principal reason why, since the time of Cuvier, the Echinoderms were included in one group, the *Radiata*, with the Medusæ and Polyps. It is only in recent times that R. Leuckart has effected the separation of the Echinoderms from the Cœlenterates.

The organization of the Echinoderms does in fact appear so different from that of the Cœlenterates, and seems to belong to a so much higher grade of development, that the combination of the two groups

* Fr. Tiedemann, "Anatomie der Röhrenholothurie, des pomeranzfarbenen Seesternes und des Stein-Seeigels," Heidelberg, 1820. Joh. Müller, "Über den Bau der Echinodermen," Abh. der Berl. Akad, 1853. Joh. Müller, "Sieben Abhandlungen über die Larven und die Entwicklung der Echinodermen." Abh. der Berl. Akad, 1846, 1848, 1849, 1850, 1851, 1852, 1854. A. Agassiz, "Embryology of the Starfish." Contributions, etc., Vol., V. 1864. E. Metschnikoff, "Studien über die Entwicklungsgeschichte der Echinodermen und Nemeriten," St. Petersburg, 1869. H. Ludwig, "Morphologische Studien an Echinodermen," Leipzig 1877 and 1878.

as *Radiata* is inadmissible, and so much the more so since the radial arrangement of the structure exhibits some transitions towards a bilateral symmetry. The *Echinodermata* are separated from the *Celenterata* by the possession of a separate alimentary canal and vascular system, and also by a number of peculiar features both of organization and of development.

The arrangement of the parts round the axis of the body is usually pentamerous. Nevertheless when the rays are more numerous, irregularities in the repetition of the similar organs are met with. If we take as the fundamental form of the Echinoderm type a spheroid with the principal axis somewhat shortened and the poles flattened and dissimilar, the long axis of the radial body will be this chief axis, and the mouth and anus the two poles (oral and anal poles).

We can imagine five planes passing through the long axis of this spheroid, each of which will divide the body into two symmetrical halves. The perfect correspondence of these halves is, in the body of Echinoderms, disturbed by the different forms and significance of the two poles, so that our representation is not an exact one. The ten meridians, which are separated from one another by equal intervals and fall in these five planes, are differently related to one another, inasmuch as five alternate ones, which are called the *chief rays*, or *radii*, contain the most important organs, the nerves, the vascular trunks, the ambu-

FIG. 206.—The shell of a regular Sea-urchin seen from above. *R*, Radius with double row of perforated plates; *J*, inter-radius with the genital organs and their pores. In the right anterior inter-radius is the madreporic plate.

lacrual feet, etc., while the other five meridians constitute the *intermediate rays* or *inter-radii*, and also contain certain organs (fig. 206). It is only in cases of complete equivalence of the radii and inter-radii that the echinoderm body presents a pentamerous radial arrangement (*regular Echinoderms*). It is, however, easy to show that this regular radial symmetry never occurs in its perfect form. Since one organ or another, *e.g.*, the madreporic plate, the stone canal, heart, etc., always remains single, and does not fall in the axis of the body, it will be only those planes, in the radius or inter-radius of which the unpaired organs fall, which can fulfil the

conditions which admit of the body being divided into two exactly symmetrical halves.

Even these planes do not exactly fulfil these conditions, since the remaining organs are not strictly symmetrical in regard to such a plane.

Very frequently one of the rays differs in size from the others, and then we have an *irregularity* in the external form of the Echinoderm, which renders the bilateral symmetry visible even from the exterior. The pentamerous body of the Echinoderm may become bilateral, the plane of the unpaired ray forming a median

FIG. 207.—*Clypeaster rosaceus*, from the dorsal side. The madreporic plate is situate in the centre and is surrounded by five genital pores and by the five-leaved rosette. The unpaired radius is directed forwards. At the side is the median portion of the ventral surface. O, mouth; A, anus.

plane, on each side of which two pairs of equal rays are repeated. We can distinguish an upper surface (apical pole) and an under (oral pole), a right and left side (the two paired rays and their inter-radii), an anterior end (unpaired radius) and a posterior (unpaired inter-radius). In the *irregular* Sea-urchins, the bilaterally symmetrical form is still more strongly marked. Not only is the unpaired radius of abnormal size and form, and not only are the angles at which the principal ray and the accessory rays cut each other equal only in pairs, but also in the *Clypeastridea* (fig. 207), the anus is removed from the dorsal pole to the ventral half of the body in the unpaired inter-radius,

FIG. 208.—*Schizaster* (*Spatangidae*), from the ventral side. O, mouth; A, anus; P, pores of the ambulacral feet.

while, in *Spatangidæ*, both poles, or only the oral pole, are shifted in the direction of the unpaired radius, and become eccentric (fig. 208).

Only a few of the regular *Echinodermata* have the means of locomotion on all the five rays, and seldom then along the whole length of their meridians; far more frequently the area surrounding the oral pole becomes with regard to the position during movement the ventral surface; it is flattened and mainly or entirely possesses the organs of locomotion (*ambulacral surface*). These relations always obtain among the irregular *Echinodermata* which do not move indifferently in the direction of all five rays, but principally in that of the unpaired one. In these animals the mouth, and therewith the oral pole, being pushed towards the anterior edge, the two posterior radii (*bivium*) seem principally concerned in the formation of the ventral surface (*Spatangidæ*). It is otherwise in the case of the cylindrical *Holothurians*. Their mouth and anus preserve the normal position at the poles of the elongated axis, and the body is not unfrequently compressed in the direction of the axis in such a manner that three radii (*trivium*) with their organs of locomotion are placed on the foot-like ventral surface. On the body of these *Holothurians* one unpaired and two paired radii can be distinguished, only in this case the unpaired radius with its inter-radius marks, not the anterior and posterior, but the dorsal and ventral surfaces.

In many Echinoderms (*Echinoidea*) the oblate spheroidal form is the prevalent one. The principal axis appears shortened, the apical pole may be either pointed or flattened, and the ventral half is

FIG. 209.—*Cucumaria* with extended dendritically branched tentacles (*T*). *Af*, ambulacral feet.

flattened out to form a more or less extended surface. The cylindrical form is obtained by an elongation of the axis (*Holothuroidea*) (fig. 209), the round form by a shortening of the same and the pentagonal disc by the latter process combined with a simultaneous elongation of the radii. If the radii are elongated till they are two or more

times the length of the inter-radii, the form takes the shape of a star (*Asteroidea*), which may be either flat or arched. The arms of the star may be simple processes of the disc, and enclose a part of the body cavity (*Stel-*

FIG. 210.—Calcareous bodies from the integument of Holothurians. *a*, calcareous wheels of *Chirodota*; *b*, anchor with supporting plate of *Synapta*; *c*, chair-like bodies; *d*, plates of *Holothuria impatiens*; *e*, hooks of *Chirodota*.

leridea, *Star-fish*), or they may be more independent moveable organs sharply marked off from the disc, and as a rule simple (*Ophiuridae*), but sometimes branched (*Euryalidae*), or they may even bear simple jointed side twigs, the *pinnulae* (*Crinoidea*).

An important characteristic of the *Echinodermata* is the induration by calcareous deposits of the deeper layers of the integument (dermal connective tissue), so as to give rise to a solid more or less moveable or even immoveable armour. In the leathery *Holo-*

FIG. 211.—Skeletal plates of *Astropecten Hemprichii* (after J. Müller). *DR*, dorsal marginal ossicles; *VR*, ventral marginal ossicles; *Ap*, ambulacral ossicles; *Jp*, intermediate interambulacral ossicles; *Adp*, anterior adambulacral ossicles projecting into the mouth.

thuroidea (fig. 210) alone these skeletal structures are confined to isolated calcareous bodies, which are embedded in the integument, and have a definite form of latticed plates, wheels, or anchors. In these

cases the dermal muscular system is strongly developed, and has the form of five pairs of bundles of longitudinal muscles, external to which is a continuous layer of circular muscular fibres covering the internal surface of the integument. In the Star-fishes and Brittle-stars a moveable dermal skeleton is formed on the arms consisting of calcareous masses (*ambulacral ossicles*), connected together like vertebræ, while the integument of the dorsal surface is filled with calcareous plates, and bears projecting processes and spicules (fig. 211).

The exoskeleton in the Sea-urchins is immovable. It consists of twenty meridional rows of solid calcareous plates immoveably connected together by their edges so as to form a firm shell, which is continuous except at the two poles, where it is interrupted by membranous structures. The rows of plates are arranged in two groups, each with five pairs; of which the one group is radial in position and consists of plates pierced by the pores for the exit of the ambulacral feet (*ambulacral plates*, fig. 212); the other belongs to the inter-radii, and the

FIG. 213. — Pedicellaria of a *Leiodidaris* (after Perrier).

FIG. 212. — Third ambulacrum of a young *Toxopneustes droebachensis* of 3 mm (after LcVén). *Op*, Ocular plate; *P*, primary plates and tentacle pores. The sutures of the primary plates are visible on the plates; *Sw*, the tubercles to which the spines are articulated.

plates are unpierced (*the interambulacral plates*, fig. 206, *R, J*). Near the apical pole, which in the *Crinoidea* and the embryonic *Echinoidea* is occupied by a single plate (central plate), there is, in the Sea-urchins, a small area covered with minute calcareous plates and containing the anus. Around this area the five ambulacral and the five interambulacral rows terminate, each in a pentagonal plate; the former ending in the smaller radial ocular plates (fig. 206), the latter in the larger inter-radial genital plates. The *Crinoidea*, in addition to the dermal skeleton of the disc, possess a stalk, which is composed of pentagonal calcareous masses, arises from the dorsal side of the body, and becomes attached to firm surrounding objects.

Amongst the appendages of the dermal armour, the numerous and variously shaped spines and the pedicellariæ must be mentioned.

The former are moveably articulated to the knobbed tubercles on the shell of the Sea-urchin, and are raised and moved laterally by special muscles developed in a soft superficial dermal layer. The pedicellariæ (fig. 213) are stalked, prehensile appendages furnished with two, three, or more rarely four jaws, which are continually snapping together. They are especially collected around the mouth of the Sea-urchin and on the dorsal surface of the Star-fish. Small transparent bodies, *sphæridia*, are found in the living Sea-urchins, and probably have the value of sense organs. In the *Spatangidae*, knobbed and ciliated bristles (*clavulæ*) are found upon the so-called *fascioles*.

FIG. 214.—Diagram exhibiting the relations of the different systems of organs in an *Echinus* (after Huxley). O, mouth; A, anus; Z, teeth; L, lips; Aur, auriculæ of the shell; re, retractor and protractor muscles of lantern; Rg, circular ambulacral vessel; Po, Polian vesicle; R, radial vessel of the same, with side branches to the ambulacral feet (Am); Sc, stone canal; M, madreporic plate; St, spine; Pe, pedicellariæ.

The *Echino-*
dermata are
especially cha-
racterised by
the possession
of the peculiar
water-vascular
system and of
the distensible
ambulacral feet
connected with
it (figs. 214,
215). This
ambulacral vas-
cular system
consists of a
circular vessel
surrounding
the œsophagus,
and of five
radial vessels

projecting into the rays. These vessels have ciliated internal walls, and contain a watery fluid. Very frequently a number of vesicles, the Polian vesicles, are connected with the circular vessel, also a number of racemose appendages, the significance of which is not fully understood. In connection with the circular vessel there is also a stone canal (in rare cases more than one are present), which permits of communication between the sea water and the fluid contents of the water vascular system. This canal, which is so

called on account of the calcareous deposits in its walls, either hangs within the body cavity, whence it takes up fluid through the pores in its walls (*Holothurians*), or ends in a porous calcareous plate, the madreporic plate, which is inserted in the external covering of the body, and through the pores of which the sea water percolates into the lumen of the canal system. The position of the madreporic plate varies considerably. In the *Clypeastridea* it is at the apical pole; in the *Cidaridea* and *Spatangidea* it is interradiar, and falls in the anterior right interradius near the apex; in the *Asteridea* it is also interradiar and dorsal; in the *Euryalidae* and the *Ophiuridae* it lies on one of the five buccal plates. Some Echinoderms, *e.g.*, species of *Ophidiaster* and *Echinaster echinites*, possess several stone canals and madreporic plates.

FIG. 215. — Diagrammatic representation of the water-vascular system of a Star-fish. *Rc*, Circular vessel; *Ap*, ampullæ or Polian vesicles; *Stc*, stone canal; *M*, madreporic plate; *P*, ambulacral feet connected with the side twigs of the radial canals; *Ap'*, the ampullæ of the same.

On the lateral branches of the five or more radial trunks are found the appendages known as the *ambulacral feet* (fig. 216).

These are extensible tubes or sacs, which pass through pores and openings in the dermal skeleton and project on the surface of the body. They are capable of being swollen out, and are frequently provided with a sucking disc at their free extremity. Contractile ampullæ are placed at the point of junction of the

FIG. 216. — Diagrammatic section through one of the arms of *Asteracanthion* (after W. Lange). *N*, Nervous system; *P*, ambulacral feet; *A*, calcareous portions of integument; *T*, dermal branchia.

tube feet with the side branch of the radial vessel; they force the

fluid into the feet and cause them to swell, and hence to project. A number of feet so distended affix themselves by means of their sucking discs; they then contract and draw the body slowly in the direction of the radii. The number and distribution of these appendages are subject to numerous modifications. Sometimes

FIG. 217.—Sea-urchin divided along the equatorial line (after Tiedemann). *D*, Digestive canal fixed to the shell by mesentery; *G*, generative organs; *J*, inter-radial plates.

they are arranged in rows along the whole length of the meridian from the oral region to the periproct (*Cidaridea* and *Pentacta*). Sometimes they are scattered irregularly over the whole surface of the body, or only over the foot-like ventral surface, as in the

FIG. 218.—Longitudinal section through the arm and disc of *Solaster endeca* (somewhat altered after G. O. Sars). *O*, mouth leading into the wide stomach; *A*, anus; *L*, radia-hepatic diverticulum of the stomach; *G*, genital organs; *Md*, madreporic plate; *Js*, inter-radial diverticulum of the rectum; *Af*, ambulacral feet

Holothurians. In some cases they are confined to the oral surface, as in all the *Asteroidea*. We are able therefore to distinguish an ambulacral and an antambulacral zone—the first coinciding with the oral and ventral surfaces, the latter with the dorsal surface. Nevertheless the ambulacral feet are variously constructed, and do not in

all cases serve for locomotion. In addition to the ambulacral feet, great tentacle-like tubes may be present as appendages of the water-vascular system; the circle of tentacles round the mouth of *Holothurians* (fig. 209) is composed of such appendages. We also find leaf-like appendages arranged over four or five-leaved rosette-shaped areas, forming the ambulacral gills of the *Spatangidea* and *Clypeastridea* (figs. 207 and 208). The irregular Sea-urchins all possess in addition ambulacral feet upon the ventral surface. These are in the *Clypeastridea* almost microscopic in size; they are very numerous, and are arranged in branched rows or are irregularly distributed over the surface.

The *Echinodermata* possess an alimentary canal distinct from the body cavity; it can be divided into three parts—oesophagus, stomach, and rectum. The anus is placed usually at the centre of the apical pole, rarely in an inter-radius on the ventral side. The intestine may, however, end blindly, as for example in all the *Ophiuridae* and *Euryalidae*, also in the genera *Asteropecten*, *Ctenodiscus*, and *Luidia*, which have no anus. The mouth

FIG. 219.—*Holothuria tubulosa*, opened longi tudinally (after M. Edwards). O, Mouth in the midst of the tentacles (T); D, digestive canal; Sc, stone canal; P, Polian vesicle; Rg, circular vessel of the water-vascular system; Ov, ovaries; Ag, ambulacral vessel; M, longitudinal muscles; Gf, vessel to the intestine; Cl, cloaca; Wl, respiratory trees.

is often surrounded by projecting skeletal plates armed with spicules. There may even be developed, as in the *Cidaridea* and *Clypeastridea*, pointed teeth covered with enamel, constituting a powerful masticatory apparatus, which again is supported around the œsophagus by a system of plates and rods. This apparatus is known as Aristotle's Lantern (fig. 214). In the *Holothurians*, on the other hand, there is a calcareous ring round the œsophagus. It is formed of ten pieces, and serves for the attachment of the longitudinal bundles of the dermal muscles.

In the Star-fishes the digestive canal is invariably short, sac-like, and beset with branched blind appendages, some of which lie in the disc, while some project a long way into the arms. In the *Asteroidea* we find five pairs of strongly developed multilobed diverticula of the middle division of the alimentary canal (fig. 218). The five diverticula of the short rectum which fall in the interradii are much shorter, and perhaps perform the function of kidneys, while the longer diverticula increase the digesting surface. In the other Echinoderms the narrow intestine is much increased in length, and is either, as in *Comatula*, coiled round a spindle in the axis of the disc, or, as in the Sea-urchins, describes some convolutions (fig. 217), and is attached to the inner surface of the shell by fibres and membranes. In the *Holothurians* also the intestine is, as a rule, much longer than the body, and is usually folded upon itself three times and attached by a sort of mesentery (fig. 219).

The true vascular system is very difficult to trace. It consists in most Echinoderms of a ring-like vascular plexus surrounding the œsophagus. From this circular vessel radial vessels pass off one to each ray, and these trunks again give off other branches. There is in addition on the dorsal surface a second circular vessel, which sends off branches to the stomach and generative organs. These two vascular rings are connected by a supposed heart, which, according to Ludwig, consists of a close plexus of contractile vessels. In the *Holothurians*, besides the vascular ring round the œsophagus, only two trunks with their branches to the intestine are known. The blood is a clear, slightly coloured fluid, in which numerous colourless blood corpuscles are suspended.

Special organs of respiration are by no means universally found. The entire surface of the external appendages, as well as the surface of the organs suspended in the body cavity, and especially of the intestine, appear to play a part in the exchange of the gases of the blood. The sea-water very likely enters by the pores in the madre-

poric plate into the body cavity, and is kept in active movement by the cilia which line the body cavity and the perihæmal canals; in this way the surface of the internal organs is continually bathed by water. The leaf-like and pinnate ambulacral appendages (*ambulacral branchiæ*) of the irregular Sea-urchins are regarded as special organs of respiration, as also are the cæcal tubes (*dermal branchiæ*), which project from the surface of the integument and communicate with the body cavity in some regular Sea-urchins and in the *Asteridea*. These dermal branchiæ are distributed in the *Asteridea* over the whole dorsal surface as simple tubes, and in the Echini they surround the mouth as five pairs of branched tubes. Lastly there are the so-called respiratory trees of *Holothurians*; these are two large tree-like branched tubes which open by a common stem into the cloaca. The water which is taken into these organs can be again ejected with great force (fig. 219).

FIG. 220.—Diagram of the nervous system of a Star-fish. *N*, The nerve ring connecting the five ambulacral centres.

The *nervous system* (fig. 220) consists of five principal nerves running down the five rays. These nerves in the *Asteridea* lie immediately beneath the epidermis of the ambulacral groove, external to the radial blood vessel and water vascular trunk: they send off numerous fibres to the ambulacral feet, the muscles of the spines, pedicellariæ, etc. These ectodermal bands may be looked upon as the central part of the nervous system ("*ambulacral brains*" of J. Müller). Near the mouth they divide into two parts, which unite with corresponding branches from the other radial trunks to form a nervous ring containing ganglion cells.

FIG. 221. — *Astropecten aurantiacus*, end of ray with the eye (*Oc*) surrounded by spicules (after E. Haeckel).

The tentacle-like ambulacral feet which in the *Asteridea* and *Ophiuridea* are present in simple number at the end of the arms are supposed to have the value of tactile organs. The same significance has been attributed to the tentacles of the *Holothurids* and to the pencil-like tactile feet of the *Spatangidae*. Organs resembling eyes

have been found in the *Echinoidea* and *Asteridea*. In the former (*Cidaridea*) there are, on special plates (*ocular plates*), at the apical pole, five tentacle-like prominences, in each of which a nerve ends. The eyes of the *Asteridea* are most accurately known. According to Ehrenberg's discovery, they have the form of red pigment spots, and lie on the ventral side of the rays at the distal end of the ambulacral groove. They are spherical pedunculated prominences, and the convex surface is covered by a simple membrane, which hides a number of conical simple eyes (fig. 221). The simple eyes appear to have their axes directed towards a common point. They each consist of a red mass of pigment surrounding a refractive body, and a nervous apparatus.

FIG. 222.—Genital organs of *Echinus*. *A*, R. cum; *G*, genital glands lying on the interambulacral plates; *a*, rows of ampullæ.

Reproduction is mainly sexual, and separate sexes are the rule. Only *Synapta* and *Amphiura* are hermaphrodite. The organs of reproduction of the two sexes are extremely alike, so that if it were not that the colour of the generative products is different,—the seminal fluid is mostly white and the ova red or yellow,—a microscopical examination of the contents of the generative glands

would be the only means of distinguishing between them. Sexual differences of the external form or of definite parts of the body are only very rarely present, since as there is no copulation the sexual functions are usually confined to the secretion and preparation of the generative material. Ova and spermatozoa, with some rare exceptions, first come in contact in the sea water outside the body of the mother. Internal fertilization, which is very rare, occurs in several viviparous species of *Amphiura* and *Phyllophorus*. The number and position of the generative organs are generally in strict correspondence with the radial structure; nevertheless there are numerous exceptions to this. In the regular *Echinoidea*, five-lobed ovaries or testes, which are composed of branched blind tubes, lie in the interradii on the internal surface of the dorsal part of the shell (fig. 222). The

ducts of these glands are five in number, and open to the exterior through five openings in the skeletal plates (genital plates) around the apical pole (figs. 206, 222). In the irregular *Spatangidæ* the generative organ of the posterior interradius is always absent, and the number of glands may be three or two. In the *Asteridea* the five pairs of genital glands have the same interradial arrangement: sometimes however, they project into the arms: the apertures for the exit of the generative products lie on the dorsal side, and in each interradius two places may be found, each of which is pierced in a sieve-like manner by a number of such openings (fig. 223). In the *Ophiuridæ* ten lobed generative glands composed of a number of blind tubes are developed around the stomach; their products pass through special passages into pouches, and from thence to the exterior through paired slits on the ventral side between the arms. The generative glands of the *Crinoidea* are concealed in the arms and pinnules. In the *Holothurians*, the generative organs are reduced to one branched gland, the duct of which opens to the exterior not far from the anterior pole of the body on the dorsal side (fig. 219).

The development of the *Echinodermata* presents as a rule a complicated metamorphosis, and is characterised by the possession of bilateral larval stages. Many *Holothurians* are developed without passing through the larval stages, as also are certain Sea-urchins, as *Anochanus*, *Hemiaster*, and some *Asteroidea*, which are either viviparous (*Amphiura squamata*) or lay only a small number of eggs, and protect them during their development in a brood pouch. In these cases also the first stage is a ciliated embryo, which is either developed directly or passes through a much simplified metamorphosis.

FIG. 223.—Part of the inter-radius of a star-fish (*Solaster*) with the generative glands (*G*) and the groups of pores (sieve plates) on the dorsal skin (after J. Müller and Troschel).

In the cases of a complicated metamorphosis, the ovum, after undergoing a nearly equal segmentation, gives rise to a spherical embryo, the cellular wall of which is ciliated and encloses a central gelatinous substance (fig. 103). A pitlike depression of the cellular wall gives rise to the first rudiment of the alimentary canal, and the opening of this depression (gastrula mouth) to the anus. The ciliated embryo becomes elongated and gradually takes the form of a long, oval, more

or less pear-shaped larva, in which a slightly arched dorsal, two symmetrical lateral, and a saddle-shaped ventral surface can be distinguished. The cilia which are concentrated upon the raised edge of the ventral depression give rise to a continuous ciliated band which serves as a locomotive apparatus. [This band first appears as two separate ciliated ridges placed transversely, one in front of, and the other behind the mouth (fig. 224, 3). These soon become connected laterally.] The alimentary canal, which has now acquired an anterior opening, the mouth, consists of three portions,—the œsophagus, the stomach, and the intestine. The wide mouth leading into the œsophagus is situated within the band of cilia on the ventral surface; the anus is also ventral, but external to the ciliated band in the region of the posterior pole. Before the appearance

FIG. 221.—Larval development of *Asteracanthion beryllinus* (after A. Agassiz) (for earlier stages see fig. 103). 1, stage where the mouth (O) has just appeared, represented in profile; A, blastopore (anus); D, intestine; Vp, vaso-peritoneal sac. 2, Somewhat older stage in surface view with two separated vaso-peritoneal sacs. 3, Later stage, from the ventral side, with two transverse ciliated ridges (W); the sac on the left side has an excretory pore. 4, Young Bipinnaria with double band of cilia (W).

of the mouth, another organ is separated from the alimentary canal: this is a sac-like ciliated tube, which opens to the exterior by a pore on the dorsal surface, and represents the first commencement of the ambulacral system. A second organ, which also has its origin from the rudimentary digestive canal, consists of the disc-shaped lateral sacs (fig. 224), from the walls of which the peritoneal lining of the body cavity is produced.

With their progressive development the larvæ of the *Sea-urchin*, the *Starfish*, and the *Holothurian* diverge more and more widely from one another. The raised edge of the depression just mentioned, with its band of cilia, becomes bent and prolonged into processes (fig.

225) of different form. These processes are arranged with a strict regard to bilateral symmetry, and their number, position, and size essentially determine the special shape of the body. An anterior and a posterior ventral region of the band of cilia can be distinguished from the lateral parts which form the dorsal portions; the latter curve round and pass into the former at the anterior and posterior ends of the body (fig. 225, *b*). The dorso-lateral parts may, however, unite anteriorly with one another without passing into the anterior ventral band; in this case the anterior continuations of the latter pass directly into one another so as to form an independent præoral ring, while the dorso-lateral and posterior ventral portions of the originally continuous band form a longitudinally directed post-oral ring. This arrangement is characteristic of the larvæ of the *Asteridea* (*Bipinnaria*, *Brachiolaria*).

In all other forms a single longitudinal band of cilia only is present. In the larvæ of Holothurians, the *Auricularia* (fig. 225), the processes remain short and soft; they are found on the dorso-

FIG. 225.—*Auricularia* larvæ (after J. Müller). *a*, from the dorsal side; *b*, from the ventral side. *O*, mouth beneath the oral shield; *Oe*, oesophagus; *M*, stomach; *D*, intestine with anus (*A*); *P*, peritoneal sac; *V*, Water-vascular rosette with pore; *R*, calcareous wheel-like bodies.

lateral edges and on the posterior dorso-ventral arch of the band of cilia; they also appear on the posterior ventral (umbrella) and the anterior ventral (oral shield) parts of the band. The processes have a similar disposition in *Bipinnaria*, where, however, they are often much longer, but are in this case also not provided with calcareous rods. The *Brachiolaria* are distinguished from the *Bipinnaria* by the possession of three anterior arms, which are placed between the anterior portions of the two rings of cilia, and serve as a fixing apparatus. The bilateral larvæ of the *Ophiurids* and *Sea-Urchins*, the so-called *Pluteus* forms, are distinguished by their large rod-shaped processes, which are supported by a system of calcareous rods.

The *Pluteus* larvæ of the *Ophiurids* possess long lateral arms on

FIG. 223.—*Pluteus* of a *Spatangus* with so-called apical rod (*St*) (after J. Müller).

the anterior dorso-ventral arch of the band, on the dorso-lateral edge, and on the edge of the posterior ventral hood. The *Pluteus* larva of the Sea-urchin has no lateral arms, but processes are developed on the edge of the anterior ventral hood (fig. 226). The larvæ of the *Spatangidæ* are characterised by an unpaired apical rod, and those of *Echinus* and *Echinocidaris* by the presence of ciliated epaulettes (fig. 227).

The transformation of the laterally symmetrical larva with its bilateral processes and complicated organization into the body of the adult Echinoderm is not in all cases effected in the same manner. In the Sea-urchins and Starfishes the young animal is developed by a process of new formation within the body of the larva, the stomach, intestine, and dorsal sac alone persisting; while the transformation of the *Auricularia* into *Synapta* takes place without the loss of so many parts of the larva, the young passing through a pupa-like intermediate stage. In the first case a mass of

FIG. 227.—*Pluteus* larva of *Echinus lividus* with four ciliated epaulettes (*We*) (after E. Metschnikoff) from the ventral side. *O*, Mouth; *A*, anus.

interstitial tissue filled with round cells is formed external to the lateral discs, and with participation of the thickening skin. This tissue becomes the seat of calcareous deposits, and forms the dermal skeleton of the adult Echinoderm (fig. 228 *a*, *b*). The canal of the dorsal pore has in the meantime changed its simple form and developed into the circular vessel with diverticula, which are destined to become the ambulacral trunks. As development progresses, the young animal appears as a more or less spherical or pentagonal body, or as a star with short arms, in propor-

FIG. 228.—*Epinnaria* from Trieste forming a stage in the development of the Star-fish (*St*) (after J. Müller). *a*, Earlier stage. *M*, stomach; *A*, anus; *V*, ambulacral rosette with ciliated tube opening by the dorsal pore. *b*, Older stage.

tion as it predominates over the larva. Finally, after the sprouting out of the ambulacral feet, the young Echinoderm becomes separated from the larval body, which not unfrequently remains attached to the former, like the remnants of a broken-down framework. The stomach, which is taken into the interior of the body of the Echinoderm, is torn from the œsophagus of the larva (*Bipinnaria*), and acquires a new œsophagus and mouth. The dorsal pore becomes the pore of the madreporic plate.

The *Synaptilæ*, on the contrary, are formed by the transformation of the entire body of the *Auricularia*. Five tentacles appear in front

of the stomach and the circular vessel, which is formed from the dorsal tube. They are at first enclosed in a cavity, from which later

FIG. 229.—Auricularia pupa of *Synapta* seen in profile (after E. Metschnikoff). The mouth is already large, so that the tentacles (*T*) can be protruded. *Wr*, Ring of cilia; *Pe*, *Pi*, somatic and visceral layers of the peritoneal sacs; *Ob*, auditory vesicle; *Po*, pore of the water-vascular system; *R*, calcareous wheel-shaped body.

on they penetrate to the exterior. The larva retracts its lateral lobes and transforms itself into a barrel-shaped body with five transverse rows of cilia, and loses the mouth and dorsal pore (fig. 229). The ambulacral system gradually develops further, the intestine becomes longer, the first five tentacles break through to the exterior, the mouth appears at the anterior pole, and the first sucktorial foot with its ambulacral vessel is seen on the ventral surface (fig. 230). The animal gradually loses the bands of cilia, and as a young *Holothurian* creeps about by means of its tentacles and of the first ambulacral foot, which is soon followed by a second new one.

In the more direct development the bilateral larva seems to be more or less completely suppressed, and the time of free-swimming life shortened or altogether dispensed with. In these cases, protective arrangements, such as brood pouches, are always present in the mother. The brood pouch of *Pteraster militaris* is the most carefully protected. It lies above the anus and generative openings; its walls are highly charged with calcareous matter, and they are raised above the spicules on the back. From eight to twenty ova (1 mm. in diameter) pass into the interior of the brood pouch, and are there developed into oval embryos, which acquire several sucking feet and assume later the form of a star with five rays.

FIG. 230.—Young *Holothurid* with extended tentacles (*T*), swimming and creeping (after J. Müller).

The formation of the embryo takes place thus: four shield-like thickenings are formed upon one segment of the ovum, and beneath them several ambulacral feet make their appearance. The star is developed by the increase in size and number of these discs and ambulacral feet. At this period of development we can distinguish the circular ambulacral vessel surrounding a central hemispherical projection of the oral disc, also the five vascular trunks and 2—3 pairs of sucking feet in each ray. In other cases, the brood pouch is formed upon the ventral surface of the Star-fish, *e.g.*, *Echinaster Sarsii*, and the embryo, which is completely ciliated, is provided at the anterior end with a knobbed process. The latter is divided into several structures (Haftzäpfchen), which serve as organs to attach the body of the embryo to the wall of the brood pouch. Suctorial feet are now formed in each ray, two paired and one unpaired, the latter lying nearest to the angle of the pentagon. The five angles come to project more and more, and acquire eye spots and ambulacral grooves. Spicules appear, and the mouth perforation is formed, the fixing organ aborts, and the embryos escape from the maternal brood pouch; and being at this time capable of creeping and of nourishing themselves independently, they gradually develop into small star-fishes. The mode of development is the same in *Asteracanthion Müllerii*, and some Ophiurids, as *Amphiura squamata*.

Amongst the Holothurids (*H. tremula*) the simple and more direct development was first observed by Danielssen and Koren, and later by Kowalevski, in *Phyllophorus urna*, and by Selenka, in *Cucumaria doliohum*. In the first case the embryo leaves the egg in the form of a ciliated larva, which soon assumes a pear shape, and develops the circular vessel of the water-vascular system, and five tentacles round the mouth. The alimentary canal and the dermal skeleton make their appearance before the five tentacles have assumed the function of locomotion in place of the cilia which have disappeared. Later on, with the progressive growth, the tentacles become branched, and two ventral feet appear, which put the bilateral symmetry of the larva beyond all doubt. In all cases, even in the cases of a more direct development, *the radial symmetry of the adult Echinoderm appears to be preceded by a bilateral symmetry of the larva.*

All the Echinoderms are inhabitants of the sea; they are capable of a slow, creeping movement, and feed on marine animals, especially on Mollusca, but also on Fuci and sea-weeds. Some are found near the coast at the bottom of the sea, others occur at considerable

depths. Many possess a great reproductive power, and are able to replace lost parts, such as arms, with all their apparatus of nerves and sense organs.

CLASS I.—CRINOIDEA.*

Globular or cup-shaped Echinodermata with segmented arms furnished with pinnulæ. They are usually attached by a segmented calcareous stalk. The skin upon the aboral side is provided with plates, the ambulacral appendages have the form of tentacles, and are situated in the ambulacral furrows of the calyx and of the segmented arms.

FIG. 231.—*Pentacrinus caput Medusæ* (after J. Müller).
O, mouth; A, anus, of the disc, which is represented from the oral side.

The greater number of *Crinoidea* are characterised by the presence of a segmented stalk bearing cirri. This stalk arises from the apical (dorsal) pole of the calyx, and is attached at the inferior end to surrounding objects (fig. 231). In some few living genera, as *Comatula* (fig. 232) and *Actinometra*, this stalk is only present in the young form. The body

with the contained viscera appears, therefore, as the calyx at the upper end of the stalk, and only in exceptional cases is directly

* J. S. Miller, "A Natural History of the Crinoidea or Lily-shaped Animals," Bristol, 1821. J. V. Thompson, "Sur le *Pentacrinus Europæus*, l'état de jeunesse du genre *Comatula*," L'institut, 1835. J. Müller, "Ueber den Bau von *Pentacrinus caput Medusæ*," *Abhandl. der Berl. Akad.*, 1841. J. Müller, "Ueber die Gattung *Comatula* und ihre Arten," *Abhandl. der Berl. Akad.*, 1847. Leop. v. Buch, "Ueber Cystideen," *Abhandl. der Berl. Akad.*, 1844. Ferd. Römer, "Monographie der fossilen Crinoideen familie der Blastoideen,"

attached by its dorsal apex. The segments of the stalk, which are mostly pentagonal, are connected by bands of tissue, and are pierced by a central canal, which serves for nutrition, and contains a central and five peripheral blood vessels; at certain distances they bear hollow and segmented cirri, which are arranged in whorls.

The dorsal surface of the calyx is covered externally by regularly arranged calcareous plates, while the upper (ventral) surface, on which the mouth and anus are situate, is clothed with a leathery

FIG. 232.—*Comatula mediterranea* represented from the ventral side. O, mouth; A, anus. The pinnulae are filled with the generative products.

skin. At the margin of the cup there arise movable, simple or forked, and often branched arms, which are supported by a solid framework consisting of dorsally placed calcareous plates, which are movable upon one another by special muscles. In almost

Arch. für Naturgesch., 1851. W. Thompson, "On the Embryology of the *Antedon rosaceus*," *Phil. Trans. Roy. Soc.*, Tom 155, 1865. W. B. Carpenter, "Researches on the Structure, Physiology and Development of *Antedon rosaceus*," *Ibid.*, Tom 156. A. Götte, "Vergl. Entwicklungsgeschichte der *Gematula Mediterranea*," *Archiv. für mikrosk. Anatomie*, Tom XII. H. Ludwig, "Morphol. Studien an Echinodermen," Leipzig, 1877.

every case the arms bear, either on their main stems or on their branches, lateral appendages, the *pinnules*, which have an alternate arrangement on each side, one being attached to each segment of the arms. Essentially the pinnules represent the ultimate ramifications of the arms.

The mouth, as a rule, lies in the centre of the cup. From it certain furrows, the *ambulacral grooves*, traverse the disc (fig. 231)

FIG. 233.—Developmental stages of *Comatula* (*Antedon*), much enlarged. *a*, free-swimming larva with tuft and rings of cilia (*Wr*), also with rudimentary calcareous plates. *b*, Attached *Pentacrinoid* form of the same animal. *O*, Oralium; *R*, Radialia; *B*, Basalia; *Cd*, Centrodorsal plate. *c*, Older stage described as *Pentacrinus europaeus* with arms and cirri (after Thomson).

and pass on to the arms, and their branches and pinnules; they are lined by soft skin, and carry the tentacle-like ambulacral appendages. The anus, when it is present, lies excentrically on the ambulacral (ventral) surface of the disc. The development of the living genus *Comatula*, which begins with a barrel-shaped larva with four bands of cilia and leads to the fixed stage of the Pen-

tacrinus form (*P. Europæus*) (fig. 233), consists of a complicated metamorphosis.

The greater number of Crinoids belong to the oldest periods of the history of the earth (the Cambrian, Silurian, Devonian, and the Carboniferous formations). Existing forms live mostly at considerable depths.

We distinguish two orders, the *Tesselata* and the *Articulata*.

The latter is represented by numerous fossil forms, but by only a few living genera as *Pentacrinus*, *Holopus*, and *Comatula* (fig. 234). The cup is always less completely provided with plates than in the fossil *Tesselata*.

ARTICULATA.

Fam. Pentacrinidæ. Crinoids with ten arms, several times bifurcated. There is a pentagonal stalk with whorled cirri. *Pentacrinus caput Medusæ*, Mill. from the Antilles. *P. Mülleri* Oerst., West Indian Ocean. The fossil forms are: *Encrinus liliiformis* Schl. (fig. 234) from the Muschelkalk; also *Apiocrinus*, allied to the existing *Rhizocrinus lofotensis* Sars, and to *Bathycrinus gracilis*, and *aldrichianus* W. Th., from the deep sea. Allied to this group is the third existing genus *Holopus*, from the West Indies, with calyx attached by a short unjointed prolongation of its apex. *H. Rangii* d'Orb.

Fam. Comatulidæ. Stalked only in the young state. The adult animal is free. There are usually ten arms at the margin of the flattened body; mouth and anus are present. The *Comatulidæ* possess the power of striking their arms towards the ventral surface and so of propelling themselves amidst the sea-weeds. The vermiform larva, with its four ciliated girdles, makes its appearance within the egg-membranes. It acquires a mouth and anus, also a tuft of cilia at the posterior end of the body, and swims about freely. It passes later, by the formation of calcareous rings and rows of plates, into the stage of the stalked *Pentacrinus*, from which the *Comatula* is produced by the separation of the cup from the stalk. *Comatula mediterranea* Lam., *Antedon rosacea* Link., known in the young attached stage as *Pentacrinus Europæus*. *Actinometra* J. Müll.

To the Crinoids are allied the fossil *Cystidea* and *Blastoidea*. The *Cystidea* were provided with short stalks and slightly developed arms. Their generative organs were enclosed in the calyx, whence their products escaped through a genital opening capable of being closed by movable valves. They are found as fossils in the Cambrian, Silurian, and Devonian formations and the Carboniferous limestone. To this group belong the genera *Sphaeronites*, *Caryocrinus*, *Apiocystites*.

The *Blastoidea* have no arms, and only possess ambulacral areas on the calyx, which is attached by a segmented column. *Pentatremites*.

FIG. 234.—*Encrinus liliiformis* from the Muschelkalk.

CLASS II.—ASTEROIDEA (STARFISHES).*

Echinoderms with dorso-ventrally compressed pentagonal or star-shaped body. The ambulacral feet are confined to the ventral surface. Internal skeletal pieces in the ambulacra articulated together like vertebrae.

The Star-fishes are chiefly characterised by the predominating pentagonal or star-like discoidal shape of the body, to the ventral

FIG. 235. *Echinaster sentus*, from the oral surface (after A. Agassiz). O, mouth; Af, ambulacral feet.

surface of which the ambulacral feet are confined (fig. 235). The radii are long in comparison with the inter-radii, which are very short in consequence of the divergence of the interambulacral rows of plates; they constitute more or less projecting movable arms, with movable skeletal structures. These latter consist of transversely arranged, paired calcareous plates (ambulacral ossicles),

* J. Müller and Troschel, "System der Asteriden," Brunswick, 1841. Compare besides the numerous papers of Krohn, Sars, Lütken, L. Agassiz, etc.

which reach from the mouth to the end of the arms, and are articulated together like vertebræ. The skeleton of the *Asteroidea* is distinguished from the globular or flattened shell of the *Echinoidea* by the fact that the ambulacral and interambulacral plates are confined to the ventral surface, and that on the outer side of the former there is a deep *ambulacral groove*, which contains, outside the ossicles and beneath the soft skin (which in *Ophiurids* possesses special calcareous plates), the nerve trunks, the perihæmal canals with the blood-vessels and the ambulacral trunks. In the *Ophiuridea* the ambulacral groove is covered by the dermal plates so that the ambulacral feet project at the sides of the arms. Upon the dorsal surface the dermal skeleton appears leathery; it is, however, as a rule, filled with small calcareous plates, on which are placed spines, protuberances, and papillæ, constituting a covering of a most varied kind.

At the margin in the dorsal integument there is usually a row of larger calcareous plates (*superior marginal plates*) (fig. 236).

Upon the ventral surface we can distin-

FIG. 236.—Skeletal plates of *Astropecten Hemprichii* (after J. Müller). DR, Dorsal marginal plates; VR, ventral marginal plates, Ap, ambulacral ossicles; Jp, intermediate interambulacral plates; Adp, anterior adambulacral plates forming an angle of the mouth.

guish, in addition to the internally placed ambulacral ossicles, *inferior marginal ossicles* (fig. 236, VR), also the *adambulacral plates* (Adp), and the *intermediate interambulacral plates* (Jp). The two last correspond to the interambulacral plates of the *Echinoidea*, where they occur as two or more rows, which are united along the whole length of the inter-radius: in the *Asteroidea*, however, they separate from one another at an angle, and are disposed along the opposed sides of adjacent arms. The ambulacral ossicles are calcareous bodies articulated together like vertebræ, with spaces between their lateral processes for the passage of the vessel connecting the ampullæ with the radial vessel and the tube feet. The right and left pieces of each double row are either (*Ophiuridea*) immovably connected by a suture, or are

(*Stelleridea*) movably articulated by teeth, which fit into one another at the bottom of the ambulacral groove; the latter only (*Stelleridea*) possess transverse muscles on the ambulacral ossicles, and are able to bend their arms together towards the ventral surface. The *Ophiuridea* are provided with longitudinal muscles only, by means of which they are able to bend their arms to the right and left in a horizontal plane with a serpentine movement.

The mouth is always placed in the centre of the ventral surface in a pentagonal or star-shaped depression, the edges of which are usually beset with stiff papillæ. The inter-radial angles are marked by the junction of two adambulacral plates, and frequently function as organs of mastication. The anus may be wanting; when present, it invariably lies at the apical pole. The madreporic plate, of which there may be one or more, is situated inter-radially and dorsally (*Stelleridea*), or on the inner surface of one of the *buccal plates* (*Ophiuridea*), on the exterior of which a pore may be present. Development in certain cases takes place without the interposition of a bilateral larval phase with bands of cilia. When such larvæ are developed, they have the form of a *Pluteus* (Ophiurid) or *Bipinnaria* and *Brachiolaria* (Stellerid).

The great power of regeneration possessed by Starfishes is not confined to the reproduction of lost arms, but may lead to the new formation of portions of the disc, or even of the entire disc from a single separated arm. This process thus amounts to a species of asexual reproduction by fission, and has been especially observed in forms with six (*Ophiactis*) or more than six (*Linckia*) arms.

Fossil star-fishes are found as far back as the lower Silurian strata (*Palæaster*), where intermediate forms between *Stelleridea* and *Ophiuridea* (*Protaster*) make their appearance.

Sub-Class 1.—STELLERIDEA (*Asteridea*) STARFISHES.

Asteroidea whose arms are prolongations of the disc, and contain the hepatic appendages of the alimentary canal, and also the generative organs. They possess a deep, uncovered ambulacral groove running along the ventral surface, in which groove the ambulacral feet are disposed in rows.

The *Stelleridea* usually possess broad arms, and are characterised by the fact that the ambulacral ossicles of the two sides are connected by transverse muscles and are movable upon one another. The anus lies at the aboral pole, but may be wanting in certain genera (*Astropecten*). The madreporic plate and the genital pores are

situate inter-radially and upon the dorsal surface. The multilobed branched diverticula of the stomach extend into the cavities of the arms (fig. 218). On the ventral surface of the latter, two or four rows of ambulacral feet project from the deep ambulacral groove, the edge of which is beset with papillæ (fig. 235). *Pedicellariæ* are also found, and dermal gills projecting through the tentacular pores of the dorsal surface.

They feed principally upon *Mollusca*, and, by means of their ambulacral feet, crawl slowly upon the bottom of the sea. Some few of them are developed by a very simple process of metamorphosis within the brood-pouch of the mother; but the greater number of them pass through the free larval stages of *Bipinnaria* and *Brachiolaria* (figs. 224 and 228).

Fam. **Asteriadæ**. The cylindrical ambulacral feet end in broad suctorial discs, and are usually arranged in four rows along each ambulacral groove. *Asterias* L. (*Asteracanthion*), *A. glacialis* O. F. Müller., *Heliantherium* Gray.

Fam. **Solasteridæ**. The cylindrical ambulacral feet are disposed in two rows. Rays long, often more than five. *Solaster papposus* Retz., *Echinaster sepositus* Retz., *Ophidiaster* Ag., *Linckia* Nardo.

Fam. **Astropectinidæ**. Ambulacral feet conical, and without suctorial disc, arranged in two rows. There is no anus. *Astropecten aurantiacus* Thil. *Luidia* Forb., *Ctenodiscus* Müll. Tr.

Fam. **Brisingidæ**. Body shaped like an Ophiurid. Rays distinct from the disc with only a narrow internal cavity. *Brisinga coronata* Sars.

FIG. 237.—*Asteriscus verruculatus*, with the dorsal skin removed. *Ld*, Radial appendages or hepatic tubes of the stomach; *G*, generative glands.

Sub-Class 2.—OPHIURIDEA (*Brittle Stars*).

Asteroidea characterised by the absence of an anus, and by the possession of long cylindrical arms which are sharply distinct from the disc, and do not contain appendages of the alimentary canal. The ambulacral groove is covered by the dermal plates so that the ambulacral feet project at the sides of the arms.

The *Ophiuridea* can be at once distinguished by the flexible cylindrical arms, which are sharply distinct from the disc, and enclose

no diverticula of the alimentary canal. The movements of the arms are principally in the horizontal plane, and in many cases permit of a creeping locomotion amongst marine plants. The ambulacral groove is always covered by special dermal plates, and the ambulacral feet project laterally between the spicules and plates on the upper surface (fig. 238). In a few cases the arms are branched, and can be rolled up in the direction of the mouth. In such cases the ventral groove is closed by a soft skin (*Astrophyton*). The anus is always wanting, as are *pedicellariæ*. The generative products pass into genital pouches (*bursæ*), and from these directly to the exterior

FIG. 238.—*Ophiothrix fragilis*. The ends of the rays have been removed. GS, Slits of the genital pouches; K, masticatory ossicles.

ambulacral groove. They are divided into special genera according to the peculiar character of the dermal covering and of the buccal armature. *Ophiothrix* Müll. Tr. The back is provided with granules, hairs, or spicules. The lateral plates of the arms bear spicules. *Oph. fragilis* O. Fr. Müller. *Ophiura* Lam. (*Ophioderma*). Two pairs of genital slits in each interbranchial space. *O. longicauda* Link., *Ophiolepis* Lüt., *Amphiura* Forb.

Fam. **Euryalidæ**. Mostly with branched arms which can be curved towards the mouth and are without plates; the ventral groove closed with soft skin. *Astrophyton verrucosum* Lam., Indian Ocean. *A. arborescens* Rond., Mediterranean. *Asteronyx Lovéni* Müll. Tr.

CLASS III.—ECHINOIDEA,* SEA-URCHINS.

Spherical, heart-shaped, or disc-shaped Echinoderms with immovable skeleton composed of calcareous plates. The skeleton encloses the body

* Besides the works of J. Th. Klein, compare E. Desor, "Synopsis des Échinides fossiles," 1854 to 1858. S. Lovén, "Études sur les Échinoidées," Stockholm 1874. Al. Agassiz, "Revision of the Echini," Cambridge, 1872-1874.

through inter-radial paired slits. The madreporic plate lies upon the ventral surface in one of the buccal plates. Some few Ophiurids are viviparous, e.g., *Amphiura squamata*; these do not undergo metamorphosis. Most pass through the *Pluteus* larval stage, e.g., *Ophioglypha* Lym., (*Ophiolepis*) *ciliata* with larval stage *Pluteus paradoxus*.

Fam. **Ophiuridæ**. With simple unbranched arms, and with ventral plates to the

after the manner of a shell, and carries movable spines. There is invariably a mouth and anus, and locomotive and often respiratory ambulacral appendages.

The dermal skeletal plates are connected together so as to form a firm immovable shell, which has no arm-like prolongations in the direction of the rays, and is sometimes regularly radial, sometimes irregular or symmetrical. With some rare exceptions among the fossil *Perischæchinidæ*, as *Lepidocentrus*, the calcareous plates are firmly connected with one another by sutures, and are usually arranged in twenty meridional rows. These rows (fig. 206) are disposed in pairs, and correspond alternately with the radii and the inter-radii. The five radial pairs are the ambulacral plates, and are pierced by rows of fine pores for the exit of tube feet (fig. 212, *P*), and bear, as do the broad interambulacral plates, spherical prominences and tubercles to which the differently shaped spines are movably articulated. The body form of the Sea-urchins, as contrasted with that of the Star-fish, depends upon the meridional arrangement of the rows of plates, and, at the same time, on the continuity of the interambulacral rows.

The position of the nerves and ambulacral vascular trunks beneath the skeleton is the special characteristic of the internal organization. *Pedicellariæ* are found between the spicules, and are especially numerous in the region of the mouth. Some *Cidaridea* are provided with branched respiratory tubes. The *genital pores* are disposed inter-radially on the genital plates near the apical pole. One of these genital plates is, as a rule, also the madreporic plate. The ocular plates, which are radial in position, are also pierced (figs. 206, 212). The regular Sea-urchins are often symmetrical, one radius being longer or shorter than the others, which are equal to each other. So we find long oval forms which are laterally symmetrical, having the mouth and anus central, and an anterior unpaired radius (*Acrocladia*, *Echinometra*). In the irregular Sea-urchins the anus is thrust away from the apical pole into the unpaired radius (*Clypeastridæ*). The mouth also often has an eccentric position in front (*Spatangidæ*, fig. 208), in which case the masticatory apparatus is always wanting.

In many regular forms all the ambulacral feet have the same shape, and are provided with a suctorial disc supported by calcareous bodies; in others the dorsal feet are unprovided with a disc, and are pointed and often have an indented edge. In addition to the ambulacral feet, the irregular Sea-urchins almost all possess ambu-

lacr branchiæ upon a rosette formed of large pores on the dorsal surface (fig. 239). The locomotive feet are very small in *Clypeastridæ*, and are distributed either over the whole surface of the ambulacra, or are confined to branching rows upon the ventral surface. In the *Spatangidæ* there are peculiar bands upon the upper surface,

FIG. 239.—*Brissopsis lyrifera* with the fascioles or semites surrounding the rosette. A, anus.

the *fascioles* or *semitæ* (fig. 239), upon which, in place of the spicules, knobbed bristles with active cilia (*clavulæ*) are distributed. Development takes place with a *Pluteus* larval stage, in which the larva is provided with ciliated epaulettes or with an apical rod.

The Sea-urchins live, as a rule, near the coast, and feed on molluscs, small marine animals, and Fuci. Some species of *Echinus* have the power of boring holes in the rocks in which they live. We find many fossil shells, especially in the chalk.

Order 1.—CIDARIDEA=REGULAR SEA-URCHINS.

Echinoidea with central mouth and equal band-like ambulacra; with teeth and masticatory apparatus; with sub-central anus in the apical space.

Fam. *Cidaridæ*. With very narrow ambulacral and broad interambulacral areas, on both of which are large perforated tubercles and club-shaped spines. There are no oral branchiæ. *Cidaris metularia* Lam., *Phyllacanthus imperialis* Lam., East Indies.

Fam. *Echinidæ*, Sea-urchins. The pores are grouped in transverse rows; there is a round, thin shell, broad ambulacral spaces bearing tubercles and spines, which are mostly short and pear-shaped. Oral branchiæ are present. *Toxopneustes variegatus*, Lam., *Echinus melo* Lam., *Strongylocentrotus lividus* Brit. *saxatilis* Lin., Mediterranean.

Fam. *Echinometridæ*. With long oval shell, imperforate tubercles and oral branchiæ. *Echinometra oblonga* Blainv., *Podophora atrata* Brdt., *Acrocladia trigonaria* Ag., Pacific.

Order 2.—CLYPEASTRIDEA.

Irregular Echinoidea compressed into the form of a shield. Mouth central and furnished with masticatory apparatus. Very broad ambulacra, five-leaved ambulacral rosette round the apical pole, and very

small tube feet. Five genital pores in the region of the madreporic plate.

Fam. **Clypeastridæ.** The edge of the disc without indentations. *Clypeaster rosaceus* Lam. (fig. 207), *Echinocyamus pusillus* O. F. Müller, Mediterranean.

Fam. **Scutellidæ.** Flattened *Echinoidea* with a shell often lobed or perforated, with rows of pores for the ambulacral feet. *Lobophora bifora* Ag., *Rotula Rumphii* Klein, Africa.

Order 3.—SPATANGIDEA.

Irregular Echinoidea of a more or less heart-shaped form, with eccentric mouth and anus. There are no teeth or masticatory apparatus, and there is usually a four-leaved ambulacral rosette and four genital plates.

As a rule there are semitæ and four genital pores, but the number of the latter may be reduced to three and two.

Fam. **Spatangidæ.** *Spatangus purpureus* O. Fr. Müll., Mediterranean; *Schizaster canaliferus* Ag., *Brissus* Klein.

CLASS IV.—HOLOTHUROIDEA.*

Wormlike elongated Echinoderms with a leathery body wall, with contractile tentacles surrounding the mouth; anus terminal.

The *Holothuria* approach the worms in possessing an elongated cylindrical shape and a bilateral symmetry, which is expressed in many ways. In particular they possess so striking a resemblance, so far as their exterior is concerned, to many *Gephyrea* that formerly they were included in the same group. The body-covering never consists of a firm calcareous shell like that which we find in other Echinoderms, but always remains soft and leathery, the calcareous matter being confined to a few isolated particles of definite form. In rare cases (*Cuvieria*), scales are present in the dorsal skin. These are arranged like the slates on a roof, and may even take the form of spicule-like appendages (*Echinocucumis*).

The bilateral symmetry results not only from the existence of unpaired organs, but from the contrast which is often very distinctly expressed between the dorsal and ventral surfaces. The ambulacral feet are not in all cases regularly arranged in the five meridional

* G. J. Jaeger, "De Holothuriis," Dissert. inaug. Turici. 1833. J. F. Brandt, "Prodromus descriptionis animalium ab H. Mertensio in orbis terrarum circumnavigatione observatorum," Fasc. I. Petropoli, 1835. J. Müller, "Ueber Synapta digitata und über die Erzeugung von Schnecken in Holothurien," Berlin, 1852. A. Baur, "Beiträge zur Naturgeschichte der Synapta digitata," Dresden, 1864. C. Semper, "Reisen im Archipel der Philippinen," Tom I., Leipzig, 1868.

rows from the oral to the anal pole, but may be principally or altogether confined to the three rays of the so-called trivium. In this latter case the *Holothurid* moves upon a more or less foot-like ventral surface. The ambulacral feet may also be distributed uniformly over the surface of the body, especially on the ventral side. As a rule, the tube-feet have a cylindrical shape, and terminate with a suctional disc: in other cases they are conical, and the suctional disc is absent. The tentacles, which are in communication with the water-vascular system, and represent specially modified ambulacral appendages, are simple or pennate, or even dendritic (*Dendrochirota*) or shield-shaped (*Aspidochirota*), that is, provided with a disc, which

FIG. 240.—*Synapta inhærens* (after Quatrefages). O, Mouth; A, anus: the intestine can be seen through the skin.

is often divided into many parts.

In certain genera (*Synapta*), the ambulacral feet are altogether wanting, and the tentacles remain as the sole appendages of the ambulacral system (fig. 240).

Locomotion is effected by the strongly developed dermal muscular system, the longitudinal fibres of which are attached to the calcareous ring surrounding the œsophagus. It is characteristic of the water-vascular system that the stone canal, which is usually simple, hangs freely in the body cavity, ending in a calcareous framework comparable to the madreporic plate.

The respiratory trees at the end of the intestine perform the function of *respiration*, while certain

glandular appendages (organs of Cuvier), which open into the rectum, may be regarded as *excretory organs*: these, as well as the respiratory trees, may be wanting. The *generative organs* consist of a bundle of branched tubes, the duct of which opens on the dorsal surface in the region of the mouth. The genus *Synapta* is hermaphrodite. The development is in many *Holothurians* direct (as *e.g.* in *Holothuria tremula* according to Koren and Danielssen); where there is a complicated metamorphosis, the larvæ have the *Auricularia* form, and pass through a barrel-shaped pupa stage.

The *Holothurians* are partly nocturnal in their habits, and live at the bottom of the sea, for the most part in shallow places near the coast, where they crawl slowly upon the bottom. The *Synaptidæ*, which have no feet, burrow in the sand. They feed on the smaller marine animals, which, in the *Dendrochirota*, are carried to the mouth by means of the branched, tree-like tentacles. The *Aspidochirota* fill their intestine with sand, which they eject from the anus by means of the current of water from the respiratory trees. It is worthy of notice that they (especially the *Aspidochirota*) can eject through the anal opening the intestine, which breaks off easily behind the vascular ring, and are able to renew it. The *Synapta*, when irritated, are able to break their body into several pieces by violent muscular contractions.

Order 1.—PEDATA.

Numerous ambulacral feet, which are sometimes arranged regularly in the meridians, and sometimes distributed over the whole surface.

Fam. **Aspidochirotæ**. With shield-shaped tentacles. *Holothuria* L. With scattered ambulacral feet, which are conical on the dorsal side, and are without suckers. *H. tubulosa* Gmel., Adriatic and Mediterranean; *H. edulis* Less., the edible Trepang of the East Indian seas.

Fam. **Dendrochirotæ**. With tree-like branched tentacles. *Cucumaria* Blainv. Ambulacral feet arranged in regular rows. *C. frondosa* Gr. *Psolus* Oken. Ambulacral feet confined to the foot-like ventral surface of the trivium. *Ps. phantapus*. Gr.

Order 2.—APODA.

No ambulacral feet; as a rule without respiratory trees; the tentacles are usually branched or pinnate.

Fam. **Synaptidæ**. Hermaphrodite and without respiratory trees. In the skin there are wheel-shaped calcareous bodies or projecting masses shaped like anchors, and affixed to calcareous plates. *Synapta digitata* Mntg. with anchor-shaped calcareous bodies. J. Müller discovered in their bodies parasitic cylindrical animals with spermatozoa and ova, which latter develop into small shell-bearing Gastropods (*Entoconcha mirabilis*). *Chirodota* Esch. Skin beset with rows of small tubercles bearing calcareous wheel-shaped bodies. The genus *Molpadia* Cuv. is furnished with respiratory trees.

ENTEROPNEUSTA.

The remarkable genus *Balanoglossus* must be placed here. It is the representative of a class, *Enteropneusta* Gegenb.,* allied to the *Echinodermata*, but usually classed with the *Vermes*, and presenting

* A. Kowalevski, "Anatomie des *Balanoglossus* Delle Chiaje," *Mémoires de l'Acad. impér. des Sciences de St. Petersbourg*, Tom X., No. 3, 1866. L. Agassiz,

I.—APLACENTALIA.

Order 1.—MONOTREMATA.*

The jaws are elongated to the form of a beak; the feet are short, five-toed, and furnished with strong claws. Marsupial bones and a cloaca are present [Oviparous,† with meroblastic ovum.]

The most important character of the Monotremes is the presence of a cloaca. The dilated end of the rectum receives the openings of the generative and urinary ducts (fig. 678 *a*). In addition to this character we must mention the simple condition of the female generative organs, the absence of teeth in the jaws, the possession of a large coracoid, and the slight development of the corpus callosum.

FIG. 681.—*Echidna hystrix*. FIG. 682.—*Ornithorhynchus paradoxus*.

The form of the body and the mode of life of the Monotremes partly recall the Anteaters and Hedgehog (*Echidna hystrix*, fig. 681) and partly the Otters and Moles (*Ornithorhynchus*); in fact, *Ornithorhynchus* received the appropriate name of "Watermole" from the Australian settlers (fig. 682). *Echidna* is covered with strong spines, and possesses an elongated edentulous snout, with a vermiform, protrusible tongue. The short five-toed legs end with powerful scratching claws, which are excellently adapted for rapid burrowing. *Ornithorhynchus*, on the contrary, has a close, soft fur, a flattened

* R. Owen, Article "Monotremata," in Todd's "Cyclopædia of Anatomy," vol. iii., 1843.

† Vide note on p. 296.

the ectoderm, and sinks into a depression of the water vascular vesicle. At the apical pole there is a thickening of the ectoderm resembling the apical plate of the larval Worms and containing two eye-spots.

The development of the larva into the adult *Balanoglossus* was first traced by E. Metschnikoff and then by A. Agassiz. The band of cilia gradually disappears, the præ-oral part of the larva becomes the proboscis, while the oral portion gives rise to the collar. The trunk is formed from the posterior elongated portion on which the posterior transverse ciliated band still persists. The anterior portion of the alimentary canal becomes pierced by paired branchial slits (figs. 243, 244).

The body of the adult animal is worm-like and completely ciliated; it can be divided by the external features into a number of different regions. The anterior end of the body is indicated by a proboscis well marked off and projecting like a head. This is fol-

lowed by a muscular collar. Posterior to the collar

there is a longer portion of the body, the branchial region, which may be divided into a median distinctly ringed part (branchiæ) and two lobed lateral portions usually filled with yellow glands. At the boundary, between the median portion and the two lateral lobes, there are on either side rows of openings which serve for the exit of the water from the branchial chamber. Then follows a third division of the body, the gastric region, upon the upper side of which there are four rows of yellow glands (*generative glands*).

FIG. 243.—Stage in the conversion of *Tornaria* into *Balanoglossus*, with one pair of branchial slits (after E. Metschnikoff), seen from the side. *Bo*, external branchial opening; *P*, peritoneal sac; *Vc*, circular vessel; *O*, mouth; *C*, heart.

FIG. 244.—Stage in the conversion of *Tornaria* into *Balanoglossus*, with four pairs of branchial slits (after Al. Agassiz). Letters as in figs. 242, 243.

Between these, brownish-green prominences are visible (the hepatic appendages of the intestine), which, towards the posterior extremity where the yellow glands disappear, are larger and more closely aggregated. Finally there follows a distinctly ringed caudal region, at the hind end of which is the anus.

The contractile proboscis serves not only as a siphon to maintain respiration, but also as a locomotory organ. It projects above the level of the mud in which the animal is buried, and is said to take in water by a terminal aperture (the existence of this opening has been recently disputed) [and to pass it out into the mouth through a pore at its base].

The mouth lies behind the anterior margin of the so-called collar, and leads into a buccal cavity, the walls of which contain a great number of unicellular mucous glands. The portion of the alimentary canal which follows the buccal cavity bears the branchial framework, and is divided into a dorsal and ventral part by two longitudinal folds, so that it almost presents in transverse section the appearance of a figure of 8. The intestine does not hang freely in the body cavity, but, except in the region of the tail, is fastened to the body wall by connective tissue; it is, however, always very closely attached in the two median lines. Beneath the dorsal and ventral median lines, where the two principal vascular trunks are visible through the skin, two grooves, beset with strong cilia, run along the whole length of the intestine. From these grooves secondary grooves are given off, and as it were divide the whole surface of the intestine into islands. Some distance behind the branchial region, on the upper side of the intestine, the peculiar cell masses begin, which gradually assume the form of sac-like diverticula with ciliated internal walls. These "hepatic appendages" are either disposed in a simple row along each side (*B. minutus* Kow.), or densely aggregated together (*B. clavigerus* Delle Ch.)

The branchial basket-work which is placed at the commencement of the alimentary canal projects on the anterior flattened part of the body in the form of a transversely ringed longitudinal fold, and contains a system of chitinous plates, which constitute its framework and are connected in a peculiar manner by transverse rods. The water taken in through the mouth passes through special openings in the wall of the anterior portion of the alimentary canal into the ciliated branchial spaces, to issue thence through the two rows of lateral pores on the dorsal surface of the branchial region.

The vascular system consists of two median longitudinal trunks,

which give off numerous transverse branches to the walls of the intestine and body, and of two lateral trunks. The branchiæ receive their rich vascular supply entirely from the lower trunk. The upper trunk, in which the blood flows from behind forwards, divides at the posterior end of the branchiæ into four branches, of which the two lateral ones pass to the lateral portions of the anterior part of the body.

Certain fibrous cords, running directly beneath the epidermis in the dorsal and ventral median lines and branching into a net-work of fine fibrillæ, have lately been interpreted as *nervous centres*. These cords are described as being connected at the posterior end of the collar by a ring-like commissure.

The *generative organs* are arranged in single rows in the branchial region, but posterior to this in double rows. During the breeding season they are extraordinarily developed, and the male and female can be easily distinguished by the difference in their colour. Each ovum is contained in a capsule, which is provided with nuclei, but is otherwise homogeneous. The eggs are probably laid in strings like those of Nemertines.

These animals live in fine sand. They saturate the sand in their immediate vicinity with mucous. They fill their alimentary canal with sand, and move themselves by means of their proboscis, which, alternately elongating and retracting, draws the body after it. Both the species named were found in the Gulf of Naples. A third northern species of *Balanoglossus* was discovered by Willemoes-Suhm, and described as *B. Kupfferi*.

CHAPTER IX.

VERMES.

Bilateral animals with unsegmented or uniformly (homonomous) segmented body. There are no segmented lateral appendages. A dermal muscular system and paired excretory canals (water-vascular system) are present.

SINCE the time of Cuvier, a number of groups of animals all characterised by the possession of an elongated laterally symmetrical body and by the absence of articulated limbs have been classed together as *Vermes*. This group includes such a variety of forms that attempts have already been made to break it up, and it will perhaps be necessary at some future time to separate the unseg-

mented from the segmented forms, under the respective heads of *Vermes* and *Annelida*.

The form of the body, which is soft and adapted to live in damp media, is usually elongated, flat, or cylindrical, sometimes without rings, sometimes ringed, and sometimes divided into segments (metameres). In every case we can distinguish a ventral and a dorsal surface. It is on the first that the animal moves or attaches itself to foreign objects. The mouth is usually placed ventrally at the end of the body which is directed forward in locomotion. The contrast between the flat, shorter form of body and the cylindrical and elongated seems, especially in the case of the non-segmented worms (*Vermes* s. str.), to be of importance, so that on this ground we can establish the classes of *Platyhelminthes* or flat worms, and of *Nemathelminthes* or round worms. The segmented worms (*Annelida*)

possess a ventral chain of ganglia in addition to the brain, and a segmentation of the organs which corresponds more or less with the external segmentation. The portions of the body which are primitively alike and are known as segments or metameres do not by any means always remain homonomous. In the most highly developed segmented worms, the two anterior segments unite to form a division of the body which foreshadows the head of the *Arthropoda*, and, like the latter, is pierced by the mouth, contains the brain, and bears the sense organs (fig. 245).

FIG. 245.—Head and anterior segments of *Eunice* seen from the dorsal surface. *T*, Tentacles or antennæ of the præstomium; *Ct*, tentacular cirri; *C*, cirri of the parapodia; *Br*, branchial appendages of the parapodia.

In the succeeding metameres there are also frequently variations of form which disturb the homonomy.

The skin of worms presents very different degrees of consistence, and covers a strongly developed muscular system. In the skin we can distinguish a layer of cells (*hypodermis*) or, at any rate, a nucleated layer of protoplasm which functions as a matrix, and a superficial homogeneous cuticular layer which is secreted by the first-named layer or matrix and in the lower worms is extremely thin and delicate. In the *Nemathelminthes* it is often laminated, and can

even be separated into several layers. It is of considerable thickness in many *Annelida* (*Chaetopoda*), and may be perforated by pores. Cilia are found principally in the larval stages of *Platyhelminthes* and *Annelida*. Where there are no cilia, the superficial cuticular membrane, which may project in the form of tubercles or spines, consists of a substance allied to the chitin of the Arthropod skin, like which it may bear cuticular formations of many kinds, such as hairs, bristles, hooks, etc. In many *Nemathelminthes*, as well as in segmented worms, this firm cuticula gives rise to a kind of exo-skeleton, which opposes the contractions of the dermal muscular envelope. In the *Chaetopoda* among the *Annelida*, but also in the *Rotifera*, the tough integument is divided into a number of sections lying one behind the other. These, like the segments of Arthropoda, are connected by soft portions of skin and moved by the dermal muscles, which are divided into corresponding groups. The cutaneous segments of the *Rotifera* are not true metameres, since there is no segmentation of the internal organs.

Cutaneous glands are very widely distributed; they are sometimes unicellular, sometimes polycellular, and are sometimes situated directly beneath the epidermis, sometimes in the deeper tissues of the body.

The tissue which lies beneath the hypodermis, and which we may call the cutis, contains in all cases longitudinal and in some cases also circular muscles, and so constitutes a *muscular cutaneous envelope*, the principal locomotory organ of worms. Taking into consideration the importance of this dermal muscular system in the locomotion of worms, we must attribute a certain systematic value to the special forms which it assumes, a value which, however, we must be careful not to exaggerate. The stratification and the direction of the fibres of this dermal muscular system is most complicated in the *Platyhelminthes* and in the *Hirudinea* amongst the *Chaetopoda*, for here we find the circular and longitudinal muscles, which are embedded in a basis of connective tissue, crossed by muscle fibres, which run in a dorso-ventral direction (sometimes also by fibres running obliquely). To these may be added groups of muscular fibres, which serve to attach the internal organs to the integument. The suckers of the parasitic worms, the pits and the parapodia with their setæ of *Chaetopoda*, must be looked upon as special differentiations of the dermo-muscular envelope. These aids to locomotion are mostly developed upon the ventral surface. The suckers and their accessory hooks, etc., are situated either near the two ends or in the middle of the

body; the parapodia are distributed in pairs on the individual segments along the whole length of the body, and belong to the dorsal as well as to the ventral surface, so that each segment bears a dorsal and a ventral pair of parapodia.

The internal organization of Worms is extraordinarily various. In those flat and round worms which live in the chyme or the other organic juices of the higher animals, as, for instance, the *Cestoda* and the *Acanthocephala*, the whole of the digestive apparatus, including the mouth and anus, may be wanting; the nutrition in such cases taking place by osmosis through the body-wall. When the alimentary canal is present, the mouth is usually situated ventrally in the anterior region of the body, while the anus is placed either terminally at the posterior end of the body, or near it on the dorsal surface. The alimentary canal is generally simple, and is only exceptionally divided into numerous portions corresponding to the special functions. A muscular pharynx can most often be distinguished, also a well developed stomach and a short rectum opening at the anus.

The *nervous system* appears in its most simple form as an unpaired ganglion or, when the two parts of which it is composed are separated, as a pair of ganglia (fig. 76), which are placed near the anterior pole of the body above the œsophagus and genetically may be referred to the apical plate of Lovén's Chaetopod larva. The nervous system has more rarely the form of a nerve ring surrounding the œsophagus and connected with groups of ganglion cells (*Nematoda*). The nerves given off from the supra-œsophageal ganglion are distributed symmetrically forwards and laterally; they supply the sense organs, and form two strong lateral nervous trunks, which run backwards. In still higher types two larger ganglia appear, which are connected by an inferior commissure (*Nemertinea*). In the *Annelids* with degenerated metamerous (*Gephyrea*) there is in addition to the supra-œsophageal ganglion (the brain) a ventral nerve cord connected with the supra-œsophageal ganglion by an œsophageal ring. This nerve cord is in all other Annelids divided into a series of paired ganglia, which, in most cases, correspond to the segmentation. The lateral nerve trunks approach each other in the middle line below the alimentary canal, and constitute, together with their ganglia, which are connected together by transverse commissures, a ventral chain of ganglia, which is connected with the brain by the circum-œsophageal commissures, and is continued to the hind end of the body, giving off in its course paired nerves to the right and left.

The sense organs are represented by eyes, auditory apparatus, and

tactile organs. The latter are joined to nervous expansions and special integumentary appendages (tactile hairs), and are present even in the parasitic Worms as papillæ of the outer skin connected with nerves. In the free-living worms, these tactile organs frequently take the form of filiform, tentacle-like appendages on the head and segments (cirri). *Auditory organs* are not so generally present, and are represented by *auditory vesicles* (otocysts) either lying on the brain (some *Turbellaria* and *Nemertinea*), or on the œsophageal ring (certain branchiate Worms among the *Annelida*). The organs of sight are simple pigment spots in connection with nerves (*eye-spots*), and may be provided with refractive bodies. The ciliated pits of the *Nemertinea* have been regarded as organs of smell. The cup-shaped organs of the *Hirudinea* and *Gephyrea* are also sense organs.

A blood vascular system is wanting in the *Nemathelminthes*, the *Rotifera*, and the *Platyhelminthes* with the exception of the *Nemertinea*. In these cases, the nutritive fluid passes endosmotically into the body parenchyma or into the body cavity, and penetrates the

FIG. 246.—Section through a body segment of *Eunice*. *Br*, branchial appendages; *C*, cirri; *P*, parapodia with tuft of bristles; *D*, intestine; *N*, nervous system.

tissues as a clear chyle, sometimes containing cellular elements. In the *Nemertinea* a blood vascular system is present, as also in the *Gephyrea* and *Annelida*. In the latter it obtains the highest development, and may have the form of a completely closed vascular system provided with pulsating trunks. In most cases a dorsal contractile longitudinal trunk and a ventral vessel can be distinguished; the two being connected in each segment by arched transverse vessels, which are sometimes pulsatile. Where a vascular system is present, the blood does not always appear clear and colourless like the fluids of the body cavity, but sometimes has a yellow, greenish, or more frequently red colour, which is in some cases connected with the presence of blood corpuscles.

The function of respiration is usually performed by the general external surface of the body. Among the *Annelida*, however, we

find in the large marine *Chaetopoda* filiform or branched gills, which are usually appendages of the parapodia (fig. 246). A respiratory function may also be attributed to the tentacles of the *Gephyrea*.

The excretory organs are represented by the so-called water-vascular system, which consists of canals of different sizes, symmetrically arranged and filled with a watery fluid in which granules are suspended; they communicate with the exterior through one or more openings. The canals begin either as small passages in the tissues of the body, or free funnel-shaped openings in the body cavity. In the last case, they may subserve other functions; for example, they may conduct the generative products out of the body cavity. In the segmented *Vermes* they are paired, and are repeated in each segment as *nephridia* or *segmental organs* (fig. 70). A different arrangement is presented by the two lateral canals of the *Nematoda*, which lie in the so-called lateral lines or areas, and open by a common excretory pore in the region of the pharynx.

In addition to sexual reproduction an asexual multiplication by means of gemmation and fission (rarely by formation of germinal cells) is widely distributed, especially among the lower forms. This asexual reproduction is, however, frequently confined to the larvæ, which differ from the sexually mature animal in form and habitation, and play the part of an asexual generation in the cycle of development. Almost all the *Platyhelminthes* and numerous *Annelida* are hermaphrodite; the *Nemathelminthes*, the *Gephyrea*, and *Rotifera*, and also the branchiate Annelids are of separate sexes. Many Worms pass through a metamorphosis; the larvæ are characterised by the possession of a præoral ring of cilia (Lovén's larva), or of several rings of cilia. In the *Cestoda* and *Trematoda*, which possess in their embryonic stage the capability of asexual reproduction, the metamorphosis assumes the form of a more or less complicated alternation of generations which is often characterised by the difference in the habitat of the two successive stages of development and by the alternation of a parasitic and free life.

The vital activity of the Worms is in general of a low order, corresponding with their habitat. Many of them (Entozoa) live as parasites in the interior of the organs of other animals, some as ectoparasites on the external surface of the body, and feed on the juices of their hosts. Others live free in damp earth, or in mud; others, and these are the most highly organized forms, inhabit fresh and salt water.

CLASS I.—PLATYHELMINTHES

Vermes with a flat, more or less elongated body, with cerebral ganglion. They are often provided with suckers and hooks, and are usually hermaphrodite.

The series of forms included under this class are mostly *Entozoa*, or else live in the mud and beneath stones in the water. In their organization they occupy the lowest place among the worms. Their body is more or less flattened, and is either unsegmented or is divided by transverse constrictions into a number of successive divisions, which, although forming parts of one animal, yet have a strong tendency towards individualisation, and frequently attain to separation and lead an independent life. These segments are products of growth in the direction of the long axis of the body, and stand in a special relation to reproduction. They are by no means to be considered as necessarily indicating a high grade of organization, as does the segmentation of the *Annelida*. The *alimentary canal* may be altogether wanting (*Cestoda*), or, if present, may be without an anus (*Trematoda*, *Turbellaria*).^{*} The *nervous system* is usually composed of a double ganglion above the œsophagus, giving off small nerves anteriorly and laterally, and two stems backwards. In many *Platyhelminthes* simple eye-spots occur, either with or without refractive bodies, and more rarely there is an auditory vesicle. Blood-vessels and organs of respiration are found only in the *Nemertinea*. The excretory (water vascular) system is everywhere developed. With the exception of the *Microstomide* and *Nemertinea*, hermaphroditism is the rule. The female generative glands consist of distinct yolk-glands and ovaries. The development very frequently takes place by a very complicated process of metamorphosis connected with alternation of generations.

Order 1.—TURBELLARIA.*

Free living Platyhelminthes with oval or leaf-shaped body, with soft skin covered with cilia. They possess a mouth and aprocous

* Dugès, "Recherches sur l'organisation et les mœurs de Planaires," *Ann. des Sc. Nat.*, Ser. I., Tom XV. A. S. Oerstedt, "Entwurf einer systematischen Eintheilung und speciellen Beschreibung der Plattwürmern," Copenhagen, 1844. De Quatrefages, "Mémoire sur quelques Planariées marines," *Ann. des Sc. Nat.*, 1845. M. Schultze, "Beiträge zur Naturgeschichte der Turbellarien," Greifswald, 1851. L. Graff, "Zur Kenntniss der Turbellarien," *Zeitschrift für Wiss. Zool.*, Tom XXIV. L. Graff, "Neue Mittheilungen über Turbellarien." *Zeitsch. f. wiss. Zool.*, xxv., 1875. P. Hallez, "Contributions à l'histoire naturelle des Turbellariés," Lille, 1879.

alimentary canal. Hooks and suckers are absent. A cerebral ganglion is present.

The *Turbellaria* usually possess an oval flattened body, and reach only a small size. The uniform ciliation of the body is connected with their existence in fresh and salt water, beneath stones, in mud, and even in damp earth. Only in exceptional cases do we meet with apparatuses for adhering, viz., small hooks and suckers.

The skin consists of a single layer of cells, or of a finely granular

FIG. 247.—Alimentary canal and nervous system of *Mesostomum Ehrenbergii* (after Graff). *G*, the two cerebral ganglia with two eye spots; *St*, the two lateral nerve trunks; *D*, alimentary canal with mouth and pharynx.

layer containing nuclei, which is supported by a stratified basal membrane, and covered externally by a special homogeneous membrane bearing cilia and comparable to a cuticula. Peculiar integumentary structures, which have the form of rods or spindles, and, like the nematocysts in *Cœlenterata*, take their origin in cells, are not unfrequently present. Various pigments are also often found embedded in the epidermis, and of these pigments the green-coloured vesicles, in *Vortex viridis* for example, which are identical with chlorophyll corpuscles, are specially worthy of remark. Pear-shaped mucous glands are also present. Beneath the conspicuous basement membrane which supports the epidermis lies the dermis. It contains the strongly developed dermal muscular system embedded in a connective tissue layer formed of round, often branched cells. A body cavity between the body wall and the alimentary canal, is, as a rule, absent; it may, however, in many cases be recognised as a system of lacunæ, or as a continuous cavity surrounding the alimentary canal.

The nervous system consists of two ganglia connected by a commissure, and giving off nerve fibres in various directions; of these, two especially large lateral trunks run backwards, one on either side (fig. 247). The latter are connected at regular intervals by delicate transverse trunks. In a number of dendrocœlous Turbellarians a

diverticulum of the stomach runs forward above the transverse commissure in a groove between the two cerebral lobes (*Leptoplana*). In some genera of *Planarians*, a ring-shaped double commissure has been shown to exist in the brain (*Polycelis*), and ganglion-like swellings, from which nerves are given off, have been observed on the lateral nerve-trunks (*Sphyrocephalus*, *Polycladus*).

With regard to sense organs, *eye spots* are tolerably widely distributed among the *Turbellaria*. They either lie in pairs upon the cerebral ganglia or are connected with short nerves given off from the latter. More frequently two larger eyes with refractive structures are developed. Otcysts are but rarely present, *e.g.*, in *Monocelis* among the *Rhabdocela* a single one is present lying upon the cerebral ganglion. The integument is without doubt endowed with a highly developed tactile sense; the large hairs and stiff bristles which project between the cilia may possibly be of importance in this relation. Lateral ciliated pits, which may also be explained as sense organs, are in rare cases present at the anterior end of the body (compare the *Nemertinea*).

Mouth and digestive apparatus are never wanting but the former is frequently removed from the ventral surface of the anterior end of the body to the middle or, indeed, even to the posterior region. According to Metschnikoff and Ulianin, a stomach may in some cases be absent (*Convoluta*, *Schizoprora*), and be replaced, as in *Infusoria*, by a soft internal parenchyma. The mouth leads into a muscular pharynx, which can usually be protruded after the manner of a proboscis. The alimentary canal, of which the internal wall is frequently ciliated, is either forked and then simple or branched (*Dendrocela*), or rod-shaped (*Rhabdocela*). An anus is never present. A peculiar tube capable of being evaginated as a proboscis, and without connection with the pharynx is sometimes also present (*Prostomum*).

The *excretory* (water-vascular) *system* consists of two transparent lateral trunks and innumerable side branches, which begin with closed ciliated funnels, and are furnished with vibratile cilia, which

FIG. 248.—*Microstomum lineare*, after Graff. A chain produced by fission; O, O', mouth openings.

shelled or *summer eggs* invariably precedes that of the hard-shelled or *winter eggs*, and the summer eggs are normally self-fertilized.

In rare cases the hermaphrodite generative organs present a segmentation recalling that of the *Cestoda* (*Alaurina composita*).

The freshwater *Turbellaria*, as well as many of the marine forms, undergo a simple direct development, and in the young state are often difficult to distinguish from *Infusoria*. Other marine *Dendrocœla* undergo a metamorphosis, the larvæ being characterised by the possession of finger-shaped ciliated lobes (fig. 251).

(1) Sub-order: **Rhabdocœla**. The body is round and more or less flat. The intestine is cylindrical, and there is usually a protrusible pharynx. They are usually hermaphrodite.

The Rhabdocœlous Turbellarians are the smallest and most simply organised forms. The intestine is cylindrical and elongated, and is sometimes provided with lateral diverticula. The position of the mouth varies exceedingly, and has been employed as a principal characteristic for distinguishing the various families. Sometimes salivary glands are present, opening into the pharynx. According to Ulianin's discovery, which has been several times confirmed, the alimentary canal may be wanting in many forms, and be replaced by a central cavity, filled with a substance containing numerous vacuoles and rich in oil globules (*Convoluta*, *Schizoprora*, *Nadina*). In those *Rhabdocœla* which possess an alimentary canal, interstices and spaces in the connective tissue parenchyma are often present: these must be related to a body cavity. In some cases (in *Prostomum*) the body cavity may be recognised as a continuous space filled with fluid and surrounding the alimentary canal. The *Rhabdocœla* live on the juices of small worms and of the larvæ of *Entomostraca* and *Insecta*, which they envelop with a cutaneous secretion containing small rods, and afterwards suck. They are mostly inhabitants of fresh water, and only a few of them are to be met with in the sea or upon the land (*Geocentrophora sphyrocephala*).

Fam. **Opisthomidæ**. The mouth is placed at the posterior end of the body and leads into a tubular pharynx, which can be protruded like a proboscis. *Monocelis agilis* M. Sch., *Opisthomum pallidum* O. S.

Fam. **Derostomidæ**. Mouth placed slightly behind the anterior margin; pharynx barrel-shaped. *Derostomum Schmidtianum* M. Sch., *Vortex viridis*, M. Sch., *Catenula lemnæ* Dug.

Fam. **Mesostomidæ**. Mouth placed nearly in the middle of the body, pharynx ringlike, cylindrical or resembling a sucker. *Mesostomum Ehrenbergii* Oerst., with two eyes.

Fam. **Convolutidæ**. (*Acoela*). Without alimentary canal. The ovaries and

yolk glands are not separate. *Convoluta* Oerst. *C. paradoxa* Oerst., North Sea, Baltic. *Schizoprora* O. S.

Fam. **Prostomidæ**. The mouth, which is situate on the ventral surface, leads into a muscular pharynx. At the anterior end there is a protrusible tactile proboscis furnished with papillæ. *Prostomum* Oerst. (*Gyrator* Ehrbg.), *P. lineare* Oerst. With pointed penial spine at the posterior end, imperfectly hermaphrodite, living principally in fresh water. *Pr. helgolandicum*, Kef., completely hermaphrodite.

Fam. **Microstomidæ**. *Rhabdocæla* with separate sexes. The small but very extensible mouth lies near the anterior end of the body. There are laterally placed ciliated pits near the anterior end of the body. Formation of metameræ and transverse fission frequently occur. *Microstomum lineare* Oerst. (fig. 248).

FIG. 250.—Anatomy of *Polycelis pallida* (after Quatre-fages). G, Cerebral ganglion with the nerves given off from it; O, mouth; D, branches of intestine; Or, ova; Od, oviduct; V, vagina; W.Goe, female generative opening; T, testes; M.Goe, male generative opening.

(2) *Sub-order: **Dendrocæla**. The body is broad and flat, and the lateral margins are often plicated. There are tentacle-like processes at the anterior end. There is a branched alimentary canal and a muscular pharynx which is usually protrusible. They are, as a rule, hermaphrodite.

The *Dendrocæla* are mostly marine, but also live in fresh water and on land. In their external appearance they resemble the Trematodes, and the branching of their straight or forked intestine is a

character common to the larger species of the latter. Compared with the *Rhabdocæla*, they are distinguished by the greater development of their bi-lobed cerebral ganglion, as well as by the greater number of their eyes (fig. 250). The rows of papillæ, or the tentacle-like processes at the anterior end of the body have

probably the function of tactile organs. The mouth usually lies in the middle of the body, and leads into a wide and protrusible pharynx. The skin is often provided with glands, the secretion of which in certain land *Planaria* (*Bipalium*, *Rhynchodemus*) hardens to a fibrous web. They are almost always hermaphrodite. The fresh-water forms possess a common generative opening, while in the marine forms the generative openings are usually separate (fig. 250). In the latter case a separate vitellarium is absent. In some marine forms development takes place with metamorphosis, as is shown by the larva discovered by J. Müller, which possessed six provisional finger-like ciliated lobes (fig. 251). In the fresh-water Planarians development is direct. The cocoon, when laid, contains four to six small eggs. At the close of segmentation there is developed a layer of cells, which is said to split into two layers, an upper or animal layer, from which are derived the body wall and muscular system, and a lower or vegetative, from which the alimentary canal is formed. The marine *Dendrocæla* frequently deposit their eggs in the form of broad bands.

FIG. 251.—Larva of *Eurylepta auriculata*, after Hallez.

1. **Monogonopora** Stimps. *Dendrocæla* with single sexual opening. The land and fresh-water Planaria belong to this group.

Fam. Planariadæ. The body is of a long, oval, flattened shape, and is often provided with lobed processes, more rarely with tentacles, and, as a rule, with two eyes, which are provided with lenses. *Planaria* O. Fr. Müller, two eyes, no tentacles. *Pl. torva*, M. Sch. (divided by O. Schmidt into *lugubris*, *polychroa*, and *torva*) (fig. 252). *Pl. dioica* Clap., with separate sexes. *Dendrocælum* Oerst. Distinguished by the possession of

FIG. 252.—*Planaria polychroa* (a), *lugubris* (b), *torva* (c), about twice the natural size (after O. Schmidt).

lobed processes on the head, also by the presence of a copulatory organ placed in a special sheath. *D. lacteum* Oerst., *Polycelis nigra*, *brunnea* O. Fr. Müll.

Fam. Geoplanidæ.* Land Planarians. They are characterised by their

* Besides M. Schultze, Stimpson, Metschnikoff, Grube, etc., compare H. N.

elongated and flattened body, which is provided with a foot-like ventral surface. *Geoplana lapidicola* Stimps., *Rhynchodemus terrestris* Gm. (*Fasciola terrestris*, O. Fr. Müller), Europe. *Geodesmus bilineatus*, Metschn., with thread cells in the integument, found in potter's earth.

2. **Digonopora.** *Dendrocaela* with double sexual opening. Almost all are marine. The proboscis is often folded and lies within a special pouch. When protruded, it spreads out like a lobe.

Fam. **Stylochidæ.** The body is flat and rather thick, and is provided with two short tentacles on the head. There are usually numerous eyes on the tentacles or on the head. The genital openings are posterior. *Stylocheus maculatus* Quatr.

Fam. **Leptoplanidæ.** Body flat and broad, usually very delicate. Cephalic region not distinct, without tentacles. The eyes are more or less numerous. The mouth is usually placed in front of the middle of the body. The genital openings lie behind it. *Leptoplana tremellaris* O. Fr. Müll., Mediterranean.

Fam. **Euryleptidæ.** Body broad, and either smooth or furnished with papillæ. There are two tentacle-like lobes on the anterior region of the head. The mouth is placed in front of the middle of the body. Numerous eyes are disposed near the anterior margin. Marine. *Thysanozoon Diesingii* Gr. Mediterranean. *Eurylepta auriculata* O. Fr. Müller, North Sea.

Order 2.—TREMATODA.*

Parasitic Platyhelminthes with unsegmented, usually leaf-shaped, rarely cylindrical body. They possess a mouth and ventrally placed organ for attachment: the intestine is forked and without an anus.

The Trematodes are with great probability to be derived from the *Turbellaria*, with which group, both in form and organization, they show a close relationship. In connection with their parasitic mode of life they develop special organs for adhering, such as suckers and hooks. Cilia are present only in larval life.

The mouth is invariably placed at the anterior end of the body, usually in the middle of a small sucker (fig. 253). It leads into a muscular pharynx with a more or less elongated œsophagus, which is prolonged into a forked intestine ending blindly.

Moseley, "Notes on the Structure of Several Forms of Land Planarians," etc. *Journal of Micr. Science*, vol. xvii.

* A. v. Nordmann, "Mikrographische Beiträge zur Kenntniss der wirbellosen Thiere," Berlin, 1832. G. G. Carus, "Beobachtung über *Leucochloridium paradoxum*, etc.," *Nov. Act.*, vol. xvii., 1835. Wagener, "Ueber *Gyrodactylus elegans*," *Müller's Archiv.*, 1860. Van Beneden, "Mémoire sur les vers intestinaux," Paris, 1861. E. Zeller, "Untersuchungen über die Entwicklung und den Bau von *Polystoma integerimum*," *Zeitschr. f. wiss. Zool.*, vol. xxii., 1872. E. Zeller, "Untersuchungen über die Entwicklung von *Diplozoum paradoxum*," *Ibid.*, vol. xxiii., 1873. E. Zeller, "Ueber *Leucochloridium paradoxum* und die weitere Entwicklung seiner Distomumbrut," *Ibid.*, Tom XXIV. E. Zeller, "Weiterer Beitrag zur Kenntniss der Polystomeen," *Ibid.*, xxvii., 1876. Compare also the works of G. Wagener and De Filippi.

The *excretory* apparatus consists of two large lateral trunks and a network of fine vessels permeating the tissues and beginning with small ciliated lobules. The two large trunks open into a common contractile vesicle, which opens to the exterior at the posterior end of the body (fig. 253, *Ep*). The excretory system contains a watery fluid with granular concretions. This fluid is probably an excretory product, corresponding to the urine of higher animals.

The *nervous system* consists of a double ganglion lying above the oesophagus, and from it several small nerves and two posteriorly directed lateral trunks are said to be given off. *Eye spots* with refractive bodies are sometimes present in the larvæ during their migrations. Locomotion is effected by the dermal muscular system and the organs of attachment, viz., the suckers and hooks, which present numerous modifications in number, form, and arrangement. In general, the size and development of these organs are related to the endoparasitic or ectoparasitic mode of life. In the endoparasitic Trematodes they are less developed, and usually consist of the oral sucker and a second larger sucker on the ventral surface, either near the mouth, as in *Distomum*, or at the opposite pole of the body (*Amphistomum*). This large sucker may, however, be absent (*Monostomum*). The ectoparasitic *Polystomea*, on the other hand, are distinguished by a much more powerful armature, for besides

FIG. 253.—Young *Distomum* (after La Valette). *Ex*, trunk of the excretory (water vascular) system; *Ep*, excretory pore; *O*, mouth with sucker; *S*, sucker in the middle of the ventral surface; *P*, pharynx; *D*, forked intestine.

two smaller suckers at the sides of the mouth, they possess one or more large suckers at the posterior end of the body (fig. 258), which, moreover, may be supported by rods of chitin. There are often in addition chitinous hooks, and very frequently two larger hooks among the posterior suckers in the middle line (*H*).

The *Trematoda* are mostly hermaphrodite. As a rule, the male and female generative openings lie side by side, or one behind the other, not far from the middle line of the ventral surface, near the anterior end of the body (fig. 254). The male opening leads into a sac, the

cirrus sac, which encloses the protrusible terminal part (cirrus) of the vas deferens. The vas deferens soon divides into two, which lead back to the two large simple or multilobed testes. The supposed third vas deferens, which, according to v. Siebold, runs from one testis to the female sexual apparatus, so as to permit of direct fertilization without copulation, has been recognized as a vagina opening to the exterior on the dorsal surface (canal of Laurer). The

FIG. 254.—*Distomum hepaticum* (after Sommer). O, Mouth; D, limb of intestine; S, sucker; T, testes; Do, vitellarium; Ov (uterus), oviduct; Dr, accessory glands.

female organs consist of a convoluted uterus and of the glands concerned in the preparation of the egg, viz., an ovary and two yolk glands. There is sometimes in addition a special shell gland. The true ovary which produces the primary ova is a round body, and is usually placed in front of the testes. The yolk glands which secrete the yolk are much ramified tubular glands, and fill the sides of the body (fig. 254). The yolk particles come in contact with the primary ova in the first portion of the uterus, and surround them in greater or less quantities. Subsequently each ovum, with its investment of yolk, is surrounded by a strong shell. The ova in their passage along the uterus become packed together, often in great numbers, and undergo the stages of embryonic development in the body of the parent. Most Trematodes lay their eggs; only a few are viviparous.

The just-hatched young either possess (in most *Polystomea*) the

form and organization of the parent; or they present the phenomenon of a complicated alternation of generations (heterogamy) connected with a metamorphosis (*Distomea*). In the first case, the large eggs become attached in the place where the mother lives; in the last case, the relatively small eggs are deposited in a damp place, usually in the water. After the completion of the segmentation and the em-

bryonic development, the contractile, usually ciliated embryos* (fig. 255, *a*), which already possess the first rudiments of an excretory system and more rarely a sucker with a mouth and alimentary canal, leave the egg and wander about independently in search of a new host. The latter is, as a rule, a snail, into the interior of which they penetrate and there become transformed into simple or branched *Sporocysts* (without mouth and alimentary canal, fig. 255, *c*), or into *Rediæ* (with mouth and alimentary canal, fig. 255, *d*). These give rise, by means of the so-called germs [cells lying in the body cavity of the

FIG. 255.—Developmental history of *Distomum* (partly after R. Leuckart). *a*, free swimming ciliated embryo of the liver fluke. *b*, the same in a state of contraction with rudimentary alimentary canal (*D*) and cell mass (*Ov*) (rudiments of the genital glands). *Ex*, ciliated apparatus of the rudimentary excretory system. *c*, sporocyst developed from a *Distomum* embryo, filled with *Cercariæ* (*C*); *B*, boring spine of a *Cercaria*. *d* Redia with pharynx, (*Ph*), and alimentary canal (*D*); *O*, mouth; *Ex*, Excretory organ; *C*, *Cercaria* inside Redia. *e*, Free *Cercaria*; *S*, sucker; *D*, alimentary canal.

sporocyst or redia], which probably correspond to the germinal cells (primitive ova) of the rudimentary ovary, to the generation of the

* As R. Leuckart has rightly observed, the *Dicymidæ*, which were regarded as *Mesozoa* by Ed. v. Beneden, as well as the *Orthonectidæ*, which have recently been especially investigated by Giard and E. Metschnikoff, and which in the reproductive stage do not rise above a form corresponding to the embryos of Trematodes, recall these *Distomum* larvæ.

tailed *Cercariæ*, or to another generation of *Sporocysts* or *Rediæ*,* which then produce the *Cercariæ*.

The *Cercariæ* are nothing else than *Distomum* larvæ, which eventually reach (often only after two migrations, an active and a passive one) the final host, where they become sexually mature. They are furnished with an exceedingly motile caudal appendage, frequently with a buccal spine, and occasionally with eyes, and they present in the rest of their organization great resemblances to the adult *Distomum*, excepting that the generative organs are not developed. In this form they leave independently the body of the *Redia* or *Sporocyst* and of the host of the latter, and move about in the water, partly creeping and partly swimming. Here they soon find a new host (Snail, Worm, Insect larva, Crustacean, Fish, Batrachian), into which they penetrate, aided by the powerful vibrations of their tail; they then lose the latter and encyst.

FIG. 256.—*a*, Embryo of *Diplodiscus subclavatus* (after G. Wagener). *D*, Alimentary canal; *Ex*, excretory system. *b*, Embryo of *Monostomum mutabile* (after v. Siebold). *P*, Pigment spots; *R*, redia in the interior of the embryo.

The *Cercariæ* from the interior of the snail thus become distributed amongst a number of hosts, and each of them gives rise to an encysted young *Distomum* without generative organs. This young *Distomum* migrates passively with the flesh of its host into the stomach of another animal, and thence, freed from its cyst, into the organ (intestine, bladder etc.), in which it becomes sexually mature.

There are, then, as a rule, three different hosts in the organs of which the different developmental stages (*Redia* or *Sporocyst*, encysted form, sexually mature animal) of the *Distomum* bury themselves. The transitions from one host to another are effected partly by independent migration (embryos, *Cercariæ*), partly by passive migration (encysted young *Distomum*).

Modifications of the ordinary course of development may, however, take place; these may be either complications or simplifications. The embryo at hatching may contain a single *Redia* (as in *Monostomum*

* In *Cercaria cystophora* from *Planorbis marginatus*; according to G. Wagener, the primary asexual individual is a *Sporocyst*, the secondary a *Redia*.

flavum and *mutabile*), which it carries about until it enters the first host (fig. 256, *b*). In other cases the course of development is simplified by the omission of the second intermediate host, viz., that which contains the encysted immature *Distomum* (*Cercaria macrocerca* of *Distomum cygnoides*, also *Leucochloridium* in the tentacles of *Helix succinea*).

(1) Sub-order: **Distomea**. Trematodes with at most two suckers, without hooks. They develop with a complicated alternation of generations. The asexual individuals and the larvæ live principally in *Mollusca*, the sexually mature animals in the alimentary canal of Vertebrates.

The sexes are completely separated in *Distomum hæmatobium* (from the veins of man); individuals of the two sexes being united in pairs (fig. 257). Dimorphic forms are found in certain species of the genera *Monostomum* and *Distomum* in connection with the division of labour of the sexual functions; one individual develops only male sexual organs, and the other only female, the former producing spermatozoa and the latter ova. The rudiment of the functionless generative gland undergoes in these cases a more or less complete degeneration. Such *Distomea* are morphologically hermaphrodite, but practically of separate sexes.

The complete biology and developmental history is unfortunately only satisfactorily known for a few species which can be followed through all the stages of development.

Fam. **Monostomidæ**. Of an oval, elongated, more or less rounded form, with only one sucker, which surrounds the mouth. *Monostomum* Zeder. Sucker surrounding the mouth; pharynx powerful. Sexual openings but slightly removed from the anterior end. *M. mutabile* Zeder, in the body cavity and in the orbit of various water-birds; viviparous. *M. flavum* Mehlis, in water-birds, develops from *Cercaria ephemera* of *Planorbis*. *M. lentis* v. Nordm., the young form without generative organs is found in the lens of the human eye. *M. bipartitum* Wedl., living in pairs enclosed in a common cyst, the one individual surrounded by the lobed posterior end of the other; branchiæ of Tunny-fish.

Fam. **Distomidæ**. Body lancet-shaped, frequently spread out, more rarely elongated and rounded with a large median sucker; in front of which lie the genital openings, usually close together.

FIG. 257.—*Distomum hæmatobium*. Male and female, the latter being in the canalis gynæcophorus of the former. S, sucker.

Distomum. Median sucker approached to the anterior one. *D. hepaticum* L. Liver fluke. With conical anterior end, and numerous spine-like prominences on the surface of the broad leaf-shaped body, which is about 30 mm. long. Lives in the bile-ducts of sheep and other domestic animals, and produces the liver disease of the sheep. It is occasionally found in Man, and bores its way into the portal vein and into the system of the vena cava. The elongated embryo only develops after the egg has remained a long time in water; it has a continuous ciliated envelope with an X-shaped eye-spot. R. Leuckart's researches have rendered it probable that the development is passed through in the young *Limnæus pereger* and *truncatulus*, that here the embryo becomes a *Sporocyst*, and that this produces *Rediæ*, in which it is supposed that tailless *Distomea* arise.

[The life-history of the liver-fluke has been completely worked out by A. P. Thomas (*Quart. Journal of Microscopical Sci.* 1883, pp. 99—133). He has shown that the ciliated embryo passes into *Limnæus truncatulus*, and there gives rise to a *sporocyst* which produces *redia*. The *redia* produce more *redia* or *Cercaria*. The *Cercaria*, which are provided with long tails, leave the host (*Limnæus truncatulus*), swim about for a short time in the water, and encyst on foreign objects, e.g. blades of grass. In this condition they are eaten by the sheep.]

D. crassum Busk., in the alimentary canal of the Chinese, one to two inches in length, and half-inch broad, without spinous prominences, with a simple forked intestine. *D. lanceolatum* Mehlis. Body elongated into the form of a lancet, 8—9 mm. long, lives in the same place with *D. hepaticum*. The embryo develops at first in water, is pear-shaped, and only ciliated on the anterior half of the body, bears a styliform spine on the projecting apex. *D. ophthalmobium* Dies. A doubtful species of which only four specimens have been observed in the lens capsule of a nine-months' child. *D. heterophyes* Bilh. v. Sieb. 1—1·5 mm. long, in the alimentary canal of man in Egypt. *D. goliath* van Ben., 80 mm. long, in *Pterobalana*. Numerous species live in the alimentary canal, lungs, and bladder of the frog. *Distomum filicollis* Rud. (*D. Okeni* Köll) in pairs in the mucous sacs in the branchial cavity of *Brama Raji*. The one individual is cylindrical and narrow, and produces spermatozoa; the other is swollen in the middle and posterior region of the body, and is filled with eggs. The dissimilar development of the two individuals is probably due to the fact that copulation only leads to the fertilization of one of them, which alone is able to perform the female sexual functions. *D. hæmatobium*. Bilh. v. Sieb. (*Gynæcophorus* Dies) (fig. 257). Body elongated; sexes separate. The female is slender and cylindrical. The male has powerful suckers, and the lateral margins of the body are bent round so as to form a groove, the *canalis gynæcophorus*, for the reception of the female. They live in pairs in the portal vein, and in the veins of the intestine and of the bladder of man in Abyssinia. According to Cobbold, the embryos are ciliated, and possess a tolerably well developed excretory system. By the deposition of masses of their eggs in the vessels of the mucous membrane of the ureter, bladder, and great intestine, inflammation is set up, which may cause hæmaturia.

(2) Sub-order: **Polystomea**.—Trematodes with two small lateral suckers at the anterior end, and one or more posterior suckers, to which two large chitinous hooks are often added. In exceptional

cases (*Tristomum coccineum*) transverse rows of bristles are found. Paired eyes are frequently present. In some species the elongated body presents a kind of external segmentation. They are for the most part ectoparasitic, to a certain extent like the *Hirudinea*, and they develop directly without alternation of generations from eggs which are usually hatched in the locality inhabited by the mother. Sometimes the development is a metamorphosis (*Polystomum*), and the young larvæ live in another place.

The development of *Polystomum integerrimum* from the bladder of the frog is the best known, owing to the researches of E. Zeller (figs. 258, 259). The production of eggs begins in the spring, when the frog awakes from hibernation and proceeds to pair. It lasts

from three to four weeks. It is easy then to observe the *Polystomea* in the process of reciprocal copulation. When the eggs are being laid, the parasite

FIG. 259.—Egg with embryo (a), and hatched larva (b) of *Polystomum integerrimum*; Dk, operculum (after E. Zeller).

forces the anterior end of the body with the genital opening through the mouth of the bladder nearly as far as the anus. The development of the embryo takes place in water and occupies a period of many weeks, so that the young larvæ are only hatched when the tadpoles have already acquired internal gills. The larvæ resemble *Gyrodactylus*, and possess four eyes, a pharynx and alimentary canal, as well as a posterior disc (for attachment), which is surrounded by sixteen hooks. They possess five transverse rows of cilia; three are ventral and anterior, two dorsal and posterior. There is also a ciliated cell upon the anterior extremity. The larvæ now migrate

FIG. 258.—*Polystomum integerrimum* (after E. Zeller). O, mouth; Go, genital opening; D, intestine; W, copulatory opening (lateral pads); Dg, yolk gland duct; S, sucker; Ov, ovary; H, hooks.

into the branchial cavity of the tadpole, lose their cilia, and are transformed into young *Polystomea* by the formation of the two median hooks and of the three pairs of suckers upon the posterior disc. The young *Polystomum*, eight weeks after the migration into the branchial cavity, at the time when the latter begins to abort, passes through the stomach and intestine into the bladder, and there

FIG. 260.—Young *Diplozoon* (after E. Zeller). *a*, Two young *Diporpa* beginning to attach themselves together. *b*, After both individuals have attached themselves. *O*, mouth; *H*, fixing apparatus; *Z*, papillæ; *G*, sucker.

only becomes sexually mature after three and more years. In some exceptional cases, and always when the larva has passed on to the gills of a very young tadpole, it becomes sexually mature in the branchial cavity of the latter. The forms then remain very small,

are without the copulatory canals and uterus, and die after the production of a single egg, without ever getting to the bladder.

FIG. 261.—Egg (*a*) and larva (*b*) of *Diplozoon* (after E. Zeller).

Polystomum Zed., with four eyes; with no lateral suckers at the anterior end, but with oral sucker; with six suckers, two large median hooks and sixteen small hooks at the posterior end. *P. integerrimum* Rud., in the bladder of *Rana temporaria*. *P. ocellatum* in the pharyngeal cavity of *Emys*. In the formation of the testis and the absence of the uterus it resembles the adult form of *P. integerrimum* from the branchial cavity of the tadpole. *Octobothrium lanceolatum* Duj. *Onchocotyle appendiculata* Kuhn, on the gills of Elasmobranchs.

Diplozoon v. Nordm. The animal is double, two individuals being fused to

Fam. *Polystomidæ*. With several posterior suckers, which are usually paired and arranged in two lateral rows, and are reinforced by an armature of hooks. The genital openings are frequently surrounded by hooks. Many species have a length of only a few lines.

form an X-shaped double animal, the posterior ends of which are provided with two large suckers divided into four pits. In the young state they live solitarily as *Diporpa*; they then possess a ventral sucker and a dorsal papilla (260 a, G and Z). In the double animals the formation of ova is confined to a definite period of the year, usually the spring. The eggs are laid singly after the formation of the thread by which they are attached, and two weeks later the embryo (fig. 261, b), which only differs from *Diporpa* in the possession of two eyespots and a ciliated apparatus upon the sides and on the posterior extremity of the body, is hatched. When an opportunity of fixing itself on the gills of a fresh-water fish occurs, the young animal loses its cilia and becomes a *Diporpa*, which possesses, besides the characteristic apparatus for attachment, the alimentary canal, and the two excretory canals with their openings at the anterior part of the body (at the level of the pharynx), and sucks the branchial blood. The junction of the two *Diporpa* soon follows; and this does not take place, as was formerly believed, by the fusion of the two ventral suckers, but in such a manner that the ventral sucker of each animal affixes itself to the dorsal papilla of the other, and fuses with it (fig. 260, b). *D. paradoxum* v. Nordm., on the gills of many fresh-water fish.

Fam. **Gyrodactylidæ**. Very small Trematodes with large terminal caudal disc and powerful hooks. They are viviparous, producing a single young one (first generation) at a time, within which, while still in the body of the parent, another young one (second generation) may be present, and in this yet another (third generation). V. Siebold believed that he had observed a young animal developing from a germ cell of *Gyrodactylus*, and that this became pregnant during its development. He regarded the *Gyrodactylus* as an asexual form, since he failed to find organs for the production of sperm. G. Wagener, however, showed that the reproduction is sexual, and conceived the idea that the germs from which the second and third generations are formed are derived from the remains of the fertilized ovum from which the first generation is formed. Metschnikoff, too, is of the opinion that the individuals of the first and second generations are formed at the same time from a common mass of similar embryonic cells. *Gyrodactylus* v. Nordm., *G. elegans* v. Nordm., from the gills of Cyprinoids and fresh-water fish.

FIG. 262.—*Tænia saginata* (*mediocanellata*), natural size (after R. Leuckart).

Order 3.—C. STODA.*

Elongated and usually segmented Platyhelminthes without mouth or alimentary canal, with organs for attachment at the anterior extremity.

The tape-worms, which may easily be recognised by their band-shaped usually segmented bodies, are parasitic in the alimentary canal of Vertebrata, and were formerly taken for single animals. Steenstrup was the first to introduce a different view, according to which the tape-worm is a colonial animal, a chain of single animals, each segment or *proglottis* being an individual. There are, however, *Cestoda*, like *Caryophyllæus*, which are destitute both of external segmentation and of segmentation of the generative organs; while in other cases the segments of the body are clearly differentiated, and each is provided with a set of generative organs, but they do not attain individual independence. The *proglottides*, however, usually become separated off, and in some cases (*Echineibothrium*) after their separation from the body of the tape-worm continue to live for a long time independently, and even increase considerably in size; so that although the individuality of the tape-worm may be justly insisted on, yet the subordinate and morphologically more restricted degree of individuality of the *proglottis* must also be admitted. This is the only satisfactory mode of regarding the *Cestoda*; especially as the entire tape-worm, and not the *proglottis* alone, corresponds to the Trematode, and is to be derived from the latter by a simplification of organization and loss of the alimentary canal.

The anterior part of the tape-worm is narrow, and presents a terminal swelling by which it attaches itself. This anterior swollen part is distinguished as the head of the tape-worm, but it is only its external form which entitles it to this name. In *Caryophyllæus*

* Besides the older works and papers of Pallas, Zeder, Bremser, Rudolphi, Diesing, and others, compare van Beneden, "Les vers cestoides ou acotyles," Brussels, 1850. Küchenmeister, "Ueber Cestoden im Allgemeinen und die des Menschen insbesondere," Dresden, 1853. V. Siebold, "Ueber die Band- und Blasenwürmer," Leipzig, 1854. G. Wagener, "Die Entwicklung, der Cestoden," *Nov. Act. Leop.-Car.*, Tom XXIV., Suppl., 1854. G. Wagener, "Beitrag zur Entwicklungsgeschichte der Eingeweidewürmer," Haarlem, 1857. R. Leuckart, "Die Blasenbandwürmer und ihre Entwicklung," Giessen, 1856. R. Leuckart, "Die menschlichen Parasiten," Bd. I., Leipzig, 1862. F. Sommer and L. Landois, "Ueber den Bau der geschlechtsreifen Glieder von *Bothriocephalus latus*," *Zeitschr. f. wiss. Zool.*, 1872. F. Sommer, "Ueber den Bau und die Entwicklungsgeschichte der Geschlechtsorgane von *Taenia mediocanellata* und *Taenia solium*," *Ibid.*, Tom XXIV., 1874.

the head armature is very weak, and consists of a lobed fringed expansion. The apex of the head often ends in a conical projection, the *rostellum*, which is armed with a double circle of hooks, while the lateral surfaces of the head are furnished with four suckers (*Tania*, fig. 263). In other cases only two suckers are present (*Bothriocephalus*); or we find suckers of more complicated structure and beset with hooks (*Acanthobothrium*), or four protrusible probosces beset with recurved hooks (*Tetrarhynchus*); while in other genera the head armature presents various special forms.

That portion of the animal which follows the head and is distinguished as the neck shows, as a rule, the first traces of commencing segmentation. The rings, which are at first faintly marked and very narrow, become more and more distinct and gradually larger the further they are removed from the head. At the posterior extremity the segments or proglottides are largest, and have the power of becoming detached. After separation they live independently for a long time, and sometimes even in the same medium.

The simplicity of the internal organization corresponds with the simple appearance of the external structure. Beneath the delicate external cuticle is a matrix consisting of small cells, in which are scattered glandular cells. Beneath the matrix there is a delicate superficial layer of longitudinal mus-

FIG. 263.—Head of *Tania solium*, viewed from the front (apical surface), with rostellum and double circle of hooks. The four suckers are visible.

cular fibres, and next a parenchyma of connective tissue, in which strongly-developed bundles of longitudinal muscular fibres, as well as an inner layer of circular muscles, are embedded; both these muscular layers are traversed, principally at the sides of the body, by groups of dorso-ventral muscular fibres. The power which the proglottis possesses of altering its form is due to the interaction of all these muscles. By means of them it is able to shorten itself considerably, at the same time becoming much broader and thicker, or to elongate to double its normal length, becoming much thinner. In the connective tissue parenchyma of the body, not only the muscles, but all the other organs are embedded. In its peripheral portion, especially in the neighbourhood of the head, we find small densely packed calcareous concretions, which are generally regarded as calcified connective tissue cells.

The *nervous system* consists of two lateral longitudinal cords passing externally to the main trunks of the excretory system. They are somewhat swollen in the head, where they are connected by a transverse commissure; these anterior swellings and the commissure may represent a cephalic ganglion. Distinct sense organs are wanting, but the tactile sense may be ascribed to the skin, especially to that of the head and the suckers. An alimentary canal is also wanting. The nutritive fluid, already prepared for absorption, passes endosmotically through the body wall into the parenchyma.

The *excretory apparatus*, on the contrary, attains a considerable development as a system of much ramified canals which are distributed throughout the whole

FIG. 264.—A portion of the excretory system of *Caryophyllæus mutabilis* (after Pintner). *Wb*, Ciliated funnels with the nucleus of the cell belonging to them.

body.* It consists primarily of two longitudinal canals (a dorsal and a ventral), running along each side of the body and connected in the head and in each segment by transverse trunks. According to the state of contraction of the muscular system, these longitudinal trunks and cross branches appear sometimes straight and sometimes bent in a wavy or zigzag manner: their breadth also presents considerable variation, so that the power of contraction has been ascribed to their walls. The longitudinal trunks only serve as the efferent ducts of a system of very fine vessels which ramify throughout the whole parenchyma and receive numerous long tubes: the latter begin in the

parenchyma with closed funnels, which contain a vibratile ciliated lappet (fig. 264). In many cases, as in the *Ligulidae* and *Caryophyllæus*, these longitudinal trunks are broken up into numerous longitudinal vessels, which are connected by transverse anastomoses. In other cases, on the other hand, the two ventral vessels are enlarged at the cost of the two dorsal, which may entirely atrophy. The external opening of the excretory system is, as a rule, placed at the

* Compare Th. Pintner, "Untersuchungen über den Bau des Bandwurm-körpers," Wien, 1880.

posterior end of the body, *i.e.*, at the hind end of the last segment, in which a small vesicle with an external opening receives the longitudinal trunks. According to the observations of Leuckart on *Tenia cucumerina*, the posterior transverse canals in the segments immediately preceding the last become, by their gradual shortening and the approach of the longitudinal trunks, transformed into the vesicle, which acquires an external opening when the segment behind it is detached. In rare cases the excretory system possesses additional openings in the anterior part of the body behind the suckers.

The *generative apparatus* is also divided into segments which correspond to the proglottides. Each proglottis possesses its own

FIG. 265.—Proglottis of *Tania mediocanellata*, with male and female organs (after Sommer).
Ov, ovary; *DS*, yolk gland (vitellarium); *Sa*, shell gland; *Ut*, uterus; *T*, testes; *Vd*, vas deferens; *Cb*, pouch of the cirrus; *K*, generative cloaca; *Va*, vagina.

male and female generative organs, and can therefore, when separated, be considered as a sexual individual of a lower order. The male apparatus consists of numerous pear-shaped vesicles, the testes (fig. 265, *T*), which are situated upon the dorsal side, and their vasa efferentia open into a common efferent duct (*vas deferens*). The coiled end of this duct lies in a muscular pouch (*cirrus sheath*), whence it can be protruded through the genital opening as the so-called cirrus. This cirrus is frequently beset with spines which are directed backwards, and serves as a copulatory organ. The female generative organs consist of *ovary*, *yolk gland*, *shell gland*, *uterus*, *receptaculum*, and *vagina*. The vagina and vas deferens usually open into a common

genital cloaca, which lies either on the ventral surface of the segment (*Bothriocephalus*), or on the lateral margin (*Tenia*) (fig. 265). In

FIG. 266.—Ripe proglottides ready to separate. *a*, of *Tania solium*; *b*, of *Tania mediocanellata*; *Wc*, water-vascular (excretory) canal.

the last case it is placed alternately on the right and on the left side. Nevertheless it may happen that the two genital openings are widely separate, the male opening being placed at the side, the female on the surface of the segment. As the segments increase in size and become further removed from the head, the contained generative organs gradually reach maturity in such a way that the male generative organs arrive at maturity rather earlier than the female.

As soon as the male elements are mature, copulation takes place, and the receptaculum seminis is filled with sperm, and then only do the female generative organs reach maturity. The ova are fertilized and pass into the uterus, which then assumes its characteristic form and size. As the uterus becomes distended, the testes and then the ovaries and vitellaria are more or less completely absorbed (fig. 266). The posterior proglottides, viz., those which are ready for separation, have alone undergone full development, and the eggs in their uterus often contain completely developed embryos. Accordingly we can recognize in a continuous series of the segments the course of development passed through by the sexual organs and products in their origin and gradual progress towards maturity. The number of segments between that with the first trace of the generative organs

FIG. 267.—Egg with embryo (*a*) of *Tan solium*; (*b*) of *Microtenia*; (*c*), of *Bothriocephalus latus* (after R. Leuckart).

and the first proglottis with fully developed organs gives us an expression for the number of stages through which each segment has to pass. The tape-worms are oviparous; either the embryo develops within the egg-shell in the body of the mother, or the development takes place outside the proglottis, for example in water (*Bothriocephalus*).

The eggs of the *Cestoda* are round or oval in shape and of small size. Their envelope is either simple or composed of numerous thin membranes, or else forms a thick and strong capsule, which in *Tænia* is formed of densely packed rods united by a connecting substance, and presents in consequence a granular appearance. In many cases the development of the embryo coincides with that of the egg-shell, so that the egg at the moment that it is laid contains a

FIG. 268.—Stages in the development of *Tænia solium* to the *Cysticercus* stage (partly after R. Leuckart). *a*, Egg with embryo. *b*, Free embryo. *c*, Rudiment of the head as a hollow papilla on the wall of the vesicle. *d*, Bladder-worm with retracted head. *e*, The same with protruded head, magnified about four times.

complete embryo with six, or more rarely, four hooks. In *Bothriocephalus* the development takes place outside the proglottis during the long period that the egg passes in water, and the embryo leaves the egg as a ciliated larva (fig. 267, *c*). The development of the embryo into the tape-worm probably never takes place directly in the same medium in the intestine of the original host. As a rule there is a complicated metamorphosis, which is sometimes (*Echinococcus*, *Cœnurus*) connected with alternation of generations: the successive stages live in different localities, and usually find the conditions necessary to their development in different species of animals, between which they migrate, partly actively and partly passively. The eggs usually leave the intestine of the host with the proglottis, and are deposited on dunghills, on plants, or in the

water, and thence pass in the food into the stomach usually of herbivorous or omnivorous animals. As soon as the egg membranes are digested or burst by the action of the juices of the stomach of the new host, the embryos which have been thus set free bore their way into the gastric or intestinal vessels by means of their six (rarely four) hooks, the points of which can be approached and removed from one another over the periphery of the small globular embryonic body. When they are once within the vascular system,

FIG. 269.—*a*, Brood-capsule of *Echinococcus* with developing heads (after R. Leuckart). *b*, Brood-capsule of *Echinococcus* (after G. Wagener). *c*, Heads of *Echinococcus* still connected with the wall of the brood-capsule—one is evaginated; *Vc*, excretory canals.

they are no doubt carried along passively by the current of blood, and transported by a longer or shorter route into the capillaries of the different organs, as the liver, lungs, muscles, brain, etc. After losing their hooks, they usually become enveloped by a cyst of connective tissue, and grow into large vesicles with liquid contents and a contractile wall (fig. 268). The vesicle gradually becomes a *cystic* or *bladder worm* by the formation of one (*Cysticercus**) or

* Exceptionally two or more heads are found in some *Cysticercus* forms.

several (*Cœnurus*) hollow buds, which are developed from the walls and project into the interior of the vesicle (fig. 268, *c*). The armature of the tape-worm head (suckers and double circle of hooks) is formed on the inside and at the bottom of this invagination of the wall of the vesicle (fig. 268, *d*). When these hollow buds are evaginated so as to form external appendages of the vesicle, they present the form and armature of the Cestode head, as well as a more or less developed neck, which presents even at this stage traces of segments (fig. 268, *e*). In some cases (*Echinococcus*) the irregularly shaped maternal vesicle produces from its internal walls one or two generations* of secondary vesicles which project into it; and the Cestode heads originate in special small brood-capsules on these secondary vesicles (fig. 269, *a*). In such cases the number of tape-worms which arise from one embryo is naturally enormous, and the parent vesicle may reach a very considerable size, being sometimes as large as a man's head. In consequence of this enormous growth the vesicles frequently obtain an irregular shape; while on the other hand, the tape-worms which are developed from them remain very small, and carry, as a rule, only one ripe proglottis (fig. 270).

So long as the tape-worm head (*scolex*) remains attached to the body of the bladder-worm and in the host of the latter, it never develops into a sexually mature tape-worm; although in many cases it grows to a considerable length (*Cysticercus fasciolaris* of the house-mouse). The bladder-worm must enter the alimentary canal of another animal before the head (*scolex*) can, after separation from the body of the bladder-worm, develop into the sexually mature tape-worm. This transportation is effected passively, the new host eating the flesh or organs of the animal infected with *Cysticerci*. The tape-worms, therefore, are principally found in the *Carnivora*, the *Insectivora*, and the *Omnivora*, which receive the bladder-worms in the flesh of the animals on which they feed. The vesicles are digested in the stomach, and the cestode head becomes free as a *scolex*. The latter is protected from the too intense action of the gastric juice by its calcareous concretions, and at once enters the small intestine, fastens

FIG. 270.—*Tænia Echinococcus* (after R. Leuckart), magnified 12 to 15 times.

* In *Cysticerci* (*O. longicollis*, *tenuicollis*) also sterile daughter vesicles are sometimes budded off.

itself to the intestinal wall, and grows by gradual segmentation into a tape-worm. From the *Scolex* the chain of proglottides proceeds as the result of a growth in length accompanied by segmentation, a process which is to be looked upon as a form of asexual reproduction (budding in the direction of the long axis). Since, however, it is the body of the *Scolex* which undergoes growth and segmentation, it seems

FIG. 271.—*Cysticercoid* of *Tænia cucumerina*, magnified 60 times (after R. Leuckart).

most natural to assume the individuality of the entire chain, and to subordinate to this the individuality of the proglottides. The development of the tape-worm is then to be explained as a metamorphosis, characterised by the individualization of certain stages of the development. It is only in those cases in which the young form produces a number of heads that the development can be explained as a case of alternation of generations.

The development of some tape-worms presents considerable simplifications. In the cysticercus stage the vesicle frequently diminishes to an excessively small appendage, and the *Cysticercus* becomes a cysticercoid form, in which one portion bearing the embryonic hooks is distinct from a larger part which represents the scolex (figs. 271, 272). In other cases the embryo becomes a *Scolex* directly without passing through a cystic stage, so that the *Scolex* stage is merely a late stage of the embryo (*Bothriocephalus*). The segments produced from the *Scolex* also show very different degrees of individuality, and finally are sometimes not developed at all. In the latter case (*Caryophyllæus*) the head and body cannot be sharply distinguished from one another, and represent only one single individual comparable to a Trematode and characterised by its single generative apparatus. Its development is to be looked upon as a metamorphosis completing itself in one individual.

Fam. Tæniadæ. The armature of the head consists of four muscular suckers, to which is frequently added a single or double circle of hooks on the *rostellum*.

FIG. 272.—*Echinococcus*-like *Cysticercoid* from the body cavity of the Earth-worm (after E. Metschnikoff). *a*, Brood-capsules with three *Cysticercoids*. *b*, *Cysticercoid* with evaginated head.

The proglottides have a marginal sexual opening. The vagina is usually long, separated from the uterus, and enlarged at the end to form a receptaculum seminis (fig. 265). The young stages are Cysticerci or Cysticercoids, rarely quite without caudal vesicle; parasitic in warm and cold-blooded animals.

Tenia L. (*Cystotenia* R. Lkt). Development takes place with large vesicles. The heads arise from the embryonic vesicle itself.

T. solium. L. 2—3 metres long. The double circle of hooks is composed of 26 hooks. The ripe proglottides are 8—10 mm. long and 6—7 mm. broad; the uterus has 7—10 dendritic branches. It lives in the human intestine. The Bladder-worms belonging to it (*Cysticercus cellulosæ*) live principally in the dermal cellular tissue and in the muscles of pigs, but also in the human body (muscles, eyes, brain), in which self-infection with them is possible if a *Tenia* is present in the digestive canal; more rarely in the muscles of the Roe-deer, the Dog, and the Cat. In the human brain the *Cysticercus* acquires an elongated form, and sometimes does not produce a head.

T. saginata Goetze=*mediocanellata* Küchenm., in the intestine of Man, distinguished by the older helminthologists as a variety of *T. solium*. Head without circle of hooks or rostellum, but with four more powerful suckers. The Tape-worm reaches a length of four metres, and becomes much stronger and thicker. The mature proglottides are about 18 mm. long and 7—9 mm. broad. The uterus forms 20—35 dichotomous side branches. The *Cysticercus* lives in the muscles of the ox (fig. 273). It appears to be principally distributed in the warmer parts of the Old World, but is often found in great numbers in many places in the north.

T. serrata Goetze, in the intestinal canal of the dog. The *Cysticercus* is known as *Cysticercus pisciformis* in the liver of the Hare and Rabbit. *T. crassicolis* Rud. in the Cat, with *Cysticercus fasciolaris* of the common mouse. *T. marginata* Batsch. of the Dog (butcher's dog) and Wolf with *Cysticercus tenuicollis* from Ruminants and Pigs, and occasionally in Man (*Cyst. visceralis*). *T. crassiceps* Rud. in the Fox with *Cysticercus longicollis* from the thoracic cavity of the Fieldmouse. *T. cœnurus* v. Sieb. in the intestine of the sheep-dog, with *Cœnurus cerebralis* in the brain of one year old sheep. The presence of *Cœnurus* in other places has been stated, as for instance in the body cavity of the Rabbit. *T. tenuicollis* Rud. in the intestine of the Weasel and the Pole-cat, with a *Cysticercus* which, according to Küchenmeister, lives in the hepatic ducts of the Field-mouse.

Echinococeifer Weinl. The heads bud on special brood-capsules, in such a way that their invagination is turned towards the lumen of the vesicle (fig. 269). *T. echinococcus* v. Sieb. (fig. 270) in the intestine of the dog, 3—4 mm. long, forming but few proglottides. The hooks on the head are numerous but small. Its Bladder-worm is distinguished by the great thickness of the stratified cuticula. It lives as *Echinococcus* principally in the liver and the lungs of Man (*E. hominis*) and of domestic animals (*E. veterinorum*). The first form is also distinguished as *E. altriciparens* on account of the frequent production of primary and secondary vesicles; it usually reaches a very considerable size and

FIG. 273.—*Cysticercus* of *Tania mediocanellata*, magnified about eight times. The head is protruded.

has a very irregular shape; while that form which inhabits domestic animals, *E. scolicipariens*, more frequently retains the form of the simple vesicle. Finally these echinococcus cysts frequently remain sterile, in which case they are called *Acephalocysts*. Another and indeed pathological form is the so-called multilocular *Echinococcus*, which was for a long time taken for a colloid cancer. It is also found in Mammalia (in cattle), and here presents a confusing resemblance to a mass of tubercles. The echinococcus disease (*hydatid plague*) was widely spread in Iceland. This disease likewise seems endemic in many places in Australia.

FIG. 274 a.—*Bothriocephalus latus* (after R. Leuckart).

perfoliata Goeze, and *T. plicata* Rud. in the horse; *T. pectinata* Goeze, in the hare; *T. dispar* Rud. in the frog; *T. expansa* Im. in the ox.

Fam. Bothriocephalidæ. With only two suckers, which are weak and flat. The generative organs, as a rule, open upon the surface of the proglottis. The proglottides do not become detached singly. Hydatid stage represented by an encysted Scolex.

T. (Microtaenia). The *Cysticercoid* form is small, and has but little fluid in the small portion which corresponds to the vesicle. The head is small, but has a small club-shaped or proboscis-like rostellum, and is furnished with weak hooks. The eggs are provided with several membranes. The embryo is usually furnished with large hooks. The *Cysticercoid* stages live principally in Invertebrates (in Slugs, Insects, etc.), and more rarely in cold-blooded Vertebrates (the Tench). *T. cucumerina* Bloch, in the intestine of dogs (house dogs). The *Cysticercoid* is entirely without the caudal vesicle, and lives (according to Melnikoff and R. Leuckart) in the body cavity of the Dog-louse (*Trichodectes canis*). The infection with the *Cysticercoids* takes place when the dog swallows the parasites which are annoying him, while the parasites swallow the eggs contained in fæces adherent to the hair of the dog. Nearly allied is *T. elliptica* Batsch, in the intestine of the Cat, occasionally in that of Man. *T. nana* Bilh. v. Sieb. in the intestine of the Abyssinians, hardly an inch long. *T. flavopunctata* Weinl. in the human intestine (North America). The *Cysticercoids* of the Meal-worm are probably developed into tape-worms in the intestines of Mice and Rats.

In other partially unarmed *Tenias* the generative organs and development are as yet not accurately known; such are—*T.*

Bothriocephalus Brems. Segmented body. Head with two pits, without hooks. The genital openings are on the middle of the ventral surface. The young stage usually in fishes. *B. latus* Brems., the largest of the tape-worms parasitic in man, twenty-four to thirty feet in length, principally found in Russia, Poland, Switzerland, and South France. The sexually mature segments are broader than they are long (about 10–12 mm. broad and 3–5 mm. long). They do not become detached singly, but in groups (fig. 274). The segments of the hindmost portion of the body are, however, narrower and longer. The head is club-shaped, and is provided with two slit-like pits. The cortical parts of the lateral regions of the body contain a number of round masses of granules, the *yolk-glands* (fig. 275, *Dst*), the contents of which are poured into the shell glands (coiled glands) through the so-called yellow ducts.

The genital openings lie close together, one behind the other, in the midst of the segment (fig. 275, *a*). The anterior and larger belongs to the male generative apparatus, and leads into the muscular terminal portion of the vas deferens, which is enclosed in the cirrus sheath and can be everted as the cirrus (fig. 275, *Cb*). The vas deferens just before its entrance into the cirrus pouch is dilated (fig. 275 *b*) to form a large muscular swelling (the vesicula seminalis?). It then becomes coiled, and passes in the direction

FIG. 274 *b*.—Larva of a *Bothriocephalus* from the Smelt (after R. Leuckart).

FIG. 275.—Generative organs of a sexually mature proglottis of *Bothriocephalus latus* (after Sommer and R. Leuckart); *a*, from the ventral surface, *b*, from the dorsal surface. *Ov* and *v*, ovary; *Ut*, uterus; *Sd*, shell gland; *Dst*, vitellarium (yolk gland); *Va*, vagina with opening; *T*, testis; *Cb*, pouch of the cirrus; *Vd*, vas deferens.

of the long axis of the segment on the dorsal surface and divides into two side branches. These receive the efferent canals of the delicate testicular sacs, which occupy the lateral parts of the middle layer (*T*). The female genital opening (fig. 275 *a*) leads into a vagina (*Va*) situated behind the pouch of the cirrus, and frequently filled with semen. This vagina runs as a tolerably

straight median canal on the ventral surface, and opens by a short, narrow tube into the oviduct. The vagina also functions as a *receptaculum seminis*. There is yet a third opening (fig. 275, *a*), situated at some distance behind the other two; this is the opening of the tubular uterus (*Ut*), the convolutions of which give rise to a peculiar rosette-shaped figure in the midst of the segment (*Wappenlilie* Pallas). Close to the hind end of the segment the ducts of the yolk-glands (*Dst*) and of the ovaries (*Or*) unite with each other and open into the uterus; the cells of the shell-gland (*Scl*) surround and open into the point of junction of these structures. Behind the uterus, and partly among its posterior lateral horns, lie the so-called coiled glands; and at its sides are the so-called lateral glands (Eschricht). The latter are, according to Eschricht, the ovaries or germaria (formerly held by Leuckart to be the vitellaria). The coiled glands (Leuckart's ovaries), an aggregation of pear-shaped cells, were considered by Stieda, with whom Landois and Sommer are in accord, to be a shell gland (fig. 275).

The ova are for the most part developed in water, and escape from the upper pole of the egg-shell through a lid-like valve. The escaped embryo is covered with cilia, by means of which it swims about for a long time. Hence it is probable that the later stages of development take place in an aquatic animal. It is unknown how and in what host the embryo with six hooks becomes a Scolex; and the question how this tape-worm gets into the human body—in spite of the researches of Knoch, who maintained that they appeared there directly and without the intervention of an intermediate host—is still undecided. *B. cordatus* Lkt. With large, heart-shaped head, without a filiform neck; with numerous deposits of calcareous bodies in the parenchyma. It attains a length of about three feet and lives in the intestines of man and of the dog in Greenland.

Schistocephalus Crepl. Head split, with a sucker on each side. The body of the cestoid form is segmented. *S. solidus* Crepl. Lives in the body cavity of the stickleback, escapes into the water, and becomes sexually adult in the intestine of water-birds. *Trienophorus* Rud. Head not distinct, with two weak suckers and with two pairs of tridentate hooks. The body has no external segmentation. The generative openings are marginal. *T. nodulosus* Rud. In the intestine of the pike. Asexual encysted form in the liver of *Cyprinus*.

Fam. **Ligulidæ** (*Pseudophyllidæ*). Without real suckers. Hooks are either present or absent. The Cestoid has no segmentation, but the generative organs are repeated. They live in the body cavity of Teleosteans and in the intestine of birds. *Ligula* Bloch. Body band-shaped and unsegmented. *L. simplicissima* Rud., in the body cavity of fishes and in the intestine of aquatic birds. *L. tuba* v. Sieb., in the intestine of the Tench.

The families of the **Tetrarhynchidæ** (*Tetrarhynchus lingualis*, Cuv., passes its young stages in Soles, and is matured in the intestine of Rays and Dog-fish), and **Tetraphyllidæ** (*Echinibothrium minimum* van Ben.) are allied here.

Fam. **Caryophyllæidæ**. Body elongated and unsegmented. The anterior margin is plicated. There are no hooks, and there are eight sinuous longitudinal canals of the excretory system. Generative organs single. The development is a simplified metamorphosis. *Caryophyllæus mutabilis* Rud., in the intestine of *Cyprinoids*. The young form possibly lives in *Tubifex rivulorum*, if the Helminth observed by d'Udekem was the same. In this worm, however, there lives another parasite, which was observed by Ratzel and has recently been more closely investigated by R. Leuckart, who has shown that it is

a sexually mature Cestoid still fixed by an appendage bearing the embryonic hooks. *Archigetes Sieboldii* Lkt. With two weak suckers and a caudal appendage.

Order 4.—NEMERTINI* = RHYNCHOCELA.

Elongated, frequently band-shaped Platyhelminthes, with straight alimentary canal opening by an anus, and with a separate protrusible proboscis. Usually with two ciliated pits in the cephalic region. The sexes are separate.

The *Nemertines* are distinguished not only by their elongated form, but also by their considerable size and high organization. Thick layers of muscles, traversed by connective tissue, are spread beneath the integument, which contains pigment as well as flask-shaped mucous glands. The external layer of longitudinal muscles, strongly developed in the *Anopla*, is wanting in the *Enopla* (Nemertines, the proboscis of which is armed with stylets), in which group there is only an outer layer of circular muscles and an inner layer of longitudinal muscles. A long tubular protrusible proboscis, which is sometimes armed with stylet-shaped rods, is always found at the anterior end of the body above the buccal cavity, and projects through a special præoral opening (fig. 276), and can be retracted into a special muscular sheath separate from the body cavity. At the bottom of the principal portion of the proboscis, there is in many *Nemertines* (*Enopla*) a large spine, which is directed forwards, and at its sides numerous small secondary spines in pouches. The posterior glandular portion of the proboscis, to which retractor muscles are attached, is, according to Claparède, to be regarded as a poison apparatus. When the proboscis is pro-

FIG. 276. — *Tetrastemma obscurum* (after M. Schultze). Young specimen about 3 lines in length; O, mouth; D, intestine; A, anus; Bg, blood vessels; R, proboscis armed with stylet; Ex, lateral trunks of the excretory system; P, excretory pore; G, ciliated pit; Nc, nerve centre; Ss, lateral nerve trunks; Oe, eyes.

* A. de Quatrefages, "Mémoire sur la famille des Némertines," *Ann. des Sc. Nat.* Ser. 3, Tom. VI., 1846. McIntosh, "On the Structure of the British Nemerteanans," *Transact. Edinb. Royal Soc.*, Tom XXV., 1 & 2. Barrois, "Mémoire sur l'Embryologie des Némertes," Paris, 1877. Hubrecht, "Untersuchungen über Nemertinen, etc.," *Niederl. Archiv.*, Tom. II.

truded, it is inverted like the finger of a glove, so that the blind end at which the spines are placed becomes the extreme front end of the protruded proboscis.

The *brain* attains a considerable development. Its two halves are connected by a double commissure which embraces the proboscis, and in them several lobes, usually a dorsal and ventral, may be distinguished. The two ventral lobes are produced into the two lateral nerve trunks, which in certain cases (*Oerstedtia*) may approach each other on the ventral surface. The nerve trunks contain not only fibres but also a superficial layer of ganglion cells, which may give rise to ganglion-like enlargements at the points of exit of the nerve branches. In the embryos of *Prosochmus Claparèdii* the nerve trunks are said to end in an enlargement. In the cephalic region there are two strongly ciliated depressions known as the cephalic slits, beneath which special lateral organs, supplied with nerves from the brain or it may be posterior lobes of the brain itself, are placed. These structures are probably sense organs. The cephalic slits were formerly erroneously taken for the openings of respiratory organs. Eyes are widely distributed, and usually consist of simple pigment spots which rarely contain refractive bodies. Exceptionally, as in *Oerstedtia pallida*, two otolithic vesicles are found on the brain.

The *Nemertines*, unlike all other *Platyhelminthes*, possess a blood-vascular system. This consists of two sinuous lateral vessels in which the blood flows from before backwards, and a straight dorsal vessel in which the blood flows in the reverse direction. This latter is connected with the ventral vessel at the posterior end of the body and in the region of the brain by wide loops, and in the rest of its course by numerous narrower transverse anastomoses. These vessels lie in the body cavity and have contractile walls. The blood is usually colourless, but in some species it is red. In *Amphiporus splendens*, *Borlasia splendida*, the red colour (hæmoglobin) is contained in the oval disc-shaped blood corpuscles.

The *Nemertines* are, with some few exceptions (*Borlasia hermaphroditica*), diœcious. The two kinds of generative organs have the same structure, and are sacs filled with ova or spermatozoa lying in the lateral portions of the body between the pouches of the intestine, and opening to the exterior by paired openings in the body wall. The ova, when laid, frequently remain connected by a gelatinous substance, and are deposited in irregular masses or in strings, from the middle of which the animal creeps out, like the leech out of its

cocoon. Some forms, as *Prosorochmus Claparèdii* and *Tetrastemma obscurum*, are viviparous.

Some of the Anopla develop with a metamorphosis. The larva is ciliated and may pass through a free-swimming stage, in which case it is known as the *Pilidium*, or it may be without such a stage (*Type of Desor*). In both cases the perfect worm is developed within the skin of the ciliated larva.

FIG. 277.—*Pilidium* (after E. Metschnikoff). *a*, free swimming larva with invaginated cavity; *b*, later stage, helmet-shaped; *E*, *E'* the two pairs of ectodermal invaginations; *D*, alimentary canal.

The *Pilidium* larva is helmet-shaped, and was formerly described as the species of a supposed independent genus, *Pilidium*, and presents

FIG. 278.—Later stage of *Pilidium*, with tuft of cilia and enclosed Nemertine (after Bütschli); *Oe*, cesophagus; *D*, alimentary canal; *Am*, amnion; *R*, rudimentary proboscis of the Nemertine; *So*, lateral pit.

many analogies to the Echinoderm larva. In the case of the *Pilidium*, the segmentation is regular, and results in the formation of a spherical ciliated embryo, which is hatched and becomes a free-swimming larva; the archenteron is then formed by invagination; and at the side of the embryo, opposite the blastopore, a long flagellum is developed (fig. 277, *a*). On each side of the mouth a broad lobe grows out, the edges of which are fringed with cilia (fig. 277, *b*).

Two pairs of invaginations of the ectoderm now make their appear-

ance, forming the first rudiment of the Nemertine body. The four discs so formed fuse together and give rise to a ventral germinal plate, which gradually grows round the alimentary canal of the *Pilidium* to form the skin of the future Nemertine. The proboscis arises as an invagination of the anterior end of the germinal plate (fig. 278). The young Nemertine subsequently breaks through the larval skin.

The Nemertines live principally in the sea, under stones in the mud, but the smaller species swim about freely. There are also forms which live on the land, as well as pelagic forms. Certain species form tubes and passages, which are lined with a slimy secretion. The food of the larger species principally consists of tubicolous worms, which they extract from their habitations by means of the proboscis. There are, however, parasitic Nemertines which infest *Crustacea* or live on the mantle and gills of *Mollusca*. In this case they are, like the *Hirudinea*, furnished with a posterior sucker (*Malacobdella*). The Nemertines are distinguished by their reproductive capacity and by their tenacity of life. Mutilated parts are quickly regenerated, and the parts into which certain species readily break are said to have the capacity, under favourable conditions, of developing into new animals.

1. Sub-order: **Enopla**.—The proboscis is armed with stylets. The short, often funnel-shaped cephalic slits are connected with lateral organs, which correspond to the posterior cerebral lobes of the *Anopla*. In the brain the upper lobes are slightly elongated posteriorly leaving the ventral lobes, from which the lateral nerves arise, quite free. Development takes place without metamorphosis.

Fam. **Amphiporidae**. The ganglia are more rounded, the lateral nerve trunks are placed inside the dermal muscles. The mouth is on the ventral surface near the anterior end of the body, in front of the commissures between the ganglia. The lateral organs are separated from the brain and connected with it by fibres; they contain a narrow water canal. *Amphiporus lactifloreus* Johnst. Lives under stones, and is distributed from the North Seas to the Mediterranean, 3—4 in. long. *A. spectabilis* Quatr. *Borlasia splendida* Kef., Mediterranean, and Adriatic. *Tetrastemma obscurum* M. Sch. Viviparous: Baltic. *T. agricola* Will. Suhm., terrestrial. *Nemertes gracilis* Johnst.

2. Sub-order: **Anopla**.—The proboscis is unarmed. The long cephalic slits occupy the whole side, or the anterior part of the head, and lead into the lateral organs, which are direct processes of the upper lobes of the brain. Development frequently by means of ciliated larvæ.

Fam. *Lineidæ*. Ganglion elongated. The head has deep slits on either side. *Lineus marinus* Mont., *L. longissimus* Sim. (sea long-worm, *Borlasia anglica* Oerst., *Nemertes Borlasii* Cuv.), grows to a length of 15 feet and more. English coast. *Cerebratulus marginatus* = *Meckelia somatotomus* F.S. Lkt., Adriatic and Mediterranean. *Micrura fasciolata* Ehrbg., North Seas to the Adriatic.

Fam. *Cephalotrichidæ*. Cephalic slits and lateral organs are wanting. Head not distinct, very long and pointed. *Cephalothrix bioculata* Oerst. Sund.

Malacobdella grossa O. Fr. Müll. Body broad and flat, with posterior sucker. Is parasitic in the mantle cavity of various Mollusca, as *Mya*, *Cyprina*, etc.

CLASS II.—NEMATHELMINTHES.

Round worms with tubular or filiform bodies. The cuticle is frequently ringed. The anterior pole is either armed with hooks or provided with papillæ. The sexes are separate.

The unsegmented body is rounded, more or less elongated, tubular or filiform, and both ends are, as a rule, tapered off. Appendages are always wanting, as are, with few exceptions, movable bristles. On the other hand, special organs for attack and attachment, such as teeth and hooks, are not unfrequently present on the anterior end of the body; and in some cases small suckers, which serve for attachment during copulation, may be developed on the ventral surface. As a rule, the integument possesses a cuticular layer of relatively considerable thickness, and a well developed muscular layer, which permits not only of the body being knotted, curved, and bent, but, in the thin filiform *Nematoda*, of undulatory movements. The body cavity is enclosed by the muscular body wall, and contains the blood fluid and the digestive and generative organs. *Blood vessels* and *respiratory organs* are wanting. A *nervous system* is, however, always present. Of *sense organs* simple eyes are not unfrequently present in the free living forms. The sense of touch is probably distributed all over the surface of the body, particularly on the anterior end, especially when papillæ and lip-like prominences or bristles are found on it. While in the *Acanthocephala* mouth and alimentary canal are completely absent, the *Nematoda* possess a mouth placed at the anterior pole of the body, an œsophagus, and an elongated straight digestive canal, which usually opens by the anus on the ventral surface near the posterior end of the body. The *excretory organs* have various forms, and always differ considerably from those of the *Platodes*. In the *Nematoda* they consist of paired canals, which open by a common pore and lie in the so-called lateral lines. In the *Acanthoceph-*

phala they are branching subcutaneous canals. With a few exceptions the *Nemathelminthes* have separated sexes, and develop directly without metamorphosis. The larvæ and sexual animals are not unfrequently distributed in two different hosts.

The majority of the *Nemathelminthes* are parasites either during the whole period of their life or at different stages. There are, however, also free living forms which often show the closest relationship to the parasitic members of the group.

Order 1.—NEMATODA (THREAD-WORMS).*

Nemathelminthes, with mouth and alimentary canal. They are principally parasites.

The Nematodes possess an extremely elongated thread-like body, which may be provided with papillæ at the anterior pole in the region of the mouth, or with hooks and spines within the oral cavity. The mouth leads into a narrow œsophagus, which usually has thick muscular walls, a chitinous lining, and a triangular lumen, and is frequently dilated behind to a muscular bulb (pharynx). In certain genera (*Rhabditis*, *Oxyuris*), the chitinous lining of the pharynx is raised into ridges or tooth-like prominences, to which the

FIG. 279.—*Oxyuris vermicularis* (after R. Leuckart). *a*, female; *O*, mouth; *A*, anus; *V*, genital opening; *b*, male with curved posterior end; *c*, the latter enlarged; *Sp*, spiculus; *d*, egg with enclosed embryo.

Zeitschr. für Wiss. Zool., Tom. XXI., 1871. And "Beiträge zur Kenntniss des Nervensystems der Nematoden," *Archiv. für Mikr Anatomie*, Tom X.

* Besides the older writings of Rudolphi, Bremser, Cloquet, Dujardin, compare Diesing, "Systema helminthum," 2 Bde Wien, 1850-51. Diesing, "Revision der Nematoden," *Wiener Sitzungsberichte*, 1860. Claparède, "De la formation et de la fécondation des œufs chez les vers Nematodes," Genève, 1856. A. Schneider, "Monographie der Nematoden," Berlin, 1866. R. Leuckart, "Untersuchungen über *Trichina spiralis*," Leipzig and Heidelberg, 1866, 2nd edition; also "Die menschlichen Parasiten," etc., Tom. II., Leipzig and Heidelberg, 1876. C. Claus, "Ueber *Leptodera appendiculata*," Marburg, 1868. O. Bütschli, "Untersuchungen über die beiden Nematoden der *Periplaneta orientalis*,"

radial muscles converge in the form of conical bundles. According to its function, the œsophagus is essentially a suctorial tube, which pumps in fluids, and by peristaltic action passes them on to the intestine. The intestine follows the pharynx, and opens by the anus not far from the hind end of the body on the ventral surface (fig. 279). Its walls are formed of cells and are non-muscular, except behind, where they have a special investment of muscular fibres which render the terminal portion contractile. Muscular fibres passing from the body wall to the wall of the rectum are also frequently present. In certain Nematodes the anus may be wanting (*Mermis*); and in *Gordius* even the alimentary canal undergoes degeneration.

Beneath the stiff cuticle, which is often transversely ringed, and is composed of several layers, lies a soft granular nucleated sub-cuticular layer (*hypodermis*), which is to be regarded as the matrix of the former. Beneath this lies the highly developed muscular layer, in which band-shaped or fusiform longitudinal muscles predominate. The surface of the body may present markings, as for instance polyhedric spaces and longitudinal ribs, also processes in the form of tubercles, spines,* and hairs. Ecdyses, *i.e.*, shedding the cuticular layer, seem only to occur in the young forms. The muscles are each composed of a single cell, in which two parts are distinguishable,—a clear, sometimes a granular protoplasmic portion (medullary substance), which projects into the body cavity and is often prolonged into processes; and an external fibrillated layer (fig. 280). The Nematodes may be distinguished as *Meromyaria* or *Polymyaria*, according to the arrangement of their muscular system. In the *Meromyaria* the number of muscle cells (which are arranged according to definite laws) in the cross section is small (eight), while in the *Polymyaria* their number is considerable. In the latter the muscle cells are often connected together by transverse processes of the medullary substance, which unite on the so-called median lines to form a longitudinal cord.

FIG. 280. — Muscle-cell of a Nematode.

* There may also be prominences of various kinds, and even in some cases a complete covering of spines (*Cheiracanthus* Dies = *Gnathostoma* Ow., *Ch. hispidum* Fedtsch.)

In almost every case, with the exception of *Gordius*, two lateral regions remain free from muscle and form the so-called *lateral lines* or *regions*, which may equal in breadth the neighbouring muscular regions. These lateral regions are formed of a finely granular nucleated substance, and enclose a clear vessel containing granules. This vessel is connected with that of the opposite side in the anterior part of the body, and the two open by a common transverse slit, the *vascular pore*, on the ventral surface in the median line. The lateral lines have the value, both as regards position and structure, of *excretory organs*. Median lines (*dorsal* and *ventral*), accessory median lines (sub-median lines), the latter being placed between the principal median line and the lateral line, are also to be distinguished. The so-called ventral cord of *Gordius*, which may be compared to the median line and has perhaps the significance of an elastic rod, is very large. Cutaneous glands, in the form of unicellular glands, have been observed principally in the region of the œsophagus and in the tail.

The **nervous system**, owing to the difficulty which its investigation offers, has only been satisfactorily recognised in a few forms. It consists of a nerve ring surrounding the œsophagus, and sending off posteriorly two and anteriorly six nerve trunks (*Ascaris megalocephala*). The posterior trunks run in the dorsal and ventral lines (*N. dorsalis*, *ventralis*), to the extremity of the tail; while of the six anterior nerves, two run in the lateral lines (*N. laterales*), four in the interspaces between the lateral and median lines (*N. sub-mediani*), and supply the papillæ around the mouth. The ganglion cells lie partly near, in front of and behind the nerve ring, partly on the fibrous cords themselves, and are arranged in groups which can be distinguished as ventral, dorsal, and lateral ganglia. There are in addition groups of ganglion cells in the median lines and in the lateral lines in the caudal region.

As **sense organs** we must mention the eyes found in the free-living *Nematoda*, and the papillæ and tactile hairs found principally in the neighbourhood of the mouth. Each papilla is supplied by one nerve fibre, which is swollen to a knob and forms the axis of the papilla.

[The *Nematoda* possess a body cavity, but are without any trace of a vascular system.]

Generative organs. The Nematodes are diœcious (with exception of the hermaphrodite *Pelodytes*, and of the *Rhabdonema*

(*Ascaris nigrovenosum*, which produces first spermatozoa and later ova). The males are characterised by their smaller size, and by the posterior end of the body being generally curved. Both kinds of generative organs consist of single or paired and often much coiled tubes, at the upper end of which the generative products are developed, the lower ends representing the efferent ducts and receptacula of the generative products. The usually paired ovarian tubes, at the upper ends of which the ova arise, terminate in a short vagina, which opens on the ventral surface, rarely near the posterior end of the body. The male generative apparatus, which contains hat-shaped spermatozoa, is almost invariably represented by an unpaired tube, and usually opens on the ventral surface near the posterior end of the body in a common opening with the intestine. As a rule, the common cloacal portion contains two pointed chitinous rods, the so-called *spicula*, in a pouch-like invagination. These spicula can be protruded and retracted by a special muscular apparatus, and serve to fasten the male body to the female during copulation. In many cases (*Strongylidæ*) an umbrella-like bursa is added, or the terminal portion of the cloaca can be protruded like a penis (*Trichina*); in this case the cloacal aperture lies almost at the extreme end but is still ventral (*Acrophalli*). In the male papillæ are almost always present in the region of the posterior end of the body, and their number and arrangement afford important specific characters.

Development. The *Nematoda* for the most part lays eggs; it is only in rare cases that they bear living young. The eggs usually possess a hard shell and may be laid at different stages of the embryonic development or before it has begun. In the viviparous Nematodes the eggs lose their delicate membranes in the uterus of the mother (*Trichina*, *Filaria*). Fertilization takes place by the entry of a spermatozoon into the ovum, which is still without a membrane. The segmentation is equal, and leads to the formation of a kind of invaginate gastrula. From the two cell layers are developed the body wall and the alimentary canal. The embryo gradually assumes an elongated cylindrical form, and comes to lie rolled up in several coils within the shell. The excretory pore and the rudiments of generative organs, as well as a nerve ring, are present in the embryo, which is also provided with mouth and anus. The free development is a metamorphosis, usually complicated by the circumstance that it is not undergone in the habitat of the mother. The young stages or *larvæ*, probably of most Nema-

todes, have a different habitat to that of the sexual animal; the young and the adult Nematode being contained in different organs of the same or even of different animals. The larvæ live for the most part in parenchymatous organs, either free or encysted in a connective tissue capsule; the adults, on the contrary, live principally in the alimentary canal.

The embryo is almost invariably characterised by the special form of the oral and caudal extremities, but sometimes also by the possession of a boring tooth, or of a circle of spines (*Gordius*). Sooner or later the skin is shed, and the animal enters its second stage, which may often still be considered as a larval stage; repeated ecdyses precede the sexually adult stage.

The post-embryonic development of the Nematodes presents numerous modifications. In the simplest cases the embryo, while

FIG. 281.—*Sclerostomum tetracanthum*, encysted (after R. Leuckart).

still enveloped in the egg membranes, is transported passively in the food (*Oxyuris vermicularis* and *Trichocephalus*). In many *Ascaridæ*—to judge by the species parasitic in the Cat—the embryos, which are provided with a boring tooth, first make their way into an intermediate host, by which they are transported into the intestine of the second host with the food or water.

More frequently the young forms encyst within the intermediate host, and, enclosed in the cyst, are transferred into the stomach and intestine of the permanent host (fig. 281). For example, the embryos of *Spiroptera obtusa* of the Mouse, while still in the egg membranes, are taken with the food by the Meal-worm, in the body cavity of which they encyst. In the viviparous *Trichina spiralis* there is a modification of this mode of development inasmuch as the migration of the embryos and their development to the encysted form found in the muscles (muscle-trichina) take place in the same animal which contains the sexually mature intestinal *Trichinas*.

The development of the Nematode larvæ often makes a considerable advance within the intermediate host into which they have migrated. Thus, for instance, in *Cucullanus elegans*, the embryos migrate into the *Cyclops*, and in the body cavity of these small *Crustacea* undergo two ecdyses and essential alterations of form, obtaining at this early

stage the characteristic oral capsule of the sexually adult stage, to which they only develop in the intestine of the Perch. According to Fedschenko,* a similar mode of development occurs in *Filaria medinensis*. The embryos pass into puddles of water, and migrate thence into the body cavity of the *Cyclopidae*; and after casting their skin assume a form which, except for the absence of the oral capsule, resembles that of the larva of *Cucullanus*. After the expiration of two weeks there is another ecdysis, with which is connected the loss of the long tail. The later history is unknown. It has not yet

FIG. 292.—*a*, *Rhabdonema (Ascaris) nigrovenosum* of about 3.5 mm. in length in the stage of maturity of the male products; *G*, genital glands; *O*, mouth; *D*, intestine; *A*, anus; *N*, nerve-ring; *Drz*, glandular cells; *Z*, isolated spermatozoa. *b*, Male and female *Rhabditis* forms from about 1.5 mm. to 2 mm. long; *Ov*, ovary; *T*, testis; *V*, female genital opening; *Sp*, spicula.

been discovered whether the migration of the Filarian larva into the permanent host (Man, see p. 356) takes place with the body of the Cyclops, or independently after copulating in the free state.

The embryos of some *Nematoda* develop in damp muddy earth, after casting their skin, to small so-called *Rhabditis* forms with a double

* Compare Fedschenko, "Ueber den Bau und Entwicklung der *Filaria medinensis*," in the *Berichten der Freunde der Naturwissenschaften in Moskau*, Tom VIII. and X.

enlargement of the œsophagus and with a pharynx armed with three teeth. They lead an independent life in this habitat, and finally migrate to lead a parasitic life within the permanent host, where, after several ecdyses and alterations of form, they attain the sexually mature condition. This mode of development occurs in *Dochmius trigenocephalus* from the intestine of the dog, and very probably in the nearly allied *D. (Ancylostomum) duodenalis* of man, and also in *Sclerostomum*.

The offspring of parasitic Nematodes may, however, attain sexual maturity in damp earth, as free *Rhabditis* forms, and represent a special generation of forms whose offspring again migrate and become parasites. Such a life history is a case of heterogamy. It occurs in *Rhabdonema nigrovenosum*, a parasite in the lungs of Batrachians. These parasites, which are about half to three-quarters of an inch long, all have the structure of females, but contain spermatozoa, which are produced (as in the viviparous *Pelodytes*) in the ovarian tubes, but earlier than the ova. They are viviparous. The embryos make their way into the intestine of their host, and accumulate in the rectum, but finally pass to the exterior in the fæces, and so reach the damp earth or muddy water, where they develop in a short time into the *Rhabditis*-like forms, which have separate sexes and are barely 1 mm. in length (fig. 282, *a* and *b*). The impregnated females of the latter produce only from two to four embryos, which become free inside the body of the mother, pass into her body cavity, and there feed on her organs, which disintegrate to form a granular detritus. They finally migrate as slender, already tolerably large Nematodes into the lungs of the *Batrachia*, passing through the buccal cavity and glottis. The *Leptodera appendiculata*, which lives in the slug *Arion empiricorum*, also presents in its development a like alternation of heteromorphic generations, which, however, are not strictly alternating, inasmuch as numerous generations of the *Rhabditis* form may succeed one another.

The *Leptodera* are peculiar in that the form parasitic in the snail is a larva characterised by the absence of a mouth, and by the possession of two long band-shaped caudal appendages; it quickly attains maturity, but only after a migration into damp earth and after losing the caudal appendages and casting the skin.

The *Nematoda* feed on organic juices, some of them also on blood, and are enabled by their armed mouth to inflict wounds and to gnaw tissues. They move by bending their body with a rapid undulatory movement towards the ventral and dorsal surfaces, which thus seem

to be the lateral surfaces of the moving animal. Most *Nematoda* are parasitic, but lead an independent life in certain stages of their life history. Numerous small *Nematoda*, however, are never parasitic, but live freely in fresh and salt water and in the earth. Some Nematodes are parasitic in plants, for example, *Anguillula tritici*, *dipsaci*, etc.; some live in decaying vegetable matter, e.g., the vinegar worm in fermenting vinegar and paste. Nevertheless very similar forms occur in the contents of the intestine and in the fæces of different animals and of man (*A. intestinalis*, *stercoralis*). The power possessed by small *Nematoda* of resisting the effects of prolonged desiccation and of coming to life again on being moistened is very remarkable.

Fam. **Ascaridæ**. Body tolerably stout. With three lips furnished with papillæ. One of these lips is directed towards the dorsal surface, while the two others meet together in the ventral line. The posterior end of the male is ventrally curved, and usually furnished with two horny spicula.

FIG. 283.—*Ascaris lumbricoides* (after R. Leuckart). *a*, Posterior end of a male with the two spicula (*Sp*). *b*, Anterior end from the dorsal side, with the dorsal lip furnished with two papillæ. *c*, The same from the ventral side with the two lateral ventral lips and the excretory pore (*P*). *d*, Egg with the external membrane formed of small clear spherules.

Ascaris L. Polymyarian, with three strongly developed lips, the edges of which are in the larger species provided with teeth. The pharynx is not separated as a distinct bulb. The caudal extremity is usually short and conical, and in the male sex invariably provided with two spicula (fig. 283, *a*). *A. lumbricoides* Cloquet, the human round worm, a smaller variety in the pig (*A. suilla* Duj.) The eggs pass into water or damp earth and remain there some months, until the embryonic development is completed; they are probably carried into the alimentary canal of their later host by means of an intermediate host. *A. megalocephala* Cloquet (horse and ox); *A. mystax* Zed. (cat and dog), sometimes parasitic in man.

Oxyuris Rud. Meromyarian; usually with three lips, which bear small papillæ. The posterior end of the œsophagus is enlarged to a spherical bulb provided with a masticatory apparatus. The posterior end of the body of the female is thin and pointed, while that of the male has only two præanal and few postanal papillæ, and a single spiculum (fig. 279). *O. vermicularis* L., in the large intestine of man, distributed in all countries. The female is about ten mm. long. *O. curcula* Rud., in the cæcum of the Horse.

Fam. **Strongylidæ**. The male genital opening is placed at the hinder end of the body, at the bottom of an umbrella- or bell-shaped bursa, the margin of which is furnished with a varying number of papillæ.

Eustrongylus Dies. With six projecting oral papillæ, and a row of papillæ on either lateral line. The bursa is bell-shaped and completely closed, with regular muscular walls and numerous marginal papillæ. There is only one spiculum. The female genital opening is far forward. The larvæ live encysted in fishes. (*Filaria cystica* from *Symbranchus*). *E. gigas* Rud., the body of the female is three feet in length, and only twelve mm. thick. It lives singly in the pelvis of the kidney of the Seal and Otter, and very rarely in Man.

Strongylus Rud. With six oral papillæ and small mouth. Two conical cervical papillæ upon the lateral lines. The posterior end of the male has an umbrella-like incompletely closed bursa. Two equal spicula, usually with unpaired supporting organ. The female sexual opening is sometimes approached to the posterior end of the body. They live for the most part in the lungs and bronchial tubes. *St. longevaginus* Dies. Body 26 mm. long, 5 to 7 mm. thick. The female sexual opening lies directly in front of the anus, and leads into a simple ovarian tube. Only once found in the lung of a six-year old boy, in Klausenburg. *St. paradoxus* Mehlis, in the bronchial tubes of the pig. *St. filaria* Rud., in the bronchial tubes of the sheep. *St. commutatus* Dies., in the trachea and bronchial tubes of the hare and rabbit. *St. auricularis* Rud., in the small intestine of *Batrachia*.

Dochmius Duj. With wide mouth and horny oral capsule, the edge of which is strongly toothed. Two ventrally placed teeth project at the bottom of the oral capsule, while on the dorsal wall a conical spine projects obliquely forwards. *D. duodenalis* Dub. (*Ancylostomum duodenale* Dub.), 10 to 18 mm. long, in the small intestine of Man, discovered in Italy; very widely distributed in the countries of the Nile (Bilharz and Griesinger). By aid of its strongly armed mouth it wounds the intestinal mucous membrane, and sucks the blood from the vessels. The frequent hæmorrhages occasioned by these *Dochmia* are the cause of the illness known by the name of Egyptian chlorosis (fig. 284). It has lately been established that this worm occurs in Brazil, and that, like *D. trigonocephalus*, it develops in puddles

FIG. 284.—*Dochmius duodenalis* (after R. Leuckart). *a*, male; *O*, mouth; *B*, bursa. *b*, Female; *O*, mouth; *A*, anus; *V*, vulva.

of water (Wucherer). *D. trigonocephalus* Rud., in the Dog. *Sclerostomum* Rud. With characters of *Dochmius*, but with a different oral capsule, into which two long granular sacs open. *Sc. equinum* Duj. = *armatum* Dies. In the intestine and the mesenteric arteries of the horse. Bollinger* has shown that the phenomena of colic in the horse may be referred to embolic processes proceeding from aneurism of the intestinal artery: Each aneurism contains about nine worms

* Bollinger, "Die Kolik der Pferde und das Wurmaneurysma der Eingeweidearterien," München, 1870.

Sc. tetracanthum Mehlis, also in the intestine of the horse. The embryos, after migrating into the intestine, become encysted in the walls of the rectum and cæcum, assume within the cyst their definite form, break out from the cyst, and escape again into the intestine. *Cucullanus elegans* Zed., in the Perch.

Fam. *Trichotrachelidæ*, with long neck-like thin anterior portion of the body. Mouth small, without papillæ. Œsophagus very long, traversing a peculiar cord of cells.

Trichocephalus Goeze. Anterior part (fig. 285) of the body elongated and whip shaped: posterior part cylindrical and sharply distinct, enclosing the generative organs, in the male it is coiled up. Lateral lines absent. Main median lines present. The penis is slender and furnished with a sheath, which is turned inside out when the former is protruded. The hard-shelled, lemon-shaped eggs undergo the first part of their development in water. *Tr. dispar* Rud. In the human colon: these worms do not live free in the intestine, but bury their filiform anterior extremity in the mucous membrane (fig. 285). The eggs pass out of the host with the fæces, as yet without a sign of beginning development, which only takes place after a prolonged sojourn in the water or in a damp place. According to the experiments of Leuckart performed with *Tr. affinis* of the sheep and *Tr. crenatus* of the pig, embryos with the egg membranes, if introduced into the intestine, develop into the adult *Trichocephalus*; and we may therefore conclude that the human *Tr. dispar* is introduced directly, and without an intermediate host either in the drinking water or in uncleaned food. The young *Tr. dispar* is at first hair-like, and resembles a *Trichina*, and only gradually acquires the considerable thickness of the hind end of the body.

Trichosonum Rud. Body thin, hair-like, but the posterior end of the body in the female is swollen. Lateral lines and the principal median lines are present. The male caudal extremity has a cutaneous fold and a simple penis (spiculum) and sheath. *Tr. muris* Creplin., in the large intestine of the house-mouse. *Tr. crassicauda* Bellingh., in the bladder of the rat. According to Leuckart, the dwarfed male lives in the uterus of the female. There are usually two or three, more rarely four or five males in a single female. There is also a second species of *Trichosonum* found in the bladder of the rat. *Tr. Schmidtii* v. Linst., the larger male of which was formerly taken for that of *Tr. crassicauda*.

Trichina Owen.* Body thin, hair-like. Principal median lines and lateral

* Compare the writings of R. Leuckart, Zenker, R. Virchow, Pagenstecher, etc.

FIG. 285.—*Trichocephalus dispar* (after R. Leuckart). a, Egg; b, female; c, male with the anterior part of the body buried in the mucous membrane; Sp, spiculum.

lines are present. The female generative opening well forward. The posterior end of the body of the male has two terminal cones between which the cloaca is

FIG. 286.—*Trichina spiralis*. *a*, Mature female *Trichina* from the alimentary canal; *G*, genital opening; *E*, embryos; *Ov*, ovary. *b*, Male; *T*, testis. *c*, Embryo. *d*, Embryo which has migrated into a muscle fibre, already considerably enlarged. *e*, The same developed into a coiled Muscle *Trichina*, and encysted.

projected. *Tr. spiralis* Owen, in the alimentary canal of Man and numerous, principally carnivorous, Mammalia; hardly two lines in length. The viviparous females begin to bring forth embryos about eight days after their migration into the alimentary canal. These embryos traverse the intestinal walls and body cavity of the host, and migrate, partly by their own movements in the bundles of connective tissue, partly with the aid of the currents of blood into the striped muscles of the body. They pierce the sarcolemma and penetrate into the primitive bundles, the substance of which degenerates, the degeneration being accompanied by an active multiplication of the nuclei. In a space of fourteen days they develop, within a sac-like swelling of the muscle fibres, into spirally coiled worms, around which and within the sarcolemma and its connective tissue investment a clear lemon-shaped capsule is excreted from the degenerated muscle substance. The young Muscle-Trichina can remain living for years within this capsule, which at first very delicate, gradually becomes thickened and hard by the formation of other layers and by the gradual deposition of calcareous matter. If the encysted animal is transferred into the intestine of some warm-blooded animal in the flesh of its first host, it is freed from its cyst by the action of the gastric juice, and the rudimentary generative organs, which are already tolerably far developed, quickly attain maturity. In from three to four days after their introduction the asexual Muscle-Trichinas become sexual Trichinas. These copulate and produce a brood of embryos which migrate into the tissues of the host (one female may produce as many as 1000 embryos) (fig. 286). The house rat is especially to be mentioned as the natural host of the *Trichina*. This animal does not hesitate to eat the carcase of its own species, and so the Trichina infection is passed on from generation to generation. Carcasses infected with Trichinas are sometimes eaten by the omnivorous pig, in whose flesh the encysted *Trichinas* are introduced into the intestine of man, and occasion the well-known disease, Trichinosis, which when the migration takes place in number, often has a fatal result.

Fam. Filariidæ. Body filiform, elongated, often with six oral papillæ, some-

FIG. 287.—*Filaria medinensis* (after Bastian and Leuckart). *a*, Anterior end seen from the oral surface; *O*, mouth; *P*, papilla. *b*, Pregnant female (size reduced more than half). *c*, Embryos strongly magnified.

times with a horny oral capsule, with four præanal pairs of papillæ, to which an unpaired papilla may be added, with two unequal spicula or with simple spiculum.

Filaria O. Fr. Müll. With small mouth and narrow œsophagus. This species, which is sometimes destitute of papillæ, lives outside the viscera, usually in connective tissue, frequently beneath the skin (divided by Diesing into numerous genera). *F. (Dracunculus) medinensis** Gmel. the Guinea worm, in the subcutaneous cellular tissue of Man in the Tropics of the Old World, reaches a length of two feet or more. The head is provided with two small and two larger papillæ. The female is viviparous, and without sexual opening. The male form is unknown. The worm lives in the connective tissue between the muscles and beneath the skin, and after reaching sexual maturity, occasions the formation of an abscess, with the contents of which the embryos escape to the exterior (fig. 287). It has lately been proved (Fedschenko) that the embryos of *Filaria* migrate into a Cyclops and there undergo an ecdysis. Whether they are then (in the body of the Cyclops) introduced into man in his drinking water, or whether they first escape and copulate in a free state, is not known. *F. immitis* lives in the right ventricle of the dog, and is very abundant in East Asia. It is viviparous. The embryos pass directly into the blood, where, however, they do not undergo their further development. Similar young Hæmatozoa are also found in the blood of man in the Tropics of the New and Old Worlds (*F. sanguinis hominis*, *F. Bancrofti*). Since these animals are also found in the urine, their appearance seems to have an ætiological connection with hæmaturia. In the East Indies, young *Filaria* also live in the blood of the street dog, and would seem to be related to the brood of *Filaria sanguinolenta*, since, according to Lewis, knotty swellings on the aorta and œsophagus are invariably found with these *Filaria*. *F. papillosa* Rud. in the peritoneum of the horse. *F. loa* Guyot., in the conjunctive of negroes on the Congo. *F. labialis* Pane. Only once observed at Naples. An immature *Filaria* described as *Filaria lentis (oculi humani)* has been found in the human capsula lentis.

Fam. **Mermithidæ**. Aproctous Nematodes, with very long filiform body, and six oral papillæ. The male caudal region is broad, and is provided with two spicula and three rows of numerous papillæ. They live in the body cavity of insects, and escape into the damp earth, where they attain sexual maturity and copulate. *Mermis nigrescens* Duj., was the occasion of the fable of the worm rain. *M. albicans* v. Sieb. v. Siebold established by experiment the migration of the embryos into the caterpillars of *Tinea evonymella*. *Sphæricularia bombi* Léon Duf.

Fam. **Gordiidæ**. Body elongated and filiform. Without oral papillæ and lateral lines, with a ventral cord. The mouth and anterior region of the alimentary canal is obliterated in the adult state. The testes and ovaries are paired and open to the exterior with the anus near the hind end of the body. Uterus unpaired, with receptaculum seminis. The male caudal region is forked, and is destitute of spicula. In the young stage they live in the body cavity of predatory insects, and are provided with a mouth. At the pairing time they pass into the water, where they become sexually mature. The embryos, which are provided with a circle of spines, bore through the egg-membranes and migrate into Insect larvæ (*Chironomus-larvæ*, *Ephemeridæ*), and there encyst. Water

* Compare H. C. Bastian, "On the Structure and Nature of the Dracunculus," *Trans. Linn. Society*, vol. xxiv., 1863. Fedschenko *l. c.*

beetles and other aquatic predatory insects eat with the flesh of the *Ephemerid* larvæ the encysted young forms, which then develop in the body cavity of their new and larger host to young *Gordiidae*. *Gordius aquaticus* Duj.

Fam. **Anguillulidæ**.* Free living Nematodes of small size. Caudal glands are sometimes present. The lateral canals are often replaced by the so-called ventral glands. Some species either live on or are parasitic in plants; others live in fermenting or decaying matter. The greater number, however, live free in earth or water. *Tylenchus* Bast. Buccal cavity small, and containing a small spine. The female genital opening lies far back. *T. scandens* Schn. = *tritici* Needham, in mildewed wheat grains. When the grains of wheat fall the dried embryos grow in the damp earth, bore through the softened membranes, and make their way on to the growing wheat plant. Here they remain some time, perhaps a whole winter without alteration, until the ears begin to be formed. They then pass into the latter, grow, and become sexually mature, while the ear is ripening. They copulate and deposit their eggs, from which the embryos creep out, and at length constitute the sole contents of the wheat grains. *T. dipsaci* Kuhn, in heads of thistles (*Cardus*) *T. Davainii* Bast, on roots of moss and grass. *Heterodera Schachtii* Schmidt., roots of the beet-root, also of the cabbage, of wheat, barley, etc. *Rhabditis* Duj., divided by Schneider into *Leptodera* Duj. and *Pelodera* Schn. *Rh. flexilis* Duj., head very sharply pointed, mouth with two lips, in the salivary glands of *Limax cinereus*. *Rh. angustoma* Duj. *Rh. appendiculata* Schn., in damp earth, 3 mm. long. The larva, which is without a mouth, and has two caudal bands, is found in *Arion empiricorum*. *Anguillula aceti* = *glutinis* O. Fr. Müll., known as the vinegar worm and pasteworm, 1 to 2 mm. long.

Of the many marine *Anguillulidæ* (*Enoplidæ*), we must mention *Dorylaimus maximus* Bütschli, *D. stagnalis* Duj., found in mud everywhere in Europe. *Enchelidium marinum* Ehrbg., *Enoplus tridentatus* Duj.

The aberrant families *Desmoscolecidae* and *Chætosomidae* are allied to the *Nematoda*.

THE CHÆTOGNATHA.

The *Chætognatha*,† containing only the genus *Sagitta*, are allied to the Nematodes. They are elongated round worms, with a peculiarly armed mouth and laterally placed horizontal fins, the membranous edges of which are supported by rays. The anterior portion of the body is sharply separated off as a head, and bears in

* Davaine, "Recherches sur l'Anguillule du blé niellé," Paris, 1857. Kühn, "Ueber das Vorkommen von Anguillulen in erkrankten Blütenköpfen von *Dipsacus fullonum*," *Zeitschr. für wiss. Zool.*, Tom IX., 1859. Bastian, "Monograph of the Anguillulidæ or free Nematoids, marine, land, and fresh water," London, 1864. O. Bütschli, "Beiträge zur Kenntniss der freilebenden Nematoden," *Nov. Acta*, Tom XXXVI., 1873. Lad. Oerley, "Monographie der Anguilluliden," Buda-Pest., 1880.

† Compare A. Krohn, "Anatomisch-physiologische Beobachtungen über die *Sagitta bipunctata*," Hamburg, 1844. R. Wilms, "De *Sagitta* mare germanicum circa insulam Helgoland incolente," Berolini, 1846. Kowalevski, "Embryologische Studien an Würmern und Arthropoden," *Mem. de l'Acad. St. Pétersbourg*, Tom XVI. O. Hertwig, "Die Chætognatha, eine Monographie," Jena, 1890.

the region of the mouth two lateral groups of hooks which function as jaws.

FIG. 288.—*Sagitta* (*Spadella*) *cephaloptera*, magnified 30 times, viewed from the dorsal side (after O. Hertwig). *F*, posterior fin; *G*, supra-oesophageal ganglion; *Te*, tentacles; *R*, olfactory organs; *Ov*, ovary; *Od*, oviduct; *T*, testis; *Vd*, vas deferens; *Sb*, vesicula seminalis.

The nervous system consists, according to Krohn, of a cerebral ganglion on which the eyes are situated, and a ventral ganglion placed in about the middle of the body length. There are in addition two ganglia near the mouth, which may be considered as the suboesophageal ganglia, and are connected with each other and with the cephalic ganglion by oesophageal commissures.

[The common view now is that the large ventral ganglion of the middle of the body, which is connected with the cerebral by commissures, is homologous with the suboesophageal ganglia of other types.]

The straight alimentary canal is attached to the body wall by a dorsal and ventral mesentery from the oesophagus backwards, and opens to the exterior at the base of the long tail, which terminates in a horizontal fin (fig. 288).

[The body cavity is well developed, and divided by the dorsal and ventral mesenteries into two parts, and again by two transverse vertical septa into a cephalic section, a section in the body, and finally a caudal section. Vascular and excretory organs are absent.]

Reproduction. The *Chaetognatha* are hermaphrodite, and possess paired ovaries, which open by two apertures at the base of the tail and are connected with seminal pouches. The testes also are paired, and situated posteriorly to the ovaries in the tail; their products pass to the exterior by openings at the sides of the tail. Segmentation is complete, and leads to the formation of a blastosphere. One side of this becomes invaginated so that the segmentation cavity is obliterated and a gastrula is formed, in the entoderm

of which two cells may already be recognised as primitive generative cells. As soon as these make their appearance in the entoderm, the latter becomes folded in such a way that the archenteron is divided into a median and two lateral cavities. The layer of cells lining the lateral cavities becomes the mesoderm, and the contained cavities the two lateral compartments of the body cavity, while that of the middle cavity gives rise to the wall of the mesenteron or alimentary canal. The permanent mouth is formed at the end opposite to that at which the blastopore, which is now closed, was situated.

There is but one genus, *Sagitta* Slab., of which several species, e.g., *Sagitta bipunctata* Krohn, *S. germanica* Lkt. Pag. from the European seas have been more accurately described.

Order 2.—ACANTHOCEPHALA.*

Elongated round worms with protrusible proboscis furnished with hooks; without mouth and alimentary canal.

The saccular, often transversely wrinkled body begins with a proboscis, which is furnished with recurved hooks and can be retracted into a tube projecting into the body cavity (sheath of the proboscis) (fig. 289, *R* and *Rs*). The posterior end of this sheath is fastened to the body wall by a ligament, and by retractor muscles. The nervous system (fig. 289, *G*) is placed at the base of the proboscis, and consists of a simple ganglion formed of large cells. Nerves are given off from the ganglion anteriorly to the proboscis, and through the lateral retractors (*retinacula*) to the body wall (fig. 289, *R*). The latter supply partly the muscular system of the body, and partly the genital apparatus, in which there are, principally in the male animal, special nerve centres consisting of ganglionic enlargements.

Sense organs are entirely wanting, as also are mouth, alimentary canal, and anus.

The nutritive juices are taken in through the whole outer surface of the body. In the soft granular subcuticular

FIG. 289.—Anterior part of an *Echinorhynchus*. *R*, Proboscis; *Rs*, sheath of proboscis; *G*, ganglion; *Le*, lemnisci; *R*, retinacula.

* Besides Dujardin, Diesing, l. c., compare: R. Leuckart, "Parasiten des Menschen," Tom II., 1876. Greeff, "Untersuchungen über Echinorhynchus miliaris," *Arch. für Naturgesch.*, 1864. A. Schneider, "Ueber den Bau der Acanthocephalen," *Müller's Archiv.*, 1868. Also the *Sitzungsberichte der Oberhessischen Gesellschaft für Natur- und Heilkunde*, 1871.

layer of the integument lies a complicated system of canals, filled with a clear fluid containing granules. Beneath the internal layer of the integument, which layer is often very extensive and of a yellow colour, is placed the powerful muscular tunic; it is composed of external transverse and internal longitudinal fibres, and bounds the body cavity. The complicated ramified system of dermal canals, of

which two principal longitudinal trunks may be recognised, is filled with juices, and probably functions as a nutritive apparatus. The portion of this system which extends into two bodies (the *lemnisci*, fig. 289, *Le*) projecting behind the proboscis through the muscular tunic into the body cavity, probably acts as an **excretory organ**, since the contents of the frequently anastomosing canals of these lemnisci is usually of a brown colour, and consists of a cellular mass rich in concretions. According to Schneider, the vessels of the lemnisci open into a circular vessel in the integument, and only communicate with the network of canals in the cephalic region, while the other dermal vessels (nutritive apparatus), the contents of which differs from that of the vessels of the lemnisci, are completely shut off from the latter.

Generative organs. The body cavity through which fluids circulate encloses the greatly developed generative organs, which are attached

FIG. 290.—Male of *Echinorhynchus angustatus* (after R. Leuckart). *R*, proboscis; *Rs*, sheath of the proboscis; *Li*, ligament; *G*, ganglion; *Le*, lemnisci; *T*, testes; *Vd*, vasa deferentia; *Pr*, prostatic sacs; *De*, ductus ejaculatorius; *P*, penis; *B*, retracted bursa.

FIG. 291.—Generative ducts of a female *Echinorhynchus gigas* (after A. Andres). *Li*, ligament; *F*, disc-shaped flocculi; *F'*, *F''*, appendages of the same; *U*, uterus; *V*, vagina; *B*, lateral pouches of the bell; *Gd*, dorsal cells at the base of the bell; *Gl*, lateral cells.

to the end of the sheath of the proboscis by a ligament (figs. 290

and 291, *Li*). The sexes are separate. The male (fig. 290) has two testes (*T*), and the same number of efferent ducts (*Vd*). The latter unite behind to form a ductus ejaculatorius (*De*), which is often furnished with six or eight glandular sacs (*Pr*), and a conical penis (*P*), at the bottom of a bell-shaped protrusible bursa (*B*), situated at the posterior pole of the body (fig. 290). The generative organs of the larger females (fig. 291) consist of the ovary developed in the ligament; of a complicated uterine bell, beginning with a free opening into the body cavity; of the oviduct and the short vagina, which is divided into several portions and opens at the posterior end of the body (fig. 291). It is only in the young stage that the ovary is a simple body enclosed by the membrane of the above-mentioned ligament. As the animal increases in size, the ovary grows, and becomes divided into numerous spherical masses of eggs, the pressure of which bursts the membrane of the ligament; the masses of ova as well as the ripe elliptical eggs, which gradually become free from them, fall into the body cavity. The egg membranes are not

FIG. 292.—Embryo of *Echinorhynchus gigas* enclosed in the egg membranes (after Leuckart).

FIG. 293.—Larvæ of *Echinorhynchus proteus* from *Gammarus* (after Leuckart). *a*, Free embryo; *Ek*, embryonic nucleus. *b*, Older stage, with more differentiated embryonic nucleus. *c*, Young female worm; *Ov*, ovary. *d*, A young male worm; *T*, testes; *Le*, lemnisci.

dilating and contracting, thence into the oviduct, and through the genital opening to the exterior.

formed till after segmentation, and ought perhaps to be interpreted as embryonic membranes. The eggs, which already contain embryos, pass out of the body cavity into the uterine bell, which is continually

Development. Segmentation is irregular and complete, and results in the formation of an embryo, which is enclosed in three egg-membranes. The embryo has a small, somewhat long body, armed with small spines at the anterior pole, and containing a central granular mass (embryonic nucleus) (fig. 292). It passes into the intestine of Amphipods (*Ech. proteus*, *polymorphus*), or of Isopods (*Ech. angustatus*), and there becomes free, bores through the wall of the intestine, and after losing the embryonic spines, develops to a small elongated larva, which, like a pupa, lies in the body cavity of the small Crustacean with its proboscis retracted and surrounded by its firm external skin as by a cyst (fig. 293). The skin of the larva gives rise only to the integument, the vessels and the lemnisci of the adult; while all the other organs enclosed within the dermal muscular envelope, viz., the nervous system, the sheath of the proboscis, and the generative organs, are developed from the so-called embryonic nucleus. It is only after their introduction into the intestine of fishes (*Ech. proteus*) or of aquatic birds (*Ech. polymorphus*), which feed on these *Crustacea*, that the larvæ attain to sexual maturity, copulate, and reach their full size.

The numerous species of the genus *Echinorhynchus* O. F. Müller live principally in the alimentary canal of different Vertebrata; the gut wall may be as it were sown with these animals. *Ech. polymorphus* Brems., in the intestine of the duck and other birds, also in the crayfish. *Ech. proteus* Westrumb., *Ech. angustatus* Rud., in fresh-water fish. *Ech. gigas* Goeze, as large as an *Ascaris lumbricoides*, in the small intestine of the pig. According to A. Schneider, the embryo completes its development in the maggot. Lambl found a small sexually immature *Echinorhynchus* in the small intestine of a child which died of leukæmia.

CLASS III.—ANNELIDA.

Segmented Vermes with brain, circum-oesophageal ring, ventral nerve cord, and vascular system.

The larva of Lovén and its development seems to throw light upon the organization of the *Annelida* and their relations to the lower worms and to the *Rotifera*; and further makes evident the relationship of the *Annelida* to the *Gephyrea*, a group of worms which possess an elongated body devoid alike of external and internal segmentation, and, as an equivalent of the ganglionic chain, a ventral nerve trunk, which is usually uniformly covered with ganglion cells.

The body of Lovén's larva, from which we must derive the body of Annelids, is unsegmented, and represents mainly the Annelid head.

Behind it is continued into an indifferent terminal portion equivalent to the whole body of the adult.

At the apical region of the larva (fig. 294, *Sp*) there is a thickening of the ectoderm, which is called the apical plate. This represents the rudiment of the cerebral ganglion (apical ganglion), and gives off nerves to either side. The wide mouth (*O*) has a

FIG. 294.—Development of *Polygordius* (after B. Hatschek). *a*, Young larva; *Sp*, apical plate with pigment spot; *Prw*, præ-oral circle of cilia; *O*, mouth; *Pow*, post-oral circle of cilia; *A*, anus; *Ms*, mesoderm; *KN*, head kidney. *b*, Older larva with commencing segmentation of the body, a second limb is developed in the head kidney. *c*, Older stage. The body is elongated to the form of a worm, and divided into a number of metameres; *HWk*, posterior circle of cilia; *Af*, eye spot; *F*, tentacle.

ventral position, and leads into an alimentary canal, which opens at the posterior end of the body (*A*). In front of the mouth there is a strongly developed circle (præoral) of cilia (*Prw*); and behind

the mouth a weaker (postoral) circle (*Pow*); to the right and left there is an excretory canal (head kidney), which begins with a ciliated funnel. By the differentiation of the cephalic region of the larva into præstomial lobe and oral segment, and by the gradual growth in length of the posterior part of the body and the segmentation of the latter into a number of successive metameres, the originally unsegmented larva is transformed into an Annelid (fig. 294, *a—d*). There is, therefore, between the segmented adult and the larva a morphological relation similar to that between the cestoid and the simple scolex, from the posterior end of which the proglottides are developed.

FIG. 294 *d*.—The young *Polygordius*; *G*, cerebral ganglion; *Wg*, ciliated pit; *D*, alimentary canal.

(*Chaetopoda*), or each internal segment corresponds to a definite number (3, 4, 5, etc.) of the external rings (*Hirudinea*).

Organs of locomotion. Special organs of locomotion may either have the form of bristle-bearing unjointed appendages (parapodia) on each ring of the body (*Chaetopoda*), or of terminal suckers (*Hirudinea*). In the first case each segment may possess a dorsal and ventral pair of appendages (the *neuropodia* and *notopodia*), which, however, are sometimes replaced by simple setæ embedded in dermal pits.

Alimentary canal. The mouth is placed on the ventral surface at the anterior end of the body, and leads into a muscular pharynx, which is often provided with a powerful armature and can be protruded like a proboscis. This is followed by the gastric region of the gut, which occupies the greatest portion of the length of the body, and is either regularly constricted in correspondence with the segments, or possesses lateral diverticula; it is only coiled in exceptional cases. The anus is usually dorsal at the hinder end of the body.

The **nervous system** consists of a cerebral or supra-œsophageal ganglion, which is derived from the apical plate of the larval præ-oral lobe, of an œsophageal ring, and of a ventral cord or ganglionic chain, the two halves of which lie more or less approached to each other in the median line. The ventral cord arises from two lateral nerve cords, which probably correspond to the lateral nerve trunks of the Ne-

mertines. These two cords are continuous with the œsophageal commissures, and, like the latter, are uniformly covered with ganglionic cells. This form of the nervous system may persist, as may also its ectodermal position (*Archiannelida*, *Protodrilus*) (fig. 295). In most *Annelida*, however, this is only a transitory condition; for at a later stage the lateral cords become separated from the ectoderm, come together in the median line, and acquire a segmentation corresponding to the metamereres of the body. The nerves of the sense organs arise from the cerebral ganglion; the other nerves pass out from the parts of the ventral cord or, as the case may be, from the ganglia of the ventral chain and from the longitudinal commissures between the latter. There is in

FIG. 295.—Transverse section through the body of *Protodrilus* (after B. Hatschek). *SS*, The two lateral trunks of the nervous system; *G*, ganglionic layer of the same; *D*, alimentary canal; *N*, nephridium; *M*, muscles; *Ov*, ova.

almost all cases a visceral nervous system (*sympathetic*). The following *sense organs* are found: *paired eye spots* with refractive structures, or larger more complicated eyes; also *auditory vesicles* upon the oesophageal ring (branchiate worms), and *tactile organs*. The latter have, in the *Chaetopoda*, the form of tentacles and tentacular cirri on the head and of cirri on the parapodia. When tentacles and cirri are absent, the anterior end of the body and the region of the mouth seem to function as tactile organs.

Vascular system. A blood vascular system is very commonly present; in many cases, however, it seems not to be completely closed, but to communicate with the body cavity, which contains blood. Two main vascular trunks, a dorsal and a ventral, connected with one another by numerous transverse anastomoses, are generally present. The blood is usually coloured (green or red), and its circulation is effected by the contractility of the walls of certain vessels; sometimes the dorsal vessel, sometimes the ventral, and sometimes the transverse connecting vessels are contractile. Lateral longitudinal vessels are often present in addition to the above. In the Hirudinea these, as well as the median contractile blood sinus, are probably to be regarded as isolated parts of the body cavity.

Special respiratory organs are found amongst the *Chaetopoda* in the branchiate worms.

The **excretory organs**, corresponding to the water-vascular or excretory system of the Platyhelminthes, have the form of coiled canals (segmental organs or nephridia), which are repeated in pairs in each segment. Each nephridium usually begins with a ciliated, funnel-shaped opening into the body cavity, and opens to the exterior by a lateral pore (fig. 70). These may assume in certain segments the function of generative ducts, *e.g.*, the nephridia of the *Gephyrea*, which, however, are much reduced in number. In the cephalic segment or head there is also a segmental organ (head kidney), which in the larva functions as a kidney and later disappears.

Reproduction.—Considering the independence of the segments, to which we ascribe the value of a subordinate (morphological) individuality, the occurrence of asexual reproduction by fission and gemmation in the long axis (*Chaetopoda*) is not surprising. Numerous *Annelida* (*Oligochata*, *Hirudinea*) are hermaphrodite; the marine *Chaetopoda*, on the contrary, are for the most part of separate sexes. Many lay their eggs in special sacs and cocoons, in which case development is direct, without metamorphosis. The marine worms, on the contrary, undergo a more or less complicated

metamorphosis. The *Annelida* comprise terrestrial and aquatic animals, and they eat, for the most part, animal food. Many of them (*Hirudinea*) are occasionally parasitic.

In the group of the *Annelida* three principal divisions may be distinguished,—the *Chætopoda*, the unsegmented *Gephyrea*, and the *Hirudinea* which are adapted for parasitism. The *Hirudinea* are not in any degree to be regarded as *Annelida* of a lower grade of organization, but they rather present, at least in the case of some organs, as alimentary canal, circulatory and generative organs, a more complicated structure, and agree most closely with the *Oligochaeta*, from which they may be derived.

Sub-class 1.—CHÆTOPODA.*

Free living Annelida, with paired tufts of setæ on the segments, frequently with distinct head, also with tentacles, cirri, and branchiæ.

The Chætopoda are divided externally into segments, which correspond with the metameres of the internal organs, and are, with the exception of the anterior region, which is distinguished as the head, usually tolerably alike (fig. 296). Parapodia provided

FIG. 296.—*Grubea fusifera* (after Quatrefages). *Ph*, pharynx; *D*, alimentary canal; *C*, cirri; *F*, tentacles.

FIG. 297.—Dorsal (DP) and ventral (VP) Parapodium with bundles of setæ of *Nereis* (after Quatrefages). *Ac*, Aciculum; *Rc*, dorsal cirrus; *Bc*, ventral cirrus.

with setæ are very frequently present on the segments; their principal function is that of locomotion, but their various appendages, the branchiæ and cirri, also discharge tactile and respiratory functions (fig. 297).

plement, 1870, and "Recherches sur la structure des Annélides sédentaires," Genève, 1873. Fr. Leydig, l. c., also "Tafeln zur vergl. Anatomie," 1864.

* Besides the older works of Savigny, Audouin et Milne Edwards, and Quatrefages, compare E. Grube, "Die Familien der Anneliden," *Archiv für Naturgesch.* 1850 and 1851. E. Claparède, "Recherches anatomique sur les Annélides, etc.," Genève, 1861. E. Claparède, "Les Annélides chætopodes du golfe de Naples," Genève et Bâle, 1868, also Sup-

The form of the movable setæ varies extremely, and affords a good character for the classification of families and genera. According to the strength, form, and mode of ending (fig. 298), the following

FIG. 298.—Setæ of different *Polychæta* (after Malmgren and Claparède). *a*, Hooked seta of *Sabella crassicornis*; *b*, of *Terebella Danielsseni*; *c*, seta with spiral ridge from *Sthenelais*; *d*, lance-shaped seta of *Phyllochaetopterus*; *e*, of *Sabella crassicornis*; *f*, of *Sabella pavonis*; *g*, Composite sickle-shaped seta of *Nereis cultrifera*.

forms can be distinguished: hair-setæ, hooked-setæ, flat-setæ (*paleæ*), lance-setæ, sickle-shaped setæ, etc. When the parapodia and their

appendages are completely wanting, the setæ are embedded in pits in the integument, and are arranged either in one or two rows on either side, that is, in a lateral ventral row on either side, or in a ventral row and a dorsal row on either side. In such cases the number of setæ is small (*Oligochaeta*). The setæ may, on the contrary, be present in great number, so that the integument on either side seems to

FIG. 299.—Anterior end of *Polynoë extenuata*, the first elytron on the left hand being removed (after Claparède). The two setæ of the oral segment are visible; *El*, Elytra.

oe covered with long hairs and setæ, and a thick felt of hairs shining with a metallic lustre is distributed over the whole dorsal

surface (*Aphrodite*). The appendages of the parapodia present an equally great variety of form and not unfrequently vary in the different parts of the body. They are either simple or ringed tentacle-like processes, the *cirri*, which are distinguishable into dorsal and ventral cirri. The cirri are for the most part filiform, and sometimes jointed or conical, and then are often provided with a special basal joint. In some cases the dorsal cirri are flattened out as broad scales and leaves, the *elytra*, which constitute a protective covering (*Aphrodite*) (fig. 299). In addition to the cirri, branchiæ which may be filiform or branched and antler-like, comb-shaped or in the form of tufts, are frequently present; sometimes they are confined to the middle region of the body, or are extended over almost the whole dorsal surface; sometimes they are confined to the head or to the anterior segments immediately following the oral segment (cephalic branchiæ).

The two anterior segments may be regarded as forming the head; they are fused together, and are, with regard to their appendages, different from the following segments (fig. 245). The anterior segment projects beyond the mouth as the frontal lobe, and bears the *tentacles* and *palps* [*palps* are tentacular structures arising from the ventro-lateral sides of the head, *vide* p. 379] and also the eyes; the posterior cephalic segment or oral segment bears the tentacular cirri. The last segment (anal segment) bears the *anal cirri*.

The **alimentary canal** is usually straight, and extends from the mouth to the anus, which is terminal and rarely dorsal; it is divided into œsophagus, intestine, and rectum (fig. 300). There is in most cases a dilated muscular pharyngeal bulb which is armed with papillæ or with movable teeth and can be protruded as a *proboscis*. The intestine usually preserves the same structure in its entire length and is divided by regular constrictions into a number of

FIG. 300. — Alimentary canal of *Aphrodite aculeata* (after M. Edwards). Ph, pharynx; D, intestine; L, hepatic appendages.

divisions or chambers, which correspond to the segments and dilate again into lateral diverticula and caeca. The constrictions are due to filamentous or membranous septa (dissepimenta), which divide the body cavity into the same number of chambers lying one behind another.

¹ The **vascular system** appears to be closed, so that the clear nutritive fluid found in the body cavity, which, like the blood, contains amoeboid corpuscles, does not communicate with the usually coloured contents of the vessels. The dorsal and ventral vessels are not only connected at each end by lateral loops, but also in each segment; and from these connecting vessels proceed peripheral networks, which extend into the integument, the wall of the alimentary canal, and the *branchiæ*.

Special **organs of respiration** are wanting in almost all the *Oligochaeta*. In the marine Worms, on the contrary, *branchiæ* are very generally present, usually as appendages of the parapodia. These *branchiæ* are either simple cirri which have delicate ciliated walls and contain blood-vessels, or are branched (*Amphinome*) or in some cases are pectinate structures (*Eunice*) which co-exist with special cirri on the notopodia (fig. 246). The *branchiæ* are sometimes confined to the middle segments (*Arenicola*), and are sometimes developed on almost all the segments on the dorsal surface, being simplified towards the posterior end of the body (*Dorsibranchiata*). In the *Tubicolæ* the *branchiæ* are confined to the two (*Pectinaria*, *Sabellidæ*) or three (*Terebella*) anterior segments. The respiratory function is, however, also shared (*Capitibranchiata*) by a number of elongated tentacles which are grouped in tufts on the head. These are, in the *Sabellidæ*, supported by a special cartilaginous skeleton, and may have secondary twigs developed upon them. They are either simply arranged in a circle round the mouth, or in two fan-like lateral groups (*Serpulidæ*), the base of which is not unfrequently drawn out into a spiral plate. Such branchial structures, however, also function as organs of touch, as organs for procuring nutriment, and even for building the tubes and shells.

Excretory organs.—There are usually in all the segments paired segmental organs, which serve as excretory organs. They begin, as a rule, with a ciliated funnel in the body cavity; they possess a glandular wall, are several times coiled upon themselves, and open to the exterior in each segment by a lateral pore. These glandular passages serve in general for the removal of matters from the body cavity, and in the marine *Chætopoda* are used during the

breeding season as oviducts or vasa deferentia, and permit of the passage outwards of the generative products, which have been set free in the body cavity.

Amongst the special glands in the body of the *Chaetopoda*, those cutaneous glands of the *Oligochaeta* which give rise to the thickening (extending over several segments) known as the clitellus or girdle, are especially worthy of remark. The secretion of these glands perhaps assists the intimate connection of the Worms during copulation. In the *Serpulidae* there are present two large glands, which open upon the dorsal surface of the anterior portion of the body and furnish a secretion used in the formation of the tubes in which the animals live.

FIG. 301.—Brain and anterior portion of the ganglionic chain, *a*, of *Serpula*; *b*, of *Nereis*, (after Quatrefages); *O*, eyes; *G*, cerebral ganglion; *c*, oesophageal commissure; *Ug*, subesophageal ganglion; *e e*, nerves to the tentacular cirri and the mouth segment.

Nervous system.—The longitudinal trunks of the ventral cord are often so closely approached that they seem to form a single cord (*Oligochaeta*). In the *Tubicolæ* (fig. 301), on the contrary, they are very widely separated from one another, especially in the anterior part of the ganglionic chain (*Serpula*). The visceral nervous system consists of paired and unpaired ganglia, which supply the oral region and especially the protrusible proboscis.

Sense organs.—Paired eyes upon the surface of the frontal (*i.e.*

præoral or cephalic) lobe are widely distributed. Eye-spots may also be present upon the posterior end of the body (*Fabricia*), or may be regularly repeated upon the sides of each segment (*Polyophthalmus*). In species of *Sabella*, pigment-spots with refractive bodies are found even upon the branchial filaments. The large cephalic eyes of the genus *Alciopæ** are the most highly developed, being provided with a large lens and a complicated retina. The presence of auditory organs seems less frequent. They appear as paired otolithic vesicles upon the œsophageal ring of *Arenicola*, *Fabricia*, some *Sabellidæ* and young *Terebellidæ*, etc. Besides the tentacles, cirri and elytra, other

FIG. 302.—*Autolytus cornutus*, with the male animal *Polybostrichus* (after A. Agassiz). *F*, Tentacles; *CT*, tentacular cirri; *f*, tentacles; *ct*, tentacular cirri of the male.

portions of the surface of the body may be sensitive to tactile sensations. On such parts there are either stiff hairs and tactile setæ, or, as in *Sphærodorum*, special tactile warts with nerve terminations.

Reproduction.—In the smaller *Chætopoda* asexual generation by fission and gemmation may occur. Either (fissiparous reproduction) a large number of segments of the parent become separate and give rise to the body of the new worm, as for example in *Syllis prolifera*, where a series of the posterior segments, which are filled with ova, become separated by a simple transverse fission, after the formation of a head provided with eyes; or (gemmaiparous reproduction) a single segment only, usually the last, becomes the starting-point for the formation of a new individual. In this way *Autolytus prolifer*, one of the *Syllidæ*, asexually reproduces itself, giving rise to a male and female sexual form, known respectively as *Polybostrichus Mülleri*† (male) and *Sacconereis helgolandica* (female). This is a case of alternation of generations, for the asexual form, *Autolytus*, gives rise by budding in the long axis to the sexual

forms (fig. 302). In this case a whole series of segments are developed

* Greeff, "Ueber das Auge der Alciopiden, etc.," Marburg, 1876; and "Untersuchungen über die Alciopiden," *Nov. Act. der K. Leop. Akad., etc.*, Tom XXXIX., Nro. 2.

† Compare besides the works of O. Fr. Müller, Quatrefages, Leuckart, and Krohn, especially A. Agassiz, "On alternate Generation of Annelids and the embryology of *Autolytus cornutus*," *Boston Journ. Nat. Hist.*, vol. iii., 1863.

in front of the last segment of the asexual form, and these segments, after the formation of a head, constitute a new individual. As this process is repeated, a chain of connected individuals is formed, and these, as soon as they are separated, represent the sexual individuals. Among the freshwater *Naidæ*, in *Chaetogaster*, a regular and continued budding in the long axis leads to the formation of chains, consisting of not less than 12 to 16 zooids, each having only four segments, while the sexual individuals consist of a greater number of segments. A similar process occurs in the mode of reproduction observed by O. Fr. Müller in *Nais proboscidea*, from the last segment of which a new zooid is produced. Both generations of *Nais*, however, become sexually mature.

[For a more complete account of the asexual reproduction of Chaetopoda, vide Balfour, "Comparative Embryology," vol. i, pp. 283, 284.]

The *Chaetopoda* are, with the exception of the hermaphrodite *Oligochaeta* and certain *Serpulidæ* (e.g., *Spirorbis spirillum*, *Protula Dysteri*) of separate sexes. Male and female individuals seem occasionally so strikingly different in the structure of their organs of sense and locomotion that they have even

FIG. 303.—A parapodium of *Tomopteris* with a mass of ova and one free ovum (after C. Gegenbaur).

been taken for species of distinct genera. Besides the above-mentioned *Sacconereis* and *Polybostrichus*, the asexual generation of which is *Autolytus*, a similar sexual dimorphism has been shown by Malmgren for *Heteronereis*, a genus of the *Lycoridæ*, in which the males and females differ both in external form and in the number of their segments. A remarkable case of heterogamy is also afforded by this genus, in that a generation of smaller animals swimming upon the surface alternates with a generation of larger forms living upon the bottom.

The generative apparatus of the *Oligochaeta* is very highly developed. The ovaries and testes lie in definite segments, and empty their contents by dehiscence of their walls into the body cavity. Special generative ducts often co-exist with segmental organs in the same segment (*O. terricolæ*), while in other cases the segmental organs are wanting in the generative segments (*O. limicolæ*). In

the marine *Chatopoda*, the ova or spermatozoa originate on the body wall (fig. 303) from cells of the peritoneal membrane, either in the anterior segments alone or along the whole length of the body. The generative products then become free in the body cavity, attain maturity, and pass through the segmental organs to the exterior. Only a few *Chatopoda*, as *Eunice* and *Syllis vivipara*, are viviparous, all the rest are oviparous; many lay their eggs in connected groups, and carry them about with them, while the *Oligochaeta* lay theirs in cocoons.

Development.—The segmentation is unequal. A primitive streak is very generally developed, though sometimes not until the embryo has left the egg. It arises on the ventral side in consequence of the development of a middle layer and from neutral plates of the upper layer.

Excepting in the *Oligochaeta*, the young forms undergo a metamorphosis and after leaving the egg appear as ciliated larvæ, which are provided with mouth and alimentary canal, and essentially resemble, with some modifications, Lovén's larva.

The capability of renewing lost portions of the body, more especially the posterior part of the body and different appendages, seems to be generally distributed. The *Lumbricinae* and certain marine Worms (*Diopatra*, *Lycaretus*) are even able to replace the head and the anterior segments, with the brain, œsophageal ring, and sense apparatus.

Fossil remains of *Chatopoda* are found from the Silurian onwards in the most different formations.

Order 1.—POLYCHÆTA.*

Marine Chatopoda, with numerous setæ embedded in the parapodia, usually with distinct head, tentacles, cirri, and branchiæ. They are for the most part diœcious, and develop with metamorphosis.

The marine *Chatopoda* must be considered as belonging to a higher grade of life, on account of the sharp distinction of the head which is composed of the præstomium (præoral lobe) and oral segment (in the *Amphinomidae* several succeeding segments are also included), and of the presence of the tentacles, tentacular cirri and

* Audouin et Milne Edwards, "Classification des Annélides et description des celles qui habitent les côtes de la France," *Annales des Sc. Nat.*, Tom. XXVII. to XXX., 1832-33. Delle Chiaje, "Descrizioni e notomia degli animali senza vertebre della Sicilia citeriore," Napoli, 1841. Quatrefages, "Histoire naturelle des Annelés," Tom. I. and II., 1865. Also the numerous writings of E. Grube and E. Claparède

gills, and also of the setæ embedded in prominent parapodia, which serve as aids to swimming. The internal organization, however, is in no way more complicated than that of the *Oligochaeta*. Nevertheless all these distinctive characters may be less and less marked, and, indeed, so completely vanish that it is difficult to draw a sharp line between the *Oligochaeta* and the *Polychaeta*. The parapodia (*Capitellidæ*) and also the setæ (*Tomopteridæ*) may be wanting.

In rare cases, bundles of setæ are present on all the segments behind the head; they are however arranged in a single row and embedded in a single pair of ventral retractile parapodia in each segment.

FIG. 304. — Head and anterior body segments of *Nereis Dumerilii* (after E. Claparède). O, Eyes; P, palps; Ct, tentacular cirri; K, pharyngeal jaws.

This arrangement, which is found in *Saccocirrus* and its allies, probably represents the primitive state, especially as in these animals the character of the nervous system, which lies in the ectoderm external to the dermal muscular envelope, and of the sense organs, which are reduced to two simple tentacles upon the cephalic lobe and to ciliated pits, indicates lower and more primitive conditions.

In another and very remarkable type, *Polygordius* Schn. and *Protodrilus* Hatsch., not only parapodia and setæ but also the external segmentation are wanting. The segmentation of this achæitous and externally unsegmented worm is entirely confined

to the internal organization and is, as compared with that of all other Annelida, to a certain extent *completely homonomous*, inasmuch as the œsophagus is confined to the cephalic segment and does not extend into the anterior segments of the body. Further, the nervous system is connected with the ectoderm along its whole length, and the cerebral ganglion maintains its primitive position at the anterior end, corresponding to the apical plate of the larva; and the ventral cord is without ganglionic swellings. In all the above points these

forms seem to have preserved the primitive Annelidan structure, and they have therefore been united by Hatchesek into a special class, the *Archiannelida*.

In the *Polychaeta* the vascular system is complicated by the appearance of branchiæ, which are provided with blood-vessels. In the forms with dorsal branchiæ the branchial blood is derived from the dorsal trunk and returned to the ventral by special vessels. When,

FIG. 305.—*Terebella nebulosa*, opened from the dorsal side (after M. Edwards). T, Tentacles; K, Branchiæ; Dg, dorsal vessel or heart.

on the other hand, as in the tubicolous capito-branchiate forms, the respiratory apparatus is concentrated on a few segments, the vascular system of that part undergoes greater modifications. In the *Terebellidæ* (fig. 305), the dorsal trunk dilates above the pharynx to a branchial heart from which lateral branches are given off to the branchiæ. In the same region the transvers loops connecting the

dorsal and ventral trunks may perform the function of hearts, as is also frequently the case in the *Oligochaeta*. Finally the vascular system is in many cases considerably reduced, and, according to Claparède, is entirely wanting in *Glycera* and *Capitella*, in which the blood is represented by the perivisceral fluid.

The generative organs, unlike those of the hermaphrodite *Oligochaeta*, are usually placed in different individuals; and the males and females are sometimes of very different forms. A number of hermaphrodite *Polychæta* are, however, known; such principally belong to genera of the *Serpulidæ*, e.g., *Spirorbis*, *Protula*.

The development, unlike that of the *Oligochaeta*, is invariably connected with a metamorphosis.

Segmentation is, as in the *Hirudinea*, usually unequal, and even the first two segmentation spheres are of unequal size. The smaller (animal) half, which segments more quickly, gives rise to smaller segments, which grow round and envelope the larger segments proceeding from the segmentation

FIG. 306.—Larvæ of *Polychæta* (after Busch). *a*, Larva of *Nereis* *F*, tentacle; *Oc*, eyes; *PrW*, præoral circle of cilia; *O*, mouth; *A*, anus. *b*, Mesotrochal larva of *Chætopterus*; *Wp*, circle of cilia.

of the larger half. In the subsequent development a primitive streak makes its appearance in all embryos of *Polychæta*, sometimes, however, not until the embryo has begun to lead a free life as larva. The ganglia become differentiated later into the ventral chain.

In the free-swimming larvæ the cilia are rarely distributed over the whole surface of the body (*Atrocha**). They are usually confined to special rows (ciliated rings); sometimes, as in Lovén's larva, there is one row placed in front of the mouth at some distance from the

* Compare E. Claparède and E. Metschnikoff, "Beiträge zur Entwicklungsgeschichte der Chætopoden," Zeitschr. für wiss. Zool., Tom. XIX., 1869.

anterior end of the body (*Cephalotrocha*, e.g., larva of *Polynoë*). Sometimes there are two rows, one at each end of the body, constituting a præoral and perianal ring (*Telotrocha*, e.g., *Spio-Nephthys-larva*). In addition to these two rings of cilia, incomplete rings may also be present on the ventral surface (*Gastrotrocha*), or both ventrally and dorsally (*Amphitrocha*). In other cases one or more rows of cilia surround the middle of the body (*Mesotrocha*), while the terminal rings (præoral and perianal) are absent (*Telepsavus-Chatop-terus larva*) (fig. 306). Many larvæ are provided with long provisional setæ, which are later replaced by the permanent structures (*Metachæta*). In spite of their great diversity of form the Chatopod larvæ can in their later development also be reduced to the type of the larva of Lovén.

Relatively few forms, as for instance the transparent *Alciopidæ*,

live at the surface (pelagic animals); most of them live near the coast. Numerous forms descend into the deep sea. Many have the power of emitting an intense light, especially species of the genus *Chætopterus* which emit light from their antennæ and appendages. The elytra of *Polynoë*, the tentacles of *Polycirrus*, and the integument of certain *Syllidæ*, are also phosphorescent. Panceri* has shown that the seat of the phosphorescence is in unicellular cutaneous glands, which, in *Polynoë*, were proved to be in communication with nerves.

FIG. 307.—*Nereis margaritacea*. Head with protruded jaw apparatus of the pharynx, from the dorsal surface (after M. Edwards). K, Jaws; F, tentacles; P, palps; Fc, tentacular cirri.

Sub-order 1. **Errantia**. Free-swimming, predacious *Polychæta*. The præstomium always remains independent and forms, with the oral segment, a well-marked head which bears eyes, tentacles, and usually tentacular cirri. The parapodia are much more developed than in the *Tubicolæ*, and, together with their very variously shaped setæ, serve as oars. The anterior portion of the pharynx can be protruded as a proboscis and is divided into several portions; it is either beset with papillæ or contains a powerful masticatory apparatus, which appears at its extremity when protruded (fig. 307). *Branchiæ* may be wanting; when present, they usually appear as comb-shaped or dendritic

* Panceri, "La luce e gli organi luminosi di alcuni annelidi," Atti della R. Acad. sciensz fi. e mat. di Napoli, 1875.

tubes on the parapodia (*Dorsibranchiata*). The *Errantia* are predatory in their habits (*Rapacia*) and swim freely in the sea; but they may also inhabit temporarily thin membranous tubes.

Fam. **Aphroditidæ**. Broad scales (*elytra*) on the notopodia. These are usually placed on alternate segments, often only on the anterior part of the body. Præstomium, with eyes, with one unpaired and usually two lateral tentacles, to which may be added two stronger lateral ventrally placed tentacles (palps). Proboscis cylindrical, protrusible, with two upper and two under jaws. *Aphrodite aculeata* Lin. (*Hystrix marina* Redi.) The back has a thick felt of hairs. Eyes sessile. Numerous setæ on the neuropodia. *Polynoë scolopendrina* Sav. Ocean and Mediterranean.

Fam. **Eunicidæ**. Body very long, composed of numerous segments. Præstomium with several tentacles. Parapodia usually uniramous, rarely biramous, usually with ventral and dorsal cirri as well as branchiæ. One upper jaw composed of several pieces, and a lower consisting of two plates; both lie in a sac, the jaw-sack, on the dorsal surface of which runs the pharyngeal tube. *Staurocephalus vittatus* Gr., *Halla* (*Lysidice*) *parthenopeia* Delle Ch., Naples. *Diopatra neapolitana* Delle Ch., Naples. *Eunice Harassii* Aud. Edw.

Fam. **Nereidæ** = *Lycoridæ*.* The elongated body is composed of numerous segments. The præstomium has two tentacles, two palps, and four eyes. The parapodia are either uni- or bi-ramous, and are furnished with dorsal and ventral cirri and with composite setæ. Proboscis usually possesses spines, and always two jaws. *Nereis Dumerilii* Aud. Edw., French and English coasts, to which belongs *Heteronereis fucicola* Oerst. *N. cultrifera* Gr., Mediterranean. *N. fucata* Sav., North Sea. The form formerly distinguished as *Heteronereis* Oerst. differs from *Nereis* in the great size of the præstomium and of the eyes, also in the extraordinary development of the parapodia, and in the abnormal formation of the hinder end of the body. It belongs, however, to the same cycle of development as *Nereis* and *Nereilepas*.

Fam. **Glyceridæ**. Body slender, composed of numerous ringed segments. The præstomium is conical and ringed, with four small tentacles at its point and two palps at its base. The proboscis can be protruded to a great length, and is provided with four strong teeth. The hæmal fluid, coloured by red corpuscles, is contained in the body cavity and the branchial sinuses. There is no special vascular system. *Glycera capitata* Oerst., North Sea.

Fam. **Syllidæ**. Body elongated and flattened, head usually with three tentacles and two to four tentacular cirri. The protrusible proboscis consists of a short proboscis tube, a pharyngeal tube lined by stiff cuticular formations, and a portion characterised by annular rows of points. Sexual and asexual individuals, differing in form, are sometimes found in the same species. Many carry their eggs about with them until the young are hatched. *Syllis vittata* Gr., Mediterranean. *Odontosyllis gibba* Clap., Normandy. *Autolytus prolifer* O. Fr. Müll., asexual form. The male has been described as *Polybostrichus Mülleri* Kef., the female as *Sacconereis helgolandica* Müll. *Sphærodorum peripatus* Gr., Mediterranean.

Fam. **Alciopidæ** (*Alciopea*). With two large hemispherical projecting eyes. Ventral and dorsal cirri leaf-like. The proboscis is protrusible, the tube of the proboscis being thin walled and its terminal portion thick walled. At

* Compare E. Grube, "Die Familie der Lycorideen," *Jahresber. der Schlesischen Gesellschaft*, 1873.

its aperture are two hook-shaped papillæ. The larvæ are in part parasitic in the *Cydippidæ*. *Alciopa Cantraii* Delle Ch., Naples.

Fam. *Tomopteridæ* (*Gymnocopa*). Head well marked, two eyes, bifid præstomium, and four tentacles, of which two in many species are only present in the young. The mouth segment has two long tentacular cirri which are supported by a strong internal seta. The mouth is without proboscis and jaws. The segments are provided with large bi-lobed parapodia without setæ. *Tomopteris scolopendra* Kef., Mediterranean. *T. onisciformis* Esch., northern seas, Heligoland.

The genus *Myzostoma* F. S. Lkt., a small group of hermaphrodite worms whose affinities are doubtful and disputed, may be placed here. They are small, disc-shaped animals, parasitic on *Comatula*. They possess a soft and ciliated skin, four pairs of laterally placed suckers on the ventral surface, and a protrusible proboscis furnished with papillæ at their anterior end, also a branched alimentary canal which opens at the posterior end of the body. On the sides of the body are five pairs of short parapodia, of which each one bears a hook (with one to three supplementary hooks) as well as supporting setæ. As a rule, double as many cirri or short wart-like protuberances are found on the margin of the body. *M. glabrum, cirriferum* F. S. Lkt.

FIG. 308.—*Spirorbis lævis* (after Claparède). *a*, The animal removed from its tube, strongly magnified; *b*, tube; *T*, tentacles; *Bs*, brood-pouch with operculum; *Dr*, glands, *Or*, ova; *Oe*, œsophagus; *M*, stomach; *D*, intestine.

The branchiæ may be entirely absent and in many cases are confined to the two or three anterior segments following the head. In exceptional cases they are placed on the dorsal part of the middle of the body (*Arenicolidæ*). As a rule, however, they are represented by numerous filiform tentacles and ten-

Sub-order 2. *Sedentaria* = *Tubicolæ*.* With indistinctly separated head and short, usually not protrusible proboscis, without jaws.

* E. Claparède, "Recherches sur la structure des Annélides sédentaires." Genève, 1873.

tacular cirri upon the head (*Capitibranchiata*), of which one or more may bear an operculum at its apex to close the tube (fig. 308). The parapodia are short, and are never used in swimming; the notopodia usually carry hair-like setæ; the neuropodia are transverse ridges with hooked setæ or plates. Eyes are very frequently absent; in other cases they are present in pairs upon the head or on the terminal segment, sometimes even on the branchial tentacles; in the latter case they are very numerous. The body is often divided into two (thorax and abdomen) or three regions, the segments of which are distinguished by their unequal size. The *Tubicolæ* live in more or less firm tubes which they construct for themselves, and feed on vegetable matter which they procure by means of their tentacular apparatus. In the construction of their tubes the animals are assisted in various ways by the long tentacles or branchial filaments of the head; thus, for example, the *Sabellidæ* are said to accumulate fine ooze at the funnel-shaped base of the branchial apparatus by means of the cilia of their tentacles, to mix it with a cement secreted by large glands, and then to transfer it to the edge of the tube; while the *Terebellidæ* procure the grains of sand for the construction of their tubes by their long and very extensible tentacles. There are also boring Annelids, which pierce limestone and mussel shells, like the horny Molluscs; e.g., *Sabella saxicola*, etc.

The development is simplest when the mother possesses a kind of brood-pouch for the development of the young, e.g., *Spirorbis spirillum* Pag., the eggs and larvæ of which remain within a dilatation of the opercular stalk until the young animals are able to construct a tube for themselves. The free-swimming larvæ of most *Tubicolæ*, on assuming the form of the worm, lose the ciliary apparatus, while tentacles and parapodia make their appearance. In this condition and sometimes surrounded by delicate membranes, they swim about for some time longer, and, having lost their eyes and auditory vesicles, gradually assume the structure and mode of life of the sexual animal (*Terebella*).

Fam. **Saccocirridæ**. With two tentacles on the præstomium, two eyes and the same number of ciliated pits. A single row of retractile parapodia, furnished with simple setæ, on either side of the segments of the body. *Saccocirrus papillocercus* Bobr., Black Sea and Mediterranean (Marseilles).

Fam. **Arenicolidæ**. Præstomium small and without tentacles. The proboscis is beset with papillæ. There are branched gills on the median and posterior segments. The animals burrow in sand. *Arenicola marina* Lin. (*A. piscatorum* Lam.), North Sea and Mediterranean.

Fam. **Spionidæ** (*Spioideæ*). The small præstomium sometimes with tentacu-

lar processes, usually with small eyes. The oral segment mostly with two long tentacular cirri, which are usually grooved. Cirriform branchiæ are present. *Polydora antennata* Clap., Naples. *Spio seticornis* Fabr., north seas.

Fam. **Chætopteridæ**. Body elongated and separated into several dissimilar regions. Usually two or four very long tentacular cirri. Dorsal appendages of the middle segments have the shape of wings and are often lobed. They live in parchment-like tubes. *Telepsarus Costarum* Clap., Naples. *Chætopterus pergamentaceus* Cuv., West Indies.

Fam. **Terebellidæ**. Body vermiform and thicker anteriorly. The thinner posterior portion is sometimes distinctly marked off as an appendage destitute of setæ. The præstomium is indistinctly separate from the mouth segment. There is frequently a lip above the mouth. Numerous filiform tentacles, usually arranged in two tufts. There are pectinate or branched, rarely filamentous, gills on a few of the anterior segments. Dorsal prominences (notopodia) furnished with simple setæ, and ventral transverse ridges (neuropodia) with hooked setæ. *Terebella conchilega* Pall., English coast, Mediterranean. *Ampharete Grubei* Malmgr., Greenland and Spitzbergen. *Pectinaria auricoma* O. Fr. Müll., North Seas, Mediterranean. *Sabellaria (Hermella) spinulosa* R. Lkt., Heligoland.

Fam. **Serpulidæ**. Body usually distinctly divided into two regions (thorax, abdomen). Præstomium fused with the mouth segment, which as a rule is provided with a collar. The mouth is situated between two semicircular or spirally coiled plates, from the anterior margin of which spring the branchial filaments. These have secondary filaments arranged in single or double rows, and may be supported by a cartilaginous skeleton, and have their bases connected by a membrane. *Spirographis Spallanzanii*, Naples. *Sabella penicillus* Lin., North Seas. *S. Köllikeri* Clap., Mediterranean. *Protula Rudolphi* Risso, Mediterranean. *Filigrana implexa* Berk., Norwegian and English coasts. *Serpula norvegica* Gunn., North Sea and Mediterranean. *Spirorbis spirillum* Lin., Ocean.

Order 2.—OLIGOCHÆTA.*

Hermaphrodite Chætopoda without pharyngeal armature and parapodia. There are no tentacles, cirri, or branchiæ. The development is direct.

The cephalic region is composed of the præstomium, which projects as an upper lip, and the mouth segment. It does not essentially differ from the following segments so as to form a special region (fig. 309). Tentacles, palps, and tentacular cirri are never found on it, but tactile papillæ are present in great number, as are also peculiar sense organs which resemble taste buds. Eyes either fail or are present as simple pigment spots. Besides the small gland cells of the

* Besides the works of W. Hoffmeister, D'Udekem, and others, compare: E. Claparède, "Recherches anatomiques sur les Annélides, etc., observés dans les Hébrides," Genève, 1860. E. Claparède, "Recherches anatomiques sur les Oligochætes," Genève, 1862. A. Kowalevski, "Embryologische Studien an Würmern und Arthropoden (*Lumbricus*, *Euaxes*)," Petersburg, 1861. B. Hatschek, "Studien über Entwicklungsgeschichte der Anneliden," Wien, 1878. Fr. Vejdovsky, "Beiträge zur vergleichenden Morphologie der Anneliden. I. Monographie der Enchytræiden," 1879.

hypodermis there is present in the clitellus a deeper glandular layer (*Säulenschicht* Clap.), which consists of finely granular cells embedded in a framework of pigmented and vascular connective tissue and situated between the hypodermis and the external muscular layer. There are but few setæ present, and they are never disposed on special parapodia, but always in simple pits in the integument, by the cells of which they are secreted. There are small secondary bristles which serve as a reserve. The blood is usually red, as in the *Hirudinea*.

The **alimentary canal** is often divided into several regions, the relations of which are most complicated in the *Lumbricidæ*. In *Lumbricus*, the buccal cavity leads into a muscular pharynx, which is probably used for sucking. This is followed by a long œsophagus extending to the 13th segment, and furnished with a thick layer of glandular cells and several glandular dilated appendages (calcareous sacs). The œsophagus is succeeded by a crop, a muscular gizzard, and finally by the intestine itself, the dorsal wall of which is pushed inwards so as to form a longitudinal fold, the *typhlosole* (comparable to a spiral valve). In the *Limicolæ* the alimentary canal is simpler by the absence of a muscular stomach; a pharynx and œsophagus are, however, always present.

Reproduction.—The *Oligochæta* are hermaphrodite; they lay their eggs either singly or united in greater number in a capsule; and they develop without a metamorphosis. The testes and ovaries are paired and placed in definite segments, usually near the anterior end of the body; they dehisce their products into the body cavity. The generative ducts possess funnel-shaped openings into the body cavity through which the generative products pass, and may

FIG. 309.—*Lumbricus rubellus* (after G. Eisen). *a*, The whole worm; *Cl*, Clitellus. *b*, Anterior end of the body from the ventral side. *c*, Isolated seta.

co-exist in the same segment with segmental organs (*Lumbricidae*). In the earth-worm, whose generative organs were first accurately described by E. Hering, the female apparatus consists of two ovaries in the 13th segment,* and two oviducts, which begin with trumpet-shaped openings into the body cavity, contain several eggs in a dilatation and open to the exterior on either side on the ventral surface of the 14th segment. There are in addition in the 9th and 10th segments two pairs of receptacula seminis, which open at the junction of the 9th and 10th and 10th and 11th segment respectively. They are filled with sperm in copulation (fig. 310).

FIG. 310.—Generative organs of *Lumbricus* in segments VIII. to XV. (after E. Hering). *T*, Testes; *St*, the two funnels of the vas deferens on either side; *Vd*, vas deferens; *Ov*, ovary; *Od*, oviduct; *Rc*, receptacula seminis.

The male genital organs consist of two pairs of testes in the 10th and 11th segments, and two vasa deferentia, each of which opens internally by two funnels and to the exterior in the 15th segment. Copulation takes place in June and July on the surface of the earth at night. The worms apply their ventral surfaces to one another and lie

in opposite directions, in such a manner that the openings of the receptacula seminis of one worm are opposite the clitellus of the other. During copulation sperm flows out from the openings of the sperm duct and passes backwards in a longitudinal groove to the clitellus, and thence into the receptaculum seminis of the other worm. In *Tubifex* and *Enchytræus* the ovaries may break up into groups of ova which float free in the body cavity. Special albumen glands and also glands which secrete the substance of the shell of the cocoon are often present. In the breeding season the above-mentioned

* The head (præstomium and buccal region) being reckoned as the first segment.

girdle or clitellus, which is formed of a thick glandular layer, is almost always present.

The embryonic development of the *Oligochæta* presents many relations to that of the *Hirudinea*. The unequal segmentation, which is very much alike in the two groups, and the similarity in the method of origin of the mesoderm, from two large cells near the blastopore at the posterior end of the embryo, point to a close relationship between these two groups of Annelids.

A few *Oligochæta*, as for example *Chaetogaster*, are parasitic on aquatic animals; the rest of them live, some free in the earth, some in fresh water, and some in the sea.

Sub-order 1. **Terricolæ.** *Oligochæta* which live principally in the earth. They have segmental organs in the genital segments.

Fam. **Lumbricidæ.** Large earthworms with compact skin and red blood. Without eyes. Tufts of vessels surround the segmental organs. Their activity in boring into the earth is of the greatest importance, loosening and exposing the soil to the action of the weather. *Lumbricus* L., Earthworm. Præstomium distinct from the mouth segment. The clitellus includes a series of segments, and is situated nearly at the end of the anterior quarter of the body *far behind the genital openings*. Setæ elongated, hook-shaped, arranged in four groups in each segment, each group containing two setæ. The earthworm lays its eggs in capsules, into each of which several small ova, with sperm from the receptacula seminis, are emptied; as a rule, however, only one or but a few embryos are developed. The developing embryo takes up with its large ciliated mouth not only the common mass of albumen, but also the other eggs. *L. agricola* Hoffm. = *terrestris* Lin., *L. fætidus* Sav., *L. americanus* E. Perr. *Criodrilus lacuum* Hoffm.

Sub-order 2. **Limicolæ.** *Oligochæta* which live principally in water. Without segmental organs in the genital segments.

Fam. **Phreoryctidæ.** Long filiform worms, with thick skin and two rows of slightly curved setæ on each side. *Phreoryctes Menkeanus* Hoffm. Found in deep springs and wells; they seem to feed on the roots of plants.

Fam. **Tubificidæ.** Aquatic worms, provided with four rows of simple or divided, hooked setæ. Hair-like setæ may also be present. The receptacula are in the 9th, 10th, or 11th segment. They live in mud tubes, from which they protrude the posterior end of the body. *Tubifex rivulorum* Lam. The heart is in the 7th, the receptacula in the 9th segment. *T. Bonneti* Clap. (*Sænuris variegata* Hoffm.) The heart in the 8th, receptacula in the 10th segment; both species live in fresh water. *Limnodrilus Hoffmeisteri* Clap., *L. D'Udekemianus* Clap. Is distinguished from *Tubifex* by the absence of hair-like setæ in the upper row of setæ. *Lumbriculus variegatus* O. Fr. Müll. Every segment is provided with a contractile vascular loop and saccular contractile appendages of the dorsal vessel.

Fam. **Naïdæ.** Small *Limicolæ* with delicate thin skin and clear, almost colourless, blood. The præstomium is often elongated like a proboscis and

fused with the mouth segment. *Nais* (*Stylaria*) *proboscidea* O. Fr. Müll. *N. parasita* Schm. Both species have a filiform præstomium. *Chætogaster vermicularis* O. Fr. Müll.

Sub-class 2.—GEPHYREA.*

Worms with cylindrical body, without external segmentation, with terminal or ventral mouth; with cerebral ganglion, œsophageal ring and ventral cord. Setæ are sometimes present.

The *Gephyrea* possess an elongated cylindrical body and live, as do the *Holothuria*, in sand and ooze in the sea. The characters which distinguish them as Annelids are the possession of an œsophageal ring connected with a cerebral ganglion and of a ventral cord partially

surrounded by ganglion cells. The larvæ of the *Chaetifera* present traces of segmentation (see below, p. 391), while in the *Achata* the body cavity remains simple. Of *sense organs*, eye spots have been observed; these in certain *Sipunculidæ* lie directly upon the brain; there are also dermal papillæ, into which nerves enter.

The structure of the integument is similar to that of the *Annelida*; the thick upper cuticular layer rests upon a cellular matrix, and is not unfrequently wrinkled. There is no external segmentation. The connective tissue dermis is of considerable thickness and en-

FIG. 311.—Young *Echiurus* from the ventral side (after Hatschek). *O*, Mouth at the base of the proboscis; *SC*, œsophageal commissure; *BS*, ventral cord; *A*, anus; *H*, hooks.

closes numerous glandular tubes, which open to the exterior by pores in the epidermis. Below this is the strongly developed dermal muscular tunic, which is regularly composed of an outer layer of circular fibres

* Quatrefages, "Mémoire sur l'Echiure," *Ann. des Sc. Nat.*, 3 Sér., Tom VII. Lacaze-Duthiers, "Recherches sur le Bonellia," *Ann. des Sc. Nat.*, 1858. W. Keferstein, "Beiträge zur anatomischen und systematischen Kenntniss der Sipunculiden," *Zeitschr für wiss. Zoologie*, Tom XV., 1865. B. Hatschek, "Ueber Entwicklungsgeschichte des Echiurus," etc. Wien, 1880. J. W. Spengel, "Beiträge zur Kenntniss der Gephyreen. I. Mittheil. aus der zoologischen station zu Neapel, 1879; II. *Zeitschr. für wiss. Zool.*, Tom XIV., 1881.

and an inner layer of longitudinal fibres. The latter are connected with the former and also amongst themselves by net-like anastomoses. These dermal muscles cause the folds of the cuticle. Internally to the longitudinal muscles there is another layer of circular muscles. In the *Chaetifera* two hooked setæ are present near the genital opening (fig. 311); these assist locomotion. There may also be present one or two circles of setæ at the posterior end of the body (*Echiurus*).

In the *Chaetifera* (fig. 311), the anterior part of the body is elongated to form a kind of proboscis, which projects immovably and corresponds to the præoral lobe (præstomium) of the *Annelida*. The mouth is placed ventrally at the base of the proboscis. In the *Achaeta* (*Sipunculidæ*) this proboscis is wanting; the mouth is placed at the extremity of the anterior region of the body, which is surrounded with ciliated tentacles, and can be retracted by means of retractor muscles (fig. 312).

FIG. 312.—*Sipunculus nudus*, laid open from the side (after W. Keferstein). *Te*, Tentacles; *G*, cerebral ganglion; *VG*, ventral nerve cord; *D*, intestine; *A*, anus; *BD* brown tubes (ventral glands).

Alimentary canal.—The mouth opens into a pharynx, which is sometimes furnished with teeth; this is followed by a ciliated intestinal canal, which is usually longer than the body and disposed in coils in the body cavity. The terminal portion of the intestine is

muscular and opens to the exterior by a terminal or dorsally placed anus (fig. 312).

The **vascular system** is probably in communication with the body cavity; it consists of a dorsal vessel, which, as in the *Annelida*, accompanies the alimentary canal, and of a ventral vessel running along the body wall. There are also branches on the alimentary canal and in the tentacles. The blood is either colourless or red, and moves in the same direction as in the Annelids, the current being maintained both by the contraction of certain parts of the vessels and by the cilia which line the walls of the vessels. The corpusculated fluid of the body cavity differs from this vascular blood.

Excretory organs.—There are two sets of organs, both of which may be interpreted as segmental organs. One kind, the *anal vesicles* (fig. 314c, *Ab*), are only present in the *Chaetifera*; they have the form of a pair of tufted tubes, which open, on the one hand, into the body cavity by numerous ciliated funnels and, on the other, into the rectum. The other kind, known as the *brown tubes* (fig. 312, *Bd*) or ventral glands, are placed (one or more pairs) in the anterior part of the body; they also open into the body cavity by a ciliated funnel, and to the exterior on the ventral surface. The latter, like the segmental organs of Annelids, assume the function of seminal vesicles and of oviducts.

Generative organs.—The *Gephyrea* are of separate sexes. There are, however, remarkable variations both in the generative glands and their ducts. In *Phascolosoma* amongst the *Achaeta* (according to Théel) the generative glands lie at the root of the ventral retractor muscles of the proboscis, and form a ridge from which the generative products are set free. Spermatozoa or ova in various stages of development are found in the body cavity, and thence are carried to the exterior through the two brown tubes (segmental organs) which open on the ventral side.

In *Bonellia* among the *Chaetifera* the ovary, which has the form of a thin cord (fold of the body wall) in the posterior half of the body, is attached by a short mesentery to the nerve cord. From the ovary the ova fall into the body cavity, and thence pass into the neighbouring single uterus (fig. 314, *b*, *U*), which is provided at its base with a trumpet-shaped opening (*Tr*) and opens to the exterior on the ventral surface behind the mouth. This uterus ought probably to be considered morphologically as a segmental organ, which has only been developed on one side. The generative organs of the small Turbellarian-like males which are met with in the uterus of

the female of *Bonellia* have the same relations (fig. 313). These rudimentary males are furnished (in many species) with two ventral hooks, in front of which in the anterior region is placed the external opening of the vas deferens. The vas deferens corresponds to the uterus of the female, and is in like manner provided with an internal opening into the body cavity. In *Echiurus* there are two pairs of brown tubes, which function as generative ducts and reservoirs. In *Thalassema* there are, according to Kowalevski, three pairs of such tubes.

The development shows many points of similarity with that of the *Annelida*. Between the *Achæta* and *Chætifera*, however, there are considerable differences. In both cases a metamorphosis follows the embryonic development. The larvæ resemble Lovén's larva (larva of *Polygordius*); but in the *Achæta* they are characterised by a great degeneration of the apical region (præoral lobe) and the absence of a præoral band of cilia.

The remarkable larva known as *Actinotrocha*, which is the young stage of the tubicolous genus *Phoronis*,* is distinguished by the possession of a contractile præoral lobe, behind which there is a circle of ciliated tentacles forming a collar.

The *Gephyrea* are all marine. Some of them live in sand and ooze at considerable depths, also in holes in the rocks and in crevices between stones and corals, and in the shells of snails. Their food is similar to that of *Holothurians* and many tubicolous *Annelids*.

Order 1.—CHÆTIFERA = ECHIUROIDEA.

Gephyrea characterised by the presence of two strong hooked setæ on the ventral side and by a terminal anus. The mouth is placed at the base of the præoral lobe, which is developed into a proboscis.

The *Echiuroidea* or chætiferous *Gephyrea* present no external segmentation of their elongated and contractile body; they have, however, in the young state the rudiments of 15 metameres. This

* There should be a third order of *Gephyrea* for these animals.

FIG. 313.—Planarian-like male of *Bonellia* (after Spengel). D. Intestine; WT, ciliated funnel of the vas deferens (Vd), which is filled with sperm.

fact, as well as the formation of the præoral lobe and the development of the ventral hooked setæ, points to a close relationship with the *Chaetopoda*. In the adult animal, however, the internal segmentation is very little marked. The dissepiments, with the exception of the first, which forms a partition between the head and the body, are lost, and the segmentation of the ventral cord is only indicated by the distribution of the nerves. The supra-oesophageal ganglion remains at the apical region of the præoral lobe (proboscis); hence the oesophageal commissures are extraordinarily long.

The strongly developed præoral lobe forms a proboscis-like

FIG. 314.—*a*, female of *Bonellia viridis* (after Lacaze-Duthiers). *b*, Integument and generative organs after the intestine has been removed. *Hd*, Cutaneous glands; *Ab*, anal vesicle; *Ad*, rectum; *Ov*, ovary; *Tr*, ciliated funnel of the uterus (*U*). *c*, Anatomy of *Bonellia viridis* (after Lacaze-Duthiers). *D*, alimentary canal with anal vesicles (*Ab*); *M*, mesentery; *U*, uterus; *R*, proboscis.

appendage which may develop to a considerable length and become forked (*Bonellia*) (fig. 314 *a*).

A pair of hooked setæ (with reserve setæ in the sheath of each seta) are always present on the first segment of the body. In *Echiurus* there are also one or two circles of setæ at the posterior end of the body. There are from one to three pairs of anterior segmental organs (so-called brown tubes or ventral glands), which open on the ventral surface and are used for the passage outwards of the generative products. Besides these there is also a pair of

posterior segmental organs (anal vesicles, fig. 314, *Ab*) in the terminal segment, each of which has a number of peritoneal funnels and opens into the rectum. In *Bonellia* the segmental organ which performs the function of uterus is, like the ovary, single (fig. 314 *b*).

Development.—The development of the ovum begins with an unequal segmentation. In *Bonellia* the small cells of the animal pole grow round the four large yolk spheres, which give rise to the entoderm, leaving a small aperture, the blastopore (fig. 110). The *Echiurus* larvæ (fig. 315) are the most accurately known. They present the type of Lovén's larva and possess a strongly developed

FIG. 315.—*a*, Larva of *Echiurus* from the ventral side (after Hatschek). *SP*, apical plate; *Prw*, præoral circle of cilia; *Pow*, postoral circle of cilia; *Kn*, head-kidney; *Vg*, ventral ganglionic cord connected with the apical plate by the long oesophageal commissures; *AS*, anal vesicle. *b*, Ventral region of the *Echiurus* larva with segmented mesodermal bands; *SC*, oesophageal commissure; *Dsp*, dissepiments of the anterior body segments; *MS*, mesodermal bands; *A*, anus.

præoral circle of cilia (*Prw*), in addition to which there is also a delicate post-oral circle of cilia (*Pow*). Early in larval life a segmental organ, the head kidney or pronephros (*KN*), is developed, one on either side; and behind it a pair of mesoblastic bands makes its appearance and gives rise in the subsequent development to the rudiments of 15 segments (fig. 315 *b*). In the terminal segment, which is surrounded by a circle of cilia, there appear segmental

organs, which give rise to the anal vesicles (fig. 315 *a*, *AS*). The rudiments both of the cerebral ganglion and of the ventral cord are derived from growths of the ectoderm,—the former from the apical plate, the latter as a paired thickening of the ventral ectoderm. The two are connected by the œsophageal ring, which is also provided with ganglion cells. In older stages, after the disappearance of the segments, the ciliary apparatus begins to degenerate and finally vanishes; after which two strong hooked setæ make their appearance at the sides of the nerve cord not far from the mouth, and

FIG. 316.—Older *Echiurus* larva seen from the side. The head kidney is atrophied. *O*, mouth; *M*, stomach; *A*, anus; *BK*, circles of setæ; *SC*, œsophageal commissure; *AS*, anal vesicles; *G*, cerebral ganglion, developed from the apical plate; *Vg*, ventral nerve cord; *H*, ventral hooks.

two circles of shorter setæ are formed at the hind end of the body (fig. 316). The præoral lobe of the larva becomes the proboscis of the young *Echiurus* (fig. 311).

Fam. *Echiuridæ*. The anterior end of the body above the mouth is elongated into a proboscis, the under surface of which is grooved. The long œsophageal commissures lie in the proboscis, and meet in front without any cerebral enlargement. Anteriorly and on the ventral side are two setæ for attachment, and on the posterior end of the body there are sometimes circles of setæ. The anus is terminal. *Echiurus Pallasii* Guérin (*Gaertneri* Quatref., St. Vaast), coast of Belgium and England. *Thalassema gigas* M. Müll., Italian coast. *Bonellia viridis* Rolando, Mediterranean. The males are small and rudimentary, and resemble Planarians. They live in the efferent ducts of the female generative organs.

Order 2.—ACHÆTA=SIPUNCULOIDEA.

Gephyrea with terminal mouth, dorsally placed anus, and without setæ. The anterior region of the body is retractile.

The *Sipunculoidea* differ from the chaetiferous *Gephyrea* in their entire want of all traces of metameric segmentation, in the degeneration of the præoral lobe and in the position of the mouth and anus.

The elongated body is destitute of a projecting præoral lobe, so that the mouth, which is frequently surrounded by a circle of tentacles, comes to be placed at the anterior end of the body. On the other hand, the anus is moved far forward on the dorsal surface (fig. 317).

The cerebral ganglion, oesophageal ring and ventral cord run inside the dermal muscular tunic. Only one pair of segmental organs, known as brown tubes or ventral glands, is present. The blood vascular system is well developed.

Development.—The segmentation is complete and is followed by the formation of a gastrula by invagination. The blastopore marks the ventral side. The two posterior marginal cells* of the entoderm move inwards as primitive mesoderm cells, and give rise to the mesoblastic bands which do not undergo segmentation. Invaginations of the ectoderm of the animal pole and ventral sur-

FIG. 316.—Larva of *Sipunculus* (after Hatschek). *O*, Mouth; *Sp*, apical plate; *A*, anus; *PoW*, postoral circle of cilia; *N*, kidney.

FIG. 317.—Quite young *Sipunculus* still without tentacles (after B. Hatschek). *O*, mouth; *A*, anus; *Bs*, ventral cord; *N*, nephridium (brown tube); *G*, cerebral ganglion; *Bg*, blood vessel.

face of the embryo give rise to cephalic and ventral plates respectively, while the remainder of the ectoderm cells

grow round these and form an external envelope for the embryo of the nature of a serous membrane (serosa). Cilia project from the latter through the pores of the vitelline membrane and are employed by the embryo in swimming.

The cephalic and ventral plates soon grow together. The mesodermal bands split into somatic and

* Compare especially B. Hatschek.

splanchnic layers, and give rise to the rudiments of the two segmental organs; while the œsophagus arises as an invagination of the ectoderm, and a postoral circle of cilia is formed around its opening (fig. 318). The serous membrane is cast off with the egg membrane, and the larva then contains all the essential organs of the adult *Sipunculus* except the ventral cord and the blood-vessels. At a later stage, during the growth of the larva, the ventral cord is developed from the ectoderm, the circle of cilia disappears, the first tentacles sprout out at the edge of the mouth, and the metamorphosis of the free-swimming larva into the creeping young *Sipunculus* is completed.

Fam. *Sipunculidæ*. Body elongated and cylindrical, the anterior part retractile. The mouth is surrounded with tentacles, and the anus is dorsal. The intestine is coiled spirally. *Sipunculus nudus* L., Mediterranean. *Phascolosoma læve* Kef., Mediterranean. *Ph. elongatum* Kef. St. Vaast.

Fam. *Priapulidæ*. Anterior part of the body without circle of tentacles. Pharynx armed with papillæ and rows of teeth. Anus at the posterior end of the body and slightly dorsal, above it there usually projects a caudal appendage which bears papilla-like tubes (branchiæ). The intestine is straight. *Priapulus caudatus* O. Fr. Müller. *Halieryptus spinulosus* v. Sieb., Baltic, Spitzbergen.

Sub-class 3.—HIRUDINEA* = DISCOPHORA, LEECHES.

Body either with short rings or not ringed, without parapodia, with terminal ventral sucker, hermaphrodite.

The body of the *Hirudinea*, so far as its external form is concerned, recalls that of the *Trematoda*, with which group the *Hirudinea* have often been incorrectly connected.

Externally the body is marked by a number of transverse rings, which are short and may be more or less indistinct or even entirely absent. These rings correspond in no way with the internal segments, which are separated by transverse partitions or dissepiments; but they constitute much shorter portions of the body, four or five of them corresponding to one internal segment. The large sucker at the posterior end of the body serves as an organ of adhesion; and there may be in addition a second smaller sucker, either in front of or

* Brandt and Ratzeburg, "Medicinische Zoologie," 1829. Moquin-Tandon, "Monographie de la famille des Hirudinées," 2nd. édit., Paris, 1846. Fr. Leydig, "Zur Anatomie von Piscicola geometrica," *Zeitschr. für wiss. Zool.*, Tom. I., 1849. H. Rathke, "Beiträge zur Entwicklungsgeschichte des Hirudineen," edited by R. Leuckart, Leipzig, 1862. R. Leuckart, "Parasiten des Menschen," Bd. I., Leipzig, 1863. Van Beneden et Hesse, "Recherches sur les Bdelloïdes ou Hirudinées et les Trématodes marins," 1863. Robin, "Mémoire sur le développement embryogénique des Hirudinées," Paris, 1875.

surrounding the mouth. There are no parapodia; and setæ, with a few exceptions, are absent. A sharply distinct head is never developed, since the first rings are not essentially different from those following and are never furnished with tentacles or cirri.

Alimentary canal.—The mouth is situated near the anterior end of the body, sometimes at the bottom of a small anterior sucker (*Rhynchobdellidæ*), sometimes at the base of a projecting spoon-shaped hood, which resembles a sucker (*Gnathobdellidæ*) (fig. 319). The mouth leads into a muscular pharynx provided with glands. The anterior part of the pharynx, which may be distinguished as the buccal

cavity, is armed (*Gnathobdellidæ*) with three serrated chitinous plates (fig. 319, *a*, *b*), or more rarely with a dorsal and ventral plate (*Branchiobdellidæ*), or it is provided with a protru-

FIG. 319.—*a* Cephalic region of the Medicinal Leech. The three jaws are visible. *b*, One of the jaws isolated with the finely serrated free edge.

sible proboscis, which lies free in its anterior part (*Rhynchobdellidæ*). The pharynx leads into a stomach, which forms a straight tube in the axis of the body and sometimes shows constrictions, which correspond with the segments; sometimes it is produced into a larger or smaller number of lateral cæca. From the stomach a short rectum, which is sometimes also provided with cæca, leads to the anus. The anus is placed at the posterior pole of the body, dorsal to the sucker.

Excretory organs.—Segmental organs are present, one pair to each segment in the middle region of the body. Their number, however,

FIG. 320.—Longitudinal section through the Medicinal Leech (after R. Leuckart). *D*, intestinal canal; *G*, cerebral ganglion; *Gk*, ganglionic chain; *Ex*, excretory canals or segmental organs (water-vascular system).

varies very considerably, since, for instance, *Branchiobdella astaci*, parasitic on the gills of the cray-fish, has but two pairs, while the *Gnathobdellidae* usually possess seventeen pairs.

Unicellular glands are present in the Hirudinea in great numbers in the skin and in the deeper layers of the connective tissue. The former secrete a finely granular mucous fluid, which covers the skin; while the more deeply situated glands, which lie beneath the dermal muscular tunic, secrete a clear viscid substance, which quickly

hardens outside the body and is used to form the cocoons when the eggs are laid. These glands are especially numerous in the region of the genital openings.

A blood-vascular system is always present, but in different degrees of development. Portions of the body cavity are transformed into vessel-like trunks, and as a result of this organs which lie in the body cavity seem to be enclosed in blood sinuses. The two lateral vessels and the median blood sinus, which always encloses the ventral ganglionic chain and sometimes also the alimentary canal (*Clepsine*, *Piscicola*), may be interpreted in this manner. In most of the *Gnathobdellidae* the blood is red, the colour being due to the fluid part of the blood and not to the corpuscles.

Special respiratory organs are wanting, excepting in *Branchellion* and some allied leeches, which possess leaf-like branchial appendages.

The nervous system* in all cases is highly developed. The

FIG 321.—Anterior end of *Hirudo* (after Leydig). *G*, Cerebral ganglion with suboesophageal ganglionic mass; *Sp*, sympathetic; *A*, eyes; *Sb*, sense organs.

cerebral ganglia are characterized by a peculiar arrangement of the nerve cells which give rise to swellings on the surface of the ganglia (described by Leydig as a follicular arrangement) (fig. 321).

* Hermann, "Das Centralnervensystem von *Hirudo medicinalis*," München, 1875.

This is also the case with the ganglia of the ventral cord, and especially with the sub-œsophageal ganglia, on which there are often four longitudinal series of such ganglionic swellings, two median and ventral, and two lateral projecting dorsally. The two longitudinal trunks of the ventral ganglionic chain are invariably closely approached to one another in the middle line, and their ganglia are connected together in pairs by transverse commissures. In the *Gnathobdellidæ* two nerve trunks are given off to the right and left from each pair of ganglia, while from the brain and the last ganglion, which may be called the caudal ganglion and is formed of several ganglia fused together, a much greater number of nerves pass off. The nerves passing off from the brain supply the sense organs and the muscles and skin of the cephalic disc (anterior sucker); the nerves of the ventral chain are distributed in their proper segments, and those of the terminal ganglion supply the ventral sucker. An unpaired median longitudinal cord (Faivre, Leydig), which passes from ganglion to ganglion between the two halves of the ventral cord, most probably corresponds to the unpaired nerve which Newport discovered in insects. A system of visceral nerves was discovered by Brandt. It consists of an intestinal nerve, which arises from the brain and runs close to and above the ganglionic chain and sends branches to supply the cæca of the intestine. Three ganglia, which in the common leech lie in front of the brain and send their nerve plexuses to the jaws and pharynx, are considered by Leydig as enlargements of cerebral nerves and very likely control the movements which occur in swallowing.

Almost all leeches possess simple eyes on the dorsal surface of the anterior ring. In addition there are cup-shaped organs (in *Hirudo medicinalis* about sixty) on the cephalic rings. These probably give rise to a sense perception comparable to the sensation of taste.

Generative organs.—The *Hirudinea* are hermaphrodite. As in many marine *Planaria*, the openings of the male and female generative organs are placed one behind the other in the middle

FIG. 322. — Generative apparatus of the Medicinal Leech. *T*, Testis; *Vd*, vas deferens; *Nh*, epididymis; *Pr*, prostate; *C*, cirrus; *Ov*, ovaries with vagina and female genital opening.

line of the anterior region of the body. The male generative opening lies in front of the female and is usually provided with a protrusible cirrus. The testes lie in pairs in several successive segments and are usually present in considerable numbers (fig. 322). In *Hirudo* there are nine or ten pairs of testicular vesicles, which are connected with a sinuous vas deferens on either side. Each vas deferens is coiled in front to form a kind of epididymis (fig. 322, *Nh*) and is then prolonged into a muscular portion, the ductus ejaculatorius, which unites with that of the other side to form an unpaired copulatory apparatus. This is in connection with a well-developed prostatic gland (*Pr*), and can be protruded either as a two-horned sac (*Rhyncobdellidæ*) or as a long filament (*Gnathobdellidæ*). The female generative apparatus consists either of two long tubular ovaries with a common opening to the exterior (*Rhyncobdellidæ*), or of two short

FIG. 323.—*a*, Cocoon, *b*, female generative apparatus of *Hirudo medicinalis* (after R. Leuckart).

saccular ovaries, two oviducts, a common duct surrounded by an albumin gland, and a dilated vagina with the genital opening (*Gnathobdellidæ*) (fig. 323). In copulation a *spermatophore* passes out of the male genital organs, and is either received into the vagina of the other animal or at least becomes attached within the generative opening. In any case the fertilization of the ovum takes place within the body of the mother. The egg is laid soon after. For this purpose

the animals seek suitable places on stones or plants, or leave the water and, as *Hirudo medicinalis*, burrow in damp earth. At this period the genital rings are swollen out into the form of a saddle, partly by the turgescence of the generative organs and partly by the great development of the cutaneous glands, the secretion of which is of special importance to the fate of the eggs which are about to be laid. When the eggs are about to be laid, the leech attaches itself firmly by its ventral sucker and, twisting itself about, envelops the anterior part of its body with a viscid mass, which covers especially the genital rings like a girdle and gradually hardens to form a firmer membrane. A number of small eggs and a considerable quantity of albuminous matter then pass out, and the animal with-

draws its anterior end from this barrel-shaped membrane, which is now filled and which, after the animal has left it, becomes in consequence of the narrowing of the terminal openings a tolerably completely closed cocoon. The number of eggs contained in a cocoon varies but is never large. The eggs are small, yet the young leeches when hatched are of considerable size, those of the *Hirudo medicinalis*, for example, are about 17 mm. long, and, excepting the fact that they are not sexually mature, have essentially the organization of the adult animal. The young of *Clepsine* alone are hatched at a very early stage, and differ essentially from the sexual animal both as regards the shape of the body and the internal organisation. They have a simple intestine, are without the posterior sucker, and live a long time attached to the ventral surface of the mother; and it is not until they have received a considerable quantity of newly secreted albuminous matter that they obtain an organization which fits them to lead a free life.

The development of the embryo of *Clepsine* among the *Rhyncobdellidæ* and *Nephelis* and *Hirudo* amongst the *Gnathobdellidæ* is better known. The segmentation is always unequal. The mouth is formed early, and through it, after the formation of the pharynx and intestinal canal, the albumen contained in the cocoon is taken into the intestine of the growing embryo by means of swallowing movements of the pharynx.

The Leeches live for the most part in water or temporarily in damp earth. They move partly by "looping" with the help of their suckers, and partly by swimming with active undulations of the usually flattened body. Many of them are parasitic on the skin or the gills of aquatic animals, *e.g.*, on fishes and the cray-fish; most of them, however, are only occasional parasites on the outer skin of warm-blooded animals. Certain forms are predaceous and, as for example *Aulastomum gulo*, eat snails and earthworms, or, like *Clepsine*, suck snails. They do not feed exclusively on any special genus of animals, and their diet is not always the same in the different periods of their existence. *Hirudo medicinalis* in its young stage lives on the blood of insects, then on that of frogs, and only when it has attained sexual maturity is a diet of warm blood necessary to it.

Fam. *Rhyncobdellidæ*. Leeches with proboscis. Body elongated, cylindrical, or broad and flat; with an anterior and posterior sucker, and a powerful protrusible proboscis in the buccal cavity; with paired eyes on the anterior sucker. Organs concerned in the formation of blood corpuscles occur (so-called valves) in the dorsal contractile vessel. *Piscicola Blainv.* (*Ichthyobdellidæ*). *P. geometra* L., on fresh water fish. *P. respirans* Tr., with lateral vesicles which dilate as

the blood enters. *Pontobdella muricata* L., on Rays. *Branchellion torpedinis* Sav., *Clepsine* Sav., (*Clepsinidæ*), *Cl. bioculata* Sav., *Cl. complanata* Sav., *Cl. marginata* O. Fr. Müll. *Hæmentaria mexicana* de Fil., *H. officinalis* de Fil., both in the Lagunes of Mexico, the latter used for medicinal purposes. *H. Ghilanii* de Fil., in the river Amazon.

Fam. *Gnathobdellidæ*. Leeches with jaws. Pharynx armed with three frequently serrated jaws, and folded longitudinally. In front of the mouth there is a ringed, spoon-shaped process, which forms a kind of oral sucker. The cocoon has a spongy shell. *Hirudo* L. Usually with 95 distinct rings, of which four are upon the spoon-shaped upper lip. The three anterior rings, the fifth and the eighth, bear the five pairs of eyes. The male genital opening lies between the 24th and 25th, the female between the 29th and 30th rings. The three jaws are finely serrated and can be moved like a circular saw in a manner well adapted to inflict a wound, which readily heals, in the external skin of man. The stomach has eleven pairs of lateral cæca, of which the last pair is very long. The cocoons are deposited in damp earth. *H. medicinalis* L., with the variety distinguished as *officinalis*, possesses 80 to 90 fine teeth on the free edge of the jaws and attains a length of about six inches. They were formerly common in Germany and are still frequently to be found in Hungary and France. They are cultivated in special ponds and take three years to attain sexual maturity. *Hæmopsis vorax* Moq. Tand, the horse-leech. 30 coarse teeth on the edge of the jaws, which enable it to inflict wounds on soft mucous membranes. The horse-leech is indigenous in Europe, and especially North Africa. It attaches itself to the interior of the pharynx of horses, cattle and men. *Aulastomum gulo* Moq. Tand. Also known as the horse-leech, feeds on Mollusca. *Nephelis* Sav., *N. vulgaris* Moq. Tand.

Fam. *Branchiobdellidæ*. The body in the extended condition is nearly cylindrical and is composed of few unequally ringed segments. There is a bilobed cephalic lobe without eyes, with a well-developed sucker at the posterior end of the body. Pharynx without proboscis, with two flat jaws lying one above the other. *Branchiobdella parasita* Henle, *B. astaci* Odier.

CLASS IV.—ROTATORIA* = ROTIFERA.

With a retractile ciliated apparatus at the anterior end of the body, with cerebral ganglion and excretory canals; without heart or true vascular system. The sexes are separate.

The *Rotifera* are Worms which can be derived from Lovén's larva and have nothing to do with the *Arthropoda*, since they are without limbs and do not develop metameres. The body of the *Rotifera* is certainly externally segmented and divided into more or less sharply

* Ehrenberg, "Die Infusionsthierchen als vollkommene Organismen," Leipzig, 1838. Dujardin, "Histoire naturelle des Infusoires," Paris, 1841. Dalrymple, *Phil. Trans. Roy. Soc.* 1844. Fr. Leydig, "Ueber den Bau und die systematische Stellung der Rädertiere," *Zeitschr. für wiss. Zool.*, Bd. VI., 1854. F. Cohn, "Ueber Rädertiere," *Zeitschr. für wiss. Zool.*, Bd. VII., 1856, Bd. IX., 1858, Bd. XII., 1862. Gosse, "On the Structure, Functions and Homologies of the Manducatory Organs of the class Rotifera," *Phil. Trans.*, 1856. W. Salensky, "Beiträge zur Entwicklungsgeschichte des *Brachionus urceolaris*," *Zeitschr. für wiss. Zool.*, Tom. XXII., 1872.

defined and very dissimilar regions, but the internal organs show no trace of any corresponding segmentation. There is therefore no true segmentation, *i.e.*, division of the body into metamereres. It is usually possible to distinguish an anterior region of the body, in which the whole of the viscera are situated, and a posterior movable foot-like region, which terminates in two opposed pincer-like styles and is used both in locomotion and for attachment. The broad anterior portion of the body, as well as the narrow posterior region, is often divided by transverse constrictions into several rings, which can be drawn into one another like the rings of a telescope and can be bent more or less freely upon one another.

The anterior ciliated and usually retractile apparatus which projects at the anterior end, and is termed the *trochal disc*, or from its likeness to a rotating wheel, the *wheel organ*, is an important characteristic of the *Rotifera*. Very frequently, especially in the parasitic forms, this trochal disc is reduced, and in certain cases entirely aborted (*Apsilus*). In *Notomata tardigrada* the trochal disc is reduced to a small ciliated

lip round the mouth; in *Hydatina* (fig. 324) to the margin of the head, the whole circumference of which is ciliated. In other cases the ciliated edge projects over the head and forms the so-called double wheel, *e.g.*, *Philodina*, *Brachionus*, or becomes a ciliated cephalic shield, *e.g.*, *Megalotrocha*, *Tubicolaria*. Finally, it may be produced into ciliated processes of various form (*Floscularia*, *Stephanoceros*). As a rule, the cilia form a continuous border, starting from the mouth and returning to it. The cilia are chiefly

FIG 324.--*Hydatina senta* (after F. Cohn). *a*, Female; *b*, male. *Wpr*, Trochal disc; *Cbl*, contractile vesicle; *Wtr*, ciliated funnel of the excretory apparatus (*Ex*); *K*, jaws; *Dr*, salivary glands; *Md*, stomach, *Ov*, ovary; *T*, testis; *P*, penis.

concerned in locomotion, but in addition they play an important part in attracting small particles of food. There is also a second row of delicate vibratile cilia, extending on either side from the dorsal edge of the trochal disc to the mouth [parts of the continuous border of cilia just mentioned as starting from the mouth], which is placed on the ventral side of the trochal disc. These cilia serve to guide the small food particles which are captured by the trochal disc into the mouth.

Alimentary canal.—The mouth leads into a dilated pharynx (fig. 324), provided with a special armature. The parts of the armature are in continual movement, and serve for mastication. Following the pharynx there is a short œsophageal tube; this leads into the digestive sac, which is lined with large ciliated cells. The anterior or gastric part of this cavity is wide, and receives two large glandular tubes, which may sometimes be resolved into unicellular glands. They may be explained from their function as salivary or pancreatic glands. The posterior narrow intestinal part usually opens into a cloacal chamber, which is likewise ciliated and opens on the dorsal surface at the point where the foot-like posterior region joins the anterior part of the body. In some *Rotifera*, as for example *Ascomorpha*, *Asplanchna*, the intestine ends blindly.

A **blood-vascular system** is always wanting, and the body cavity is filled with a clear vascular fluid. The structures, erroneously described by Ehrenberg as vessels, are in reality the transversely striped muscles and muscular networks beneath the integument.

Respiration is carried on by the general surface of the body; special organs of respiration are wanting.

Excretory organs.—The so-called respiratory canals are excretory, and correspond to segmental organs. They consist of two sinuous longitudinal canals with cellular walls and with fluid contents, and they communicate with the body cavity by ciliated funnel-shaped openings placed at the end of short ciliated lateral branches (vibratile organs). They open into the cloaca either directly or by means of a contractile vesicle (respiratory vesicle).

The **nervous system** is allied to that of the Platyhelminthes. The central part of it consists of a simple or bi-lobed cerebral ganglion placed above the œsophagus, and giving off nerves to peculiar cutaneous sense organs and to the muscles. Eyes are often present, and lie upon the brain either as an x-shaped unpaired pigment body or as paired pigment spots provided with refractile spheres. The above-mentioned cutaneous sense organs, which are probably tactile, have

the form of prominences beset with hairs and setæ, or even of tubular elongated processes of the skin (respiratory organs of the neck), beneath which the sensory nerves end in ganglionic swellings.

Generative organs.—The sexes are separate, and are distinguished by a strongly marked dimorphism. The very small males have neither œsophagus nor intestinal canal, which are reduced to a string-like rudiment; and they leave the egg completely developed. Their generative organs are reduced to a testicular sac filled with spermatozoa, the muscular duct of which opens at the hinder end of the body, sometimes on a papilliform protuberance. The generative organs of the females, which are far larger than the males, consist of a roundish ovary filled with developing ova, and of a short oviduct which contains one or but few ripe ova, and usually opens into the cloaca. Almost all *Rotifera* are oviparous; and their eggs are distinguishable into thin-shelled *summer eggs* and thick-shelled *winter eggs*. They carry both kinds of eggs about on their body, but the summer eggs not unfrequently undergo their embryonic development in the oviduct. The summer eggs probably develop parthogenetically, since at the season of the year when they appear the males are not to be found. The thick-shelled winter eggs, which are often dark coloured, are produced in the autumn and fertilized.

Development.—As far as the embryonic development is known, it shows a great agreement with that of many *Gasteropoda* (*Calyptrea*). The ova undergo an irregular segmentation. The cells proceeding from the smaller segmentation spheres become accumulated at one pole, and finally enclose the darker coloured yolk cells completely, so that a two-layered embryo is formed. The cells of the outer layer are much poorer in granules than are those of the central entoderm layer, and form the ectoderm. A depression of the ectoderm is formed on the (later) ventral surface, from the side walls of which the two lobes of the trochal disc grow out (like the oral lobes of mollusc embryos). The hinder portion of the depression becomes the posterior part of the body, at the base of which a pit forming the first rudiment of the cloaca makes its appearance. The mouth and the anterior part of the alimentary canal are developed anteriorly at the bottom of the depression. The ganglion arises from the ectoderm in the cephalic region. There are no reliable observations on the formation of the mesoblast. In the male embryo the development takes a different course, the alimentary canal not being completely developed. The free development takes place either

without or with an inconsiderable and sometimes retrogressive metamorphosis. This latter is most striking in the *Floscularidæ*, which are fixed in the adult state.

The *Rotifera* principally inhabit fresh water, in which they swim about by means of the trochal disc, and sometimes they attach themselves to foreign objects by means of the forked glandular foot. When thus attached, they extend the anterior part of the body, and the cilia begin to move. The currents set up by the latter convey to the mouth food material, such as small Infusoria, Algæ, Diatoms. Some species live in gelatinous sheaths and delicate tubes, others (*Conochilus*) are fixed by their foot in a common gelatinous mass, and are united to form a free-swimming colony. A relatively small number are parasitic. It seems that many species are able to endure drying, if it be not too prolonged.

Fam. Floscularidæ. Fixed *Rotifera* with a long transversely ringed foot, usually surrounded by gelatinous coverings and tubes. The margin of the head has a lobed or deeply cleft wheel-organ. *Floscularia proboscidea* Ehrbg., *Stephanoceros Eichhornii* Ehrbg., *Tubicolaria najas* Ehrbg., *Melicerta ringens* L., *Conochilus volvox*, Ehrbg.

Fam. Philodinidæ. Free, often creeping (in a looping manner) *Rotifera*; with double-wheeled rotatory organ, and jointed, telescopically retractile foot, without gelatinous investment. *Callidina elegans* Ehrbg., *Rotifer vulgaris* Oken (*R. redivivus* Cuv.), *Philodina erythrophthalma* Ehrbg.

Fam. Brachionidæ. *Rotifera* with bifid or multifid wheel-organ; with broad, shield-shaped armoured body; and foot ringed, or with short segments. *Brachionus Bakeri* O. Fr. Müll., *B. militaris* Ehrbg., *Euchlanis triquetra* Ehrbg.

Fam. Hydatinidæ. Edge of wheel-organ prolonged into numerous processes (multifid) or only sinuous; skin delicate, often ringed; foot short, usually forked, with two setæ or pincer-shaped. *Hydatina* Ehrbg., *H. senta* O. Fr. Müll. with *Enteroplea hydatinæ* Ehrbg., as male. *Notommata tardigrada* Ldg., *N. Brachionus* Ehrbg., *N. parasita* Ehrbg.

Fam. Asplanchnidæ. The sac-like unarmoured body is destitute of rectum and anus. *Asplanchna Sieboldii* Ldg., *A. myrmeleo* Ehrbg., *Ascomorpha germanica* Ldg.

Two groups of small animals are allied to the *Rotifera*:—(1) the **Echinoderidæ** which Dujardin and Greef regarded as connecting links between *Vermes* and *Arthropoda* (*Echinoderes Dujardinii* Clap., *E. setigera* Greef); and (2) the **Gastrotricha** * or *Ichthydina* (*Chaetonotus*).

* Compare *E. Metschnikoff*, "Ueber einige wenig bekannte niedere Thierformen," *Zeitschr. für wiss. Zool.*, Tom. XV., 1865. Also the works of H. Ludwig and O. Bütschli.

CHAPTER X.

ARTHROPODA.

Laterally symmetrical animals with heteronomously segmented body and jointed segmental appendages ; with brain (supraesophageal ganglia) and ventral nerve cord (ganglionic chain).

The most important characteristic which distinguishes the *Arthropoda* from the closely allied segmented worms, and is an essential condition of a higher organization and grade of life, is the possession of jointed segmental appendages which serve as organs of locomotion. In place of the unjointed parapodia of the *Chaetopoda*, jointed appendages more adapted for locomotion and confined to the ventral surface, are present. Every segment may possess a ventral pair of appendages which, in the simplest case, are short and consist of only a few joints (*Peripatus*) (fig. 325). While in the *Annelida* loco-

FIG. 325.—*Peripatus capensis* (after Moseley).

motion is effected by the movements of the segments and undulatory movements of the whole body, in the *Arthropoda* the function of locomotion is removed from the chief axis of the body to the secondary axes, *i.e.*, to the paired appendages, with the result of the possibility of a much more efficient discharge of the function. The appendages enable the *Arthropoda* not only to swim and creep with much greater ease and speed, but also to execute various kinds of more complicated movement, *e.g.*, running, climbing, springing, and flying. The *Arthropoda* are, therefore, true terrestrial and aerial animals.

The high development of the organs of locomotion as paired appendages leads of necessity to a second essential property, *viz.*, to the *heteronomy* of the segmentation, and in connection with this to the hardening of the outer layer of the skin to form a firm exo-skeleton. If the function of the limbs is to be perfectly discharged, there will be need of a considerable mass of muscle, the points of attachment of which can only be furnished by the integument of the body. The insertions of the appendages and their muscles, therefore, require

rigid surfaces, which are obtained partly by the development of internal chitinous tendons and plates, and partly by the hardening of the integument and the fusion of several segments to form larger armoured regions. It is only when the movements are simpler and resemble those of Annelids, that all the segments remain independent and bear similar appendages along the whole

FIG. 326.—Head, thorax and abdomen of an *Acridium*, seen from the side. *St*, Stigmata; *T*, tympanum.

length of the body (larvæ, *Myriapoda*). In general, three regions of the body can be distinguished, the head, the thorax, and the abdomen, the appendages of which possess respectively a different structure and function (fig. 326).

The head constitutes the short and compact anterior region of the body, is covered by a hard integument, encloses the brain and bears the sense organs and mouth-parts (jaws). The appendages of this region are modified to form the *antennæ* and *jaws*. The head of Arthropods, as compared with that of Annelids, contains, besides the frontal (præcoral) or antennal segment and the oral segment, in

FIG. 327.—*Squilla mantis*. *A'*, *A''* Antennæ; *Kf'*, *Kf''* the anterior maxillipeds on the cephalo-thorax; *B'*, *B''*, *B'''*, the three pairs of biramous feet.

addition at least one jaw segment, the appendages of which may, in larval life (*Nauplius*), still function as legs. Usually, however, several of the succeeding segments whose appendages function as jaws form part of the head.

The middle portion of the body, or **thorax**, is likewise distinguished by a relatively intimate fusion of some or all of its segments, as well as by the hardness of its integument. It is sometimes sharply marked off from the head, sometimes fused with the head to form a

region of the body called the *cephalothorax* (fig. 327). The thorax bears the appendages which are of most importance in locomotion.

The posterior portion of the body, or **abdomen**, is composed of distinctly separate rings, and is, as a rule, without appendages. When the latter are present, they serve partly as aids to locomotion (abdominal feet), partly for respiration, or for carrying the eggs and for copulation. More rarely, as for example in the scorpions, the abdomen is divided into a broad anterior region, the *præabdomen*, and a narrow movable posterior region, the *postabdomen*.

The skin, as in the *Annelida*, consists of two different layers,—an external firm, usually homogeneous chitinous layer, and an internal soft layer, which is composed of polygonal cells (*matrix*, *hypodermis*) and secretes in layers the at first soft chitinous cuticle (fig. 22). The latter usually becomes hardened by the deposition of calcareous salts in the chitinous basis, so as to form the firm exoskeletal armour, which, however, is interrupted between each segment by thin connecting membranes. The various cuticular appendages of the skin (fig. 22, *a*, *b*, *c*), which may have the form of simple or pennate hairs, of filaments, setæ, spines and hooks, originate as processes and outgrowths of the cellular matrix. The chitinous cuticle together with its appendages is from time to time, principally in the young stage during the period of growth, renewed, the old cuticle being cast off as a continuous membrane (ecdysis, or moult).

The muscular system never constitutes a continuous envelope, but the muscles are usually broken up into segments which correspond with the segmentation of the animal. The muscles of the body are arranged in longitudinal and transverse bundles in the different segments, and are frequently interrupted. There are in addition large groups of muscles, which move the appendages. The muscular fibres are always cross-striped.

The internal organization is allied to that of the *Annelida*, but does not present such a well-marked internal segmentation.

The **nervous system** consists of brain, œsophageal commissures and a ventral cord. The latter usually has the form of a ganglionic chain (fig. 328), and is placed beneath the alimentary canal. Sometimes, however, it exhibits great concentration, and may have the form of an unsegmented ganglionic mass beneath the œsophagus. The segmentation of the ventral ganglionic chain presents in details the greatest variations; in general, however, it corresponds to the heteronomous segmentation of the animal, in that in the larger regions of the body, which have arisen by fusion of several segments,

an approximation or fusion of the corresponding ganglia has taken place. In one case only, viz., in the *Pentastomidæ*, which in form and grade of life resemble the intestinal worms, the dorsal part of the œsophageal commissure is not swollen out to form a cerebral ganglion, and the central parts of the nervous system are com-

pressed together into a common ganglionic mass beneath the œsophagus. In all other cases the brain is a large ganglionic mass lying above the œsophagus, and connected by means of the œsophageal ring with the anterior ganglion of the ventral chain, which is usually placed in the head and is known as the subœsophageal ganglion (fig. 328). The sense nerves arise from the brain, while the ganglia of the ventral chain send nerves to the muscles, organs of locomotion and the body covering.

Visceral nervous system.—In addition to the brain and ventral ganglionic chain, which are comparable to the cerebro-spinal system of *Vertebrata*, we can distinguish in the larger and more highly organised *Arthropoda* a visceral nervous system (*sympathetic*), which consists of special ganglia and plexuses connected with the other system and specially distributed to the alimentary canal. In the higher *Arthropoda*, paired and unpaired *visceral* nerves are very generally present, both of which have their origin in the brain.

Sense organs.—Eyes are most generally distributed, and are only absent in a few parasitic forms. In their simplest form they are paired or unpaired structures placed upon the brain, provided with refractive bodies, and with or without a simple lens (stemmata, or simple eyes).

The compound eyes, which are always paired, are much more complicated. They are distinguished by the presence of nervous rods and crystalline cones, and may be divided into faceted eyes

FIG. 328.—Nervous system of the larva of *Coccinella* (after Ed. Brandt). *Gfr*, Frontal ganglion; *G*, brain; *Sg*, sub-oesophageal ganglion; *G'* to *G''*, ganglia of the ventral chain in the thorax and abdomen.

and eyes with smooth cornea (*Cladocera*). The former possess numerous lenses, and are sometimes placed on movable stalks (*Decapoda*). Occasionally accessory eyes are found on other parts of the body, on the jaws and between the legs of the abdomen (*Euphausia*).

Auditory organs are found most frequently in the Crustacea as auditory vesicles with otoliths in the basal joint of the anterior antennæ, or rarely in the appendage of the abdomen known as the fan (tail of Mysis). In *Insecta*, auditory organs of a very different structure have been discovered.

Olfactory organs are also widely distributed. They are situated on the surface of the antennæ, and consist of delicate tubes or peculiar conical projections, beneath which the sense nerves end in ganglionic swellings.

Tactile organs. The antennæ and palps of the oral appendages and the ends of the limbs have a tactile function. These parts are provided with peculiar hairs and setæ, beneath which nerves end in ganglionic swellings.

Alimentary canal.—An independent digestive apparatus is always present, but its structure and degree of development are very various. The alimentary canal is only exceptionally degenerated and absent (*Rhizocephala*). The mouth is placed on the ventral surface of the head. It is furnished with a projecting upper lip, and usually with paired appendages, which are used either for masticating or for piercing and sucking. A narrow or wide œsophagus leads into the intestine, which either simply traverses the axis of the body or is disposed in several coils. The œsophagus and midgut (chyle stomach) may even be divided into several regions, and may possess salivary glands and hepatic appendages of various size.

Excretory organs.—Urinary organs are widely distributed. In the simplest form they appear as cells on the surface of the intestine (lower Crustacea), in a more highly developed state as tubular filiform diverticula of the hindgut (*Malpighian tubes*) (fig. 329). In the *Crustacea*, glands are present in the shell (*shell glands*) and in the base of the posterior antennæ; they are regarded as the morphological equivalents of segmental organs.

The **circulatory and respiratory organs** present the greatest differences in the various groups of the Arthropoda. In the simplest case the clear, more rarely coloured blood fluid, which is often corpusculated, fills the body cavity and the interstices of all

the organs, and is circulated in an irregular manner by the movements of the different parts of the body. Not unfrequently (*Achtheres* and *Cyclops*) the circulation is effected by the regularly repeated movements of certain organs (intestine, vibratile plates, etc.); in other cases, a short saccular heart is present dorsally above the intestine; or a long vascular tube (the *dorsal vessel*), divided into chambers, serves as a propelling organ. From this, vessels (*arteries*)

may arise, which conduct the blood in definite directions. Vessels for returning the blood (*veins*) may also be present. These either begin in the body cavity, or are connected with the ends of the arteries by capillary vessels. The vascular system seems never to be completely closed, since even when the circulation is most complete, lacunar spaces of the body cavity are found inserted in the course of the vessels.

Respiration is very frequently effected, especially in the smaller and more delicate species of *Arthropoda*, by means of the entire surface of the body. In the larger aquatic forms, the function of respiration is assumed by special tubular, usually branched appendages of the limbs (*branchiae*); while in the air-breathing *Insects*, *Centipedes*, *Scorpions*, and *Spiders*, respiration is performed by means of internal branched tubes filled with air (*tracheae*) or by pulmonary sacs (*fan tracheae*).

The reproduction of the *Arthropoda* is usually sexual, but sometimes takes place by the development of unfertilized ova (*parthenogenesis*). Ovaries and testes are in their origin paired, as are also the generative ducts, which often have a common terminal portion and open by a median generative aperture (*Insecta*, *Arachnoidea*). With a few exceptions (*Cirripedia*, *Tardigrada*), the sexes are separate. Males and females frequently differ essentially in their entire form and organization. In rare cases, for example in the parasitic

FIG. 329.—Alimentary canal of *Pontia brassicae* (after Newport). *R*, Proboscis (Maxillae); *Sp*, salivary glands; *Oe*, oesophagus; *S*, sucking stomach; *Mg*, Malpighian tubes; *Ad*, rectum.

generative ducts, which often have a common terminal portion and open by a median generative aperture (*Insecta*, *Arachnoidea*). With a few exceptions (*Cirripedia*, *Tardigrada*), the sexes are separate. Males and females frequently differ essentially in their entire form and organization. In rare cases, for example in the parasitic

Crustacea, there is such a marked sexual dimorphism that the males remain small and dwarfed, and are attached like parasites to the body of the female. During the act of copulation, which is often limited to the external union of the two sexes, the spermatophores are fastened to the female genital segment or thrust into the vagina by the organ of copulation, whence they sometimes pass into a special receptaculum seminis. Most *Arthropoda* are oviparous, but in almost every group there are viviparous forms. The eggs are frequently carried about by the mother, or deposited in protected places where food may easily be obtained. The embryonic development (*i.e.*, development within the egg) is characterised, except in the case of the small stout embryos of the *Cyclopidae*, *Pentastomidae* and *Acarina*, by the presence of a ventrally placed primitive streak, from which especially the ganglionic chain and the ventral parts of the segments proceed. The more or less complex embryonic development is usually followed by a complicated metamorphosis, during which the young form as larva undergoes several ecdyses. Numerous segments and parts present in the adult are not unfrequently wanting in the just-hatched larva; in other cases, all the segments of the adult are indeed present, but are not as yet fused together to form regions. In such cases, the larvæ resemble the *Annelida* in their homonomous segmentation, and in their locomotion and mode of life. The metamorphosis may however be retrogressive; the larvæ are hatched with sense organs and appendages, but in the further course of development they become parasitic, lose their eyes and organs of locomotion, and develop into strange unsegmented (*Lernææ*) or entozoon-like (*Pentastomidae*) forms.

The *Arthropoda* are no exception to the general rule that the aquatic forms which breathe by gills are lower and, from a genetic point of view, older than the air-breathing members of the same group, inasmuch as the *Branchiata* or *Crustacea* are the older, the *Tracheata* the younger types.

CLASS I.—CRUSTACEA.*

Aquatic Arthropoda, which breathe by means of gills. They have two pairs of antennæ; numerous paired legs on the thorax, and usually also on the abdomen.

* Milne Edwards, "Histoire naturelle des Crustacés," 3 vol. and atlas, 1838-1840. C. Claus, "Untersuchungen zur Erforschung der genealogischen Grundlage des Crustaceensystems," Wien, 1876.

The *Crustacea*, whose name is derived from the body-covering (which is often hardened), are principally aquatic animals. Some forms, however, can live on land, and possess respiratory organs adapted for breathing air. An important character of the group is the great number of paired appendages. The appendages of all the segments, even those of the head, may be used in locomotion (fig. 330). As a rule, the head fuses with the thorax, or at any rate with one or more of the thoracic segments, to form a *cephalothorax*; which is followed by the remaining free thoracic segments. Sometimes, however, these two regions of the body remain distinct. The head and thorax are seldom so sharply marked off from one another as, for example, in the *Insecta*: usually certain appendages, the so-called maxillipeds, occupy an intermediate position between legs and jaws, and being placed at the boundary between the two

FIG. 330.—*Gammarus neglectus* (after G. O. Sars). *A'*, *A''*, The two antennæ; *Kf*, maxilliped; *F'*, *F''*, first to seventh thoracic feet; *Sf'*, anterior swimming feet.

regions may be reckoned either as belonging to the head or the thorax. The fusion of the segments may be very extensive; not only may the head and thorax be united, but the boundary between thorax and abdomen may vanish, and the segmentation

may even disappear. As a general rule, the form of the body presents extraordinary differences in the various groups. A reduplication of the skin arching over the thorax and covering the body as a shell is frequently present. This fold of the integument constitutes, in extreme cases, a mantle-like investment, which may develop calcareous plates and occasion a certain resemblance to Lamelli-branches (*Cirripedia*). In other cases the body has quite lost its segmentation, and the animal resembles a worm (*Lernææ*, *Sacculina*).

On the head there are usually two pairs of antennæ, which function as sense organs and sometimes also as organs of locomotion or of prehension. There is a pair of large jaws (the *mandibles*), one on each side of the mouth, over which a small plate, known as the *upper lip*, often projects. The mandibles are simple but very rigid and hard masticating plates, which are usually toothed and correspond

morphologically to the coxal joint of a limb, the following joints developing into a palp-like appendage (*mandibular palp*). Then follow one or more pairs of weaker jaws (*maxillæ*), and one or more pairs of maxillipeds, which more or less resemble the legs and, in parasitic forms, are often used for adhering (fig. 331). In parasitic forms, the upper and under lips not unfrequently give rise to a suctorial proboscis, in which the styliform mandibles are placed. The appendages of the thorax, of which at least three pairs are present (*Ostracoda*), present an extremely various structure, in accordance with the mode of life and the use made of them. They are either broad leaf-shaped swimming feet (*Phyllopoda*), or biramous appendages (*Copepoda*); they may serve to produce currents in the water like the feet of the *Cirripedia*, or they may be used for crawling, walking, and running (*Isopoda*, *Decapoda*). In the latter case, some of them end with hooks or chelæ. Finally the appendages of the abdomen, which frequently itself moves *in toto* and assists in locomotion, are either exclusively locomotory as jumping or swimming feet (*Amphipoda*), in which case they usually differ from the appendages of the thorax; or they serve with their appendages for respiration, as well as for carrying the eggs, and for copulation (*Decapoda*).

The internal organization is not less varied than is the external form.

In the lower forms, the nervous system often consists of a ganglionic mass, which surrounds the œsophagus and is not further

FIG. 331.—Young stage (larva) of the Lobster (after G. O. Sars). *a*, The larva seen from the side; *R*, rostrum; *A'*, *A''*, antennæ; *Kf'''* third maxilliped; *F'*, anterior ambulatory leg. *b*, mandible with palp; *c*, anterior maxilla with two blades and palp; *d*, posterior maxilla with vibratile plate (scaphognathite); *e*, first, *f*, second maxilliped.

segmented. This ganglionic mass corresponds to the brain and ventral cord and gives off all the nerves. In the higher *Crustacea*, a distinct brain and ventral ganglionic chain, which is usually elongated and of very varied form, as well as a rich plexus of visceral nerves and ganglia of the sympathetic system are always present.

Of **sense organs**, eyes are the most widely distributed. They may have the form either of simple eyes (paired or unpaired), or compound eyes with smooth or faceted cornea; in the latter case they are often placed on movable stalks, which are attached to the lateral regions of the head. *Auditory organs* are also present usually in the basal joint of the anterior antenna, rarely in the caudal plate at the posterior end of the body (*Mysis*). The delicate hairs and filaments of the anterior antenna are probably *olfactory organs*.

The **digestive canal** is, as a rule, straight, extending from the mouth to the anus at the posterior end of the body. In the higher forms the œsophagus is usually dilated in front of the mesenteron (midgut) into a stomach or crop, which is armed with chitinous plates. The mesenteron is provided with simple or ramified hepatic cæca.

Excretory organs.—The so-called shell glands of the lower *Crustacea* are regarded as urinary organs, as are also the glands opening at the base of the posterior antenna in the *Malacostraca*. In the *Entomostraca* the latter are only preserved during larval life. Short tubes, which correspond to the Malpighian tubes of the Tracheata, may also be present on the rectum (*Amphipoda*).

The **circulatory organs** present every possible degree of perfection, from the greatest simplicity to the highest complication of an almost closed system of arterial and venous vessels. The blood is usually colourless, but is sometimes green or even red, and as a rule contains cellular blood corpuscles.

Respiratory organs are either entirely wanting, or are represented by branchial tubes on the thoracic or abdominal appendages. In the first case they are often contained in a special branchial cavity at the sides of the cephalothorax.

Generative organs.—With the exception of the hermaphrodite *Cirripedia* and *Isopoda*, all *Crustacea* are of separate sexes. The male and female generative organs usually open on the boundary of the thorax and abdomen, either on the last or the antepenultimate thoracic ring, or on the first abdominal segment. The two sexes are very often distinguished by a number of external characteristics.

The males are smaller, sometimes even dwarfed, and then attached to the females like parasites. They almost always possess apparatuses for holding the females and for transferring the spermatophores during copulation. The larger females, on the other hand, frequently carry the eggs about with them in sacs, the membranes of which are secreted by the so-called cement glands.

Development takes place either directly or by metamorphosis. The metamorphosis is sometimes retrogressive. When the development is direct, the young animals, on leaving the egg, already have the body form of the adult. The larva known as the *Nauplius* (fig. 332) is of great importance as a point of departure. This larva possesses an oval body, on the ventral side of which are present three pairs of appendages for the sense of taste, the prehension of food, and for locomotion. These appendages correspond to the two pairs of antennæ and mandibles respectively. Parthenogenesis is said to occur in certain groups (*Phyllopoda*).

Almost all *Crustacea* are carnivorous. Some of them suck the juices of living animals on which they are parasitic.

For the systematic review of this heterogeneous group, it is convenient to divide the numerous orders into two series.

1. The small simply organized *Crustacea*, the number and form of whose appendages is very various, will be included as *Entomostraca* (O. Fr. Müller). To this group belong the orders *Phyllopoda*, *Ostracoda*, *Copepoda*, and *Cirripedia*.

2. The higher *Crustacea*, characterised by a definite number of segments and appendages, may be grouped together as *Malacostraca* (Aristotle). In this group are included the orders of *Arthrostraca* (*Amphipoda* and *Isopoda*), and *Thoracostraca* (*Cumacea* *Stomatopoda*, *Schizopoda*, and *Decapoda*).

In addition there is the genus *Nebalia*, which has been hitherto erroneously placed with the *Phyllopoda*, but which is to be regarded as the representative of an ancient group connecting the *Phyllopoda* with the *Malacostraca*, and may be opposed to the latter as *Leptostraca*.

Finally, in addition to these chief divisions, there is a number

FIG. 332.—Nauplius larva of *Balanus*, seen from the side. *A'* First appendage (first antenna); *A'''*, second appendage (second antenna); *Mdf*, third appendage (mandible); *Ob*, upper lip; *D*, intestine.

of Crustacean orders, for the most part fossil and belonging to the oldest formations, which present in their development no certain trace of the Nauplius form so characteristic of the true Crustacea, and are in all probability related to the *Arachnoidea*. These orders, which may be grouped together as the *Gigantostraca*, are the *Merostomata* and *Xiphosura*, to which the *Trilobita* are possibly allied.

1.—ENTOMOSTRACA.

Order 1.—PHYLLOPODA.*

Crustacea with elongated and often distinctly segmented body ; usually with a flat, shield-like carapace, or laterally compressed bivalve shell, formed by a reduplication of the skin. There are, at least, four pairs of leaf-like lobed swimming feet.

The animals belonging to this order differ very considerably in form and size, in the number of their segments and appendages, as well as in their internal structure. They all, however, agree in the structure of their lobed, leaf-like feet. In their form, internal organization and development they appear to be the most primitive of Crustacea, and may be regarded as the least modified descendants of ancient types.

The body is either cylindrical, elongated and clearly segmented, without free reduplication of the skin, *e.g.* *Branchipus* (fig. 333), or it may be covered by a broad and flattened shield, which only allows the posterior part of the body to project uncovered, *e.g.* *Apus*. In other cases the body is laterally compressed and is enclosed by a bivalve shell, from which the anterior part of the head projects (*Cladocera*) ; or finally the laterally compressed body is completely covered by a bivalve shell (*Estheridæ*). Sometimes the head is more sharply distinct, while the thorax and abdomen are not so clearly distinguishable from each other. As a rule, the posterior segments only are without appendages. The hind end of the abdomen is very often curved ventralwards and forwards, and bears two rows of posteriorly directed claws, the two last of which arise at the point of the caudal appendage, and are by far the

* Besides the works of O. Fr. Müller, Jurine, M. Edwards, Dana, compare Zaddach, "De Apodis cancriformis anatome et historia evolutionis," Bonnæ, 1841. E. Grube, "Bemerkungen über die Phyllopoden," *Archiv für Naturgesch.*, 1853 and 1855. Fr. Leydig, "Monographie der Daphniden," Tübingen, 1860.

strongest. In other cases a pair of fin-like appendages are present constituting the caudal fork (*Branchipus*).

Appendages.—On the head there are two pairs of antennæ, which however, in the adult animal, may be rudimentary or peculiarly modified. The anterior antennæ are small, and bear the delicate olfactory hairs. The posterior antennæ frequently have the form of large biramous swimming appendages, but in the male may also have a prehensile function, *e.g.*, *Branchipus*. In other cases (*Apus*) they are rudimentary and may even be entirely absent.

Two large mandibles are always present beneath the well developed upper lip; they possess a toothed, biting edge, and in the fully developed condition are *invariably destitute of palps*. The mandibles are followed by one or two pairs of slightly developed maxillæ. A kind of underlip is in many cases present, in the form of two prominences behind the mandibles.

The *legs*, which are placed on the thorax, are usually very numerous, and are smaller towards the posterior end of the body. They are lobed, leaf-like, biramous structures, and function as swimming feet; they also assist in procuring food. They consist of the

following parts: a short basal portion, which is usually provided with a masticatory process and is followed by a long foliaceous stem with setæ on its inner edge; this is continued into the multilobed internal branch [endopodite] of the biramous limb, while it bears on its outer side the external ramus [exopodite] with marginal setæ, and nearer

FIG. 333.—Male of *Branchipus stagnalis*. *Rg*, Heart or dorsal vessel with a pair of slit-like openings in each segment; *D*, intestine; *M*, mandible; *Sd*, shell gland; *Br*, branchial appendages of the eleven pairs of legs; *T*, testis.

its base a vesicular branchial appendage. The anterior, or even all the legs (*Leptodora*) may have the form of prehensile feet, and be destitute of branchial appendages.

The Phyllopods possess a large pair of **eyes**, which are sometimes fused together in the median line. In addition a small median simple eye (Entomostracan eye) may persist. They have a saccular or chambered **heart**, which controls the regular circulation. Coiled **excretory organs**, known as *shell glands*, are sometimes present; they open to the exterior by a special aperture on the posterior maxilla. The function of **respiration** is performed by the entire surface of the body, the area of which is much increased by the reduplication of the skin forming the carapace; also by the foliaceous swimming feet, and especially by the surface of the branchial appendages.

Reproduction.—The *Phyllopoda* are of separate sexes. The males are distinguished from the females by the structure of the first pair of antennæ which are larger and more richly provided with olfactory hairs, and also by their anterior swimming feet which are armed with prehensile hooks. In general the males are less frequently met with than are the females, and, as a rule, only at definite seasons of the year. The females of the smaller *Phyllopoda* (*Cladocera*) are able to produce eggs without copulation and fertilization; and these eggs, the so-called summer eggs, develop spontaneously and produce generations containing no males. In certain genera of the *Branchiopoda*, e.g., *Artemia* and *Apus*, parthenogenesis is the rule; the males, indeed, have only been known a few years. The females usually carry the eggs about with them on special appendages, or in a brood pouch beneath the shell on the dorsal surface. The just hatched young either possess the form of the sexually mature animal (*Cladocera*), or undergo a complicated metamorphosis, leaving the egg membranes as a nauplius larva with three pairs of appendages (*Branchiopoda*).

A few of the *Phyllopoda* live in the sea, the greater number inhabit stagnant freshwater; some of them are found in brine pools.

Sub-order 1. **Branchiopoda.*** *Phyllopoda*, with clearly segmented body, often enclosed in a flat, shield-shaped, or laterally compressed bivalved shell, with from ten to about thirty or more pairs of foliaceous swimming feet.

* Schäffer, "Der krebartige Kieferfuss," etc. Regensburg, 1756. A. Kozubowski, "Ueber den männlichen *Apus cancriformis*," *Archiv für Naturgesch.*, Tom XXIII, 1857. C. Claus, "Zur Kenntniss des Baues und der Entwicklung von *Branchipus* und *Apus*," etc., Göttingen, 1873.

The alimentary canal is provided with two lateral hepatic appendages, which are, as a rule, branched and racemose and only exceptionally short and simple. The heart appears as an extended dorsal vessel with numerous paired lateral slits, and may extend throughout the whole length of the thorax and abdomen (*Branchipus*). The genital organs, which are always paired, are placed by the side of the alimentary canal, and open at the boundary between the thorax and abdomen. In the females the genital openings are small slits; in the male there may be protrusible copulatory organs at the openings (*Branchipus*).

The males are distinguished from the females principally by the fact that the anterior, or two anterior pairs of legs, are armed with hooks (*Estheridæ*), or by the modification of the posterior antennæ to form a prehensile apparatus (*Branchipus*). Remarkable is the rare occurrence of the males; they seem only to appear under certain conditions and in definite generations, which alternate with parthenogenetic generations. The eggs during development are generally protected within the body of the mother, and are carried about either in a saccular brood-pouch of the abdomen or between the valves of the shell on filiform (*Estheria*, *Branchipus*), or in vesicular (*Apus*) appendages of different pairs of legs (9th to 11th). The eggs, so far as is known, undergo a complete segmentation. When hatched, the young animal has the form of a Nauplius larva with three pairs of appendages, of which the anterior (which become the anterior antennæ) are in the *Estheridæ* only represented by slightly developed setigerous prominences. On the other hand, in *Apus* the third pair is small and rudimentary.

Almost all the *Branchiopoda* belong to inland waters, and principally inhabit shallow fresh-water pools. When the latter dry up, the eggs, preserved in dry mud, remain capable of development. Some species, as *Artemia salina*, are found in brine pools.

Branchipus pisciformis Schöff = *B. stagnalis* L., without a shell, found in the lakes of Germany, together with *Apus cancriformis*. *B. diaphanus* Prév., France. *Artemia salina* L., in salt pools, near Trieste, Montpellier. They sometimes lay eggs with a hard shell, sometimes they are viviparous. *Apus cancriformis* Schöff, with shield-shaped shell, Germany. The males, which are rare, can be recognized by the normal formation of the eleventh pair of appendages. They live in puddles and fresh-water lakes, together with *Branchipus*. *Estheria cycladoides* Joly L., with perfect shell.

Sub-order 2. **Cladocera**.* Water-fleas. Small laterally com-

* Besides the works already quoted, compare H. E. Strauss, "Mémoire sur les Daphnia de la classe des Crustacés," *Mem. du Mus. d'hist nat.*, Tom V. and

pressed *Phyllopoda*, whose body, with the exception of the head, which projects freely, is usually enclosed in a bivalve shell. They have two large antennæ, which are used in swimming, and four to six pairs of swimming feet.

The *Cladocera* are small simply organized Phyllopods, whose resemblance to the larvæ of the shelled Branchiopoda, particularly to the larva of *Estheria* with its six pairs of legs, gives the best indication of the probable origin of the group. Unlike the anterior antennæ, which are short, the posterior are modified to form biramous swimming appendages beset with numerous long setæ. The four to six pairs of legs are not always foliaceous swimming feet, but in many cases have the form of cylindrical ambulatory or prehensile appendages. The abdomen, which is ventrally flexed, develops on its dorsal side several prominences, which serve to close the brood pouch. It usually consists of three free segments, as well as the terminal anal portion, which is beset with rows of hooks. The anal portion begins with two dorsal tactile setæ and ends with two hooks or styles, representing the caudal fork (fig. 334).

The internal organization is simple in correspondence with the small size of the body. The compound eyes fuse together in the middle line to form a large, continually trembling, frontal eye, beneath which the unpaired simple eye usually remains. A special sense apparatus, whose function is not quite clear, appears in the region of the neck, in the form of an aggregation of ganglion cells.

The heart has the form of an oval sac, with two transverse lateral venous ostia and an anterior arterial opening. Its pulsations are rhythmic, and succeed one another quickly. In spite of the want of arteries and veins, the circulation of the blood, which contains amœboid cells, is completed in definite tracts marked out by lacunæ and spaces in the body. The looped and coiled shell gland is always present. The cervical gland, which functions as an organ of attachment, is less widely distributed. The sexual glands lie in the thorax as paired

VI, 1819 and 1820, Leydig, "Naturgeschichte der Daphniden," Tübingen, 1860. P. E. Müller, "Bidrag til Cladocerernes Fortplantings historie," Kjöbenhavn, 1868. G. O. Sars, "Om en dimorph Udvikling samt Generationsvexel hos Leptodora," *Vidensk. Selsk. Forh.*, 1873. A. Weismann, "Beiträge zur Kenntniss der Daphnoiden," I—IV., Leipzig, 1876 and 1877. C. Claus, "Zur Kenntniss der Organisation und des feineren Baues der Daphniden," *Zeit. f. wiss. zool.*, Tom XXVII, 1876. C. Claus, "Zur Kenntniss des Baues und der Organisation der Polyphemiden," Wien, 1877. C. Grobben, "Die Embryonalentwicklung von *Moina rectirostris*," *Arbeiten aus dem zool. vergl. anatom. Institut*. II Band, Wien, 1879.

tubes by the side of the alimentary canal. In the ovaries groups of four cells are separated ; one cell of each group becomes an ovum, while the rest are employed as nutritive cells for the nourishment of the ovum, which increases in size and absorbs fat globules. The ovary is directly continuous with the oviduct, which opens dorsally beneath the shell into the brood-pouch. The testes, like the ovaries, lie at the sides of the intestine and are continuous with the vasa deferentia,

FIG. 334.—*Daphnia*. C, Heart—the slit-like opening of one side is visible ; D, alimentary canal ; L, hepatic diverticulum ; A, anus ; G, cerebral ganglion ; O, eye ; Sd, shell gland ; Br, brood-pouch beneath the dorsal reduplication of the shell.

which open to the exterior ventrally behind the last pair of appendages or at the extreme end of the body, the openings being sometimes situated on small slightly protrusible prominences.

The smaller males usually appear in the autumn ; they may, however, also be present at any other time of the year, and, as recent investigations have proved in a tolerably satisfactory manner, always when

the conditions of life and nourishment are unfavourable. Before the appearance of the males, hermaphrodite forms * sometimes make their appearance with an organization which is half male and half female.

At the season when males are not present, normally in the spring and summer, the females produce the so-called summer eggs, which contain a large quantity of oil globules and are surrounded by a delicate vitelline membrane. They develop rapidly within the brood-pouch between the shell and the dorsal surface of the mother, and after the space of only a few days give rise to a fresh generation of young *Cladocera*, which escape from the brood-pouch. The embryonic development takes place accordingly under extremely favourable conditions, which depend upon the rich supply of food yolk in the large eggs, and are sometimes favoured by the secretion of additional food material within the brood-pouch.

At the season when the males appear, the females, under the like influence of unfavourable nourishment and independently of copulation, begin to produce so-called winter eggs, which are incapable of developing without fertilization. The number of these hard-shelled winter eggs is always relatively small. They are, therefore, distinguished from the summer eggs by their larger size and the greater quantity of food yolk; and their origin in the ovary is accompanied by much more extensive processes of absorption.

The *Daphnidæ* live for the most part in fresh water. Certain species inhabit deep inland lakes, brackish water, and the sea. They swim quickly, and usually with a jumping movement. Some of them attach themselves to solid surrounding objects by means of a dorsally placed organ of attachment, the cervical gland. When the body is thus fixed, the swimming feet seem to be able by their vibrations to set up currents in which small food particles are swept towards the animal.

Sida crystallina O. Fr. Müller. The six pairs of lamellar legs beset with long swimming setæ. The rami of the swimming antennæ two- to three-jointed. *Daphnia pulex* De Geer. *D. sima* Liev. Five pairs of legs, of which the anterior are more or less adapted for prehension. One ramus of the swimming antennæ is three-jointed, the other four-jointed. *Polyphemus pediculus* De Geer. In the lakes of Switzerland, Austria, and Scandinavia. *Eradne Nordmanni* Lovén, North Sea and Mediterranean. *Leptodora hyalina* Lillj., in lakes.

* Compare especially W. Kurz, "Ueber androgyne Missbildung bei Cladoceren," *Sitzungsber der Akad. der Wissensch. Wien*, 1874. Also Schmanke-witsch.

Order 2.—OSTRACODA.*

Small, usually laterally compressed *Entomostraca*, with a bivalve shell and seven pairs of appendages, which function as antennæ, jaws, creeping and swimming legs. There is a pediform mandibular palp, and a short abdomen.

The body of these small *Crustacea* is unsegmented and is completely enclosed in a bivalve shell, which gives the animal a resemblance to a mussel. The two valves of the shell join together in the middle line, and are fastened together by an elastic ligament along the middle third of the back. The action of this ligament is opposed by a two-headed adductor muscle, which passes from one valve of the shell to the other and causes impressions discernible from without. The common tendon of the two heads of this muscle lies nearly in the

FIG. 335.—Female *Cypris* before sexual maturity; the right valve of the shell has been removed, *A'*, *A''*, first and second pair of antennæ; *Ob*, upper lip; *Md*, mandible with pediform palp; *G*, cerebral ganglion with unpaired eye; *SM*, adductor muscle; *Mx'*, *Mx''*, first and second pair of maxillæ; *F'*, *F''*, first and second pair of feet; *Fu*, caudal fork; *M*, stomach; *D*, intestine; *L*, hepatic tube; *Ge*, rudimentary genital organs.

middle of the body. The edges of the valves are free at both ends and along the ventral side. In the marine *Cypridinidæ* there is a deep indentation in the edges of the valves, to allow the antennæ to pass out. When the valves of the shell are open, several pediform appendages can be protruded on the ventral side, which enable the animal to move in the water either by crawling or by swimming.

* H. E. Strauss-Dürkheim, "Mémoire sur les Cypris de la classe des Crustacés," *Mém. du Mus d'hist. nat.*, Tom VII., 1821. W. Zenker, "Monographie der Ostracoden," *Archiv. für Naturgesch.*, Tom. XX., 1854. C. Claus, "Beiträge zur Kenntniss der Ostracoden. Entwicklungsgeschichte von Cypris." Marburg, 1868. C. Claus, "Neue Beobachtungen über Cypridinen," *Zeitschr. für wiss. Zool.*, Tom XXIII. C. Claus, "Die Familie der Halocypriden." *Schriften zoologischen Inhalts*, Wien, 1874. G. S. Brady, "A Monograph of the Recent British Ostracoda," *Transact. of the Lin. Soc.*, Vol. XXVI.

The abdomen can also be protruded; it either ends in a caudal fork (*Cypris* and *Cythere*), or has the form of a plate armed with spines and hooks on its posterior margin (*Cypridina*).

Appendages.—The two pairs of antennæ are placed on the anterior region of the body (fig. 336, A', A''), and are used as creeping and swimming legs. In *Cypridina*, however, the anterior pair is provided with olfactory hairs. The antennæ of the second pair in *Cypris* and *Cythere* resemble legs, and end with strong hooked bristles, by help of which the animal can attach itself to surrounding objects. In the exclusively marine *Cypridinidæ* and *Halocypridæ* this pair of appendages has the form of biramous swimming feet, which consist of a broad triangular basal plate, a many-jointed endopodite beset with long swimming setæ, and a rudimentary exopodite, which, however, is stronger in the male and furnished with hooks of a considerable size.

In the region of the mouth beneath and to the side of a tolerably large upper lip there are two powerful mandibles with a broad and strongly toothed biting edge. The mandibular palps, which are leg-like and elongated, are usually three-jointed and can be used as legs (*Mdf*). In exceptional cases (*Paradoxostoma*), the mandibles are styliform and are enclosed in a suctorial proboscis formed from the upper and under lips.

The mandibles are followed by the first pair of maxillæ, which are in all cases distinguished by the great development of their basal portion and by the reduction of the palp. In the *Cypridæ* and *Cytheridæ* the basal joint of the first maxilla bears a large comb-like setose plate, which by its swinging movements aids the function of respiration, but does not itself function as a gill. A similar branchial plate may also occur on the two following appendages (the 5th and 6th pair), which sometimes have the form of jaws, sometimes of legs. The anterior of these appendages (maxilla of the second pair or better maxilliped, fig. 336, *Mx''*) functions, in *Cypris*, chiefly as a jaw, but bears, besides the rudimentary branchial appendage, a short, backwardly directed, usually two-jointed palp, which, however, in certain genera and in *Halocypris* becomes a short, three-jointed or even four-jointed leg. In *Cythere* it acts exclusively as a leg, and represents the first of the three pairs of legs present in this animal. In the *Cypridina*, however, it has completely the form of a jaw, and is provided with an enormously developed branchial plate (fig. 336 a, *Mx''*). The appendage of the sixth pair is usually modified to an elongated, many-jointed, creeping and ad-

hering foot. The appendage of the seventh pair is always elongated to the form of a leg; in *Cythera* it is formed like the preceding one,

FIG. 336.—*Cypridina mediterranea*. *a*, Female; *b*, male. *M*, Stomach; *H*, heart; *SM*, adductor muscle; *O*, eye; *O'*, unpaired eye; *G*, brain; *Stz*, frontal organ; *T*, testis; *P*, copulatory organ; *Mdf*, mandibular palp; *Mx'*, first maxilla; *Mx''*, second maxilla; *Fu*, caudal fork.

but in *Cypris* it is curved upwards, and is furnished with a short claw and terminal setæ. It has probably the same function (Putzfuss)

as the long cylindrical appendage of *Cypridina*, which arises in place of the seventh pair of legs, almost on the back of this animal.

The nervous system consists of a bilobed cerebral ganglion and a ventral chain with closely approximated pairs of ganglia, which may unite to form a single ganglionic mass.

Sense organs.—In addition to the already mentioned olfactory hairs there is a median eye (*Cypris*, *Cythere*), composed of two (often separated) halves; or there are, in addition to a small unpaired eye, two larger compound and movable lateral eyes (*Cypridina*). In *Halocypris* and *Cypridina* there is a frontal appendage, which probably functions as a sense organ.

Alimentary canal.—The mouth, which is frequently (*Cypris*) armed with toothed lateral bands, leads through a narrow œsophagus into a dilated crop-like portion of the alimentary canal. This is followed by a broad and long stomach, provided with two long

FIG. 337.—Alimentary canal and generative organs of a female *Cypris* (after W. Zenker). Oe, œsophagus; PF, crop; V, stomach; D, intestine; L, liver; Ov, ovary; SM, adductor muscle; R, receptaculum; Vu, vulva; Fu, caudal fork.

lateral hepatic tubes, which project into the lamellæ of the shell. The anus opens at the base of the abdomen (fig. 337). Of special glands a club-shaped, dilated glandular tube (poison-glands?) found in *Cythere* must be mentioned, the duct of which opens to the exterior through a spinous appendage of the posterior antennæ.

A heart is present in *Cypridina* and *Halocypris* on the dorsal surface, where the shell is connected to the animal. The function of respiration is performed by the whole surface of the body, over which an uninterrupted current of water is maintained by the swinging movements of the leaf-shaped setose branchial appendages. In many *Cypridinidæ* (*Asterope*) there is a double row of branchial tubes on the back, near the last pair of appendages.

Generative organs.—The sexes are always separate and are distinguished by well marked differences in their entire structure. The males, in addition to the greater development of the organs of sense, possess apparatuses on different appendages—in *Cypridina* on the second antennæ, in *Cypris* on the maxilliped—for holding the females; or a pair of legs may be completely modified for this pur-

pose. In addition a large copulatory organ, which may be derived from a modified pair of appendages and often possesses a very complicated structure, is always present. The male genital organs consist on either side of several elongated or globular testes, of a vas deferens and the copulatory organ; the presence in *Cypris* of a very peculiar paired mucous gland and the size and form of the spermatozoa seem to be worthy of notice (Zenker). The female of *Cypris* possesses two ovarian tubes which project into the reduplication of the carapace, two receptacula seminis, and the same number of genital openings at the base of the abdomen.

Development.—The greater number of *Ostracoda* lays eggs, which they either attach to water-plants (*Cypris*), or, as in *Cypridina*, carry about with them between the shell valves until the young are hatched. The free development of *Cypris* consists of a complicated metamorphosis. The larvæ, when hatched, possess, like the Nauplius form, only three pairs of appendages, but are strongly compressed laterally, and are already enclosed in a thin bivalve shell (fig. 338). In the marine *Ostracoda* the development is simplified, so that the metamorphosis is entirely absent.

The *Ostracoda* feed altogether on animal matter, as it seems especially on the carcasses of different aquatic animals.

Numerous fossil forms are known from almost all formations, but, unfortunately, only the remains of their shells are preserved.

FIG. 338.—Very young larva of *Cypris*. Nauplius stage, with three pairs of appendages. *M*, stomach; *D*, intestine; *SM*, shell muscle; *A'*, *A''*, first and second antennæ; *Mf*, mandible.

Cypridina. With heart and large movable paired eye. With deep excavation in the edges of the shell for the passage of the antennæ. The anterior antennæ are bent, furnished with strong setæ, and have olfactory hairs at their extremity. The posterior antennæ are biramous swimming feet. The biting part of the mandible is weak or entirely aborted; palp is five-jointed, pediform, and of considerable length. The seventh pair of appendages is represented by a cylindrical ringed appendage (Putzfuss). *Cypridina mediterranea* Costa. *Asterope oblonga* Gr., Trieste. *Halocypris* Dana.

Cythere O. Fr. Müll. Without heart. The anterior antennæ are bent at their base and beset with short setæ. The posterior antennæ are strongly developed, with hooks on the terminal joint. Three pairs of legs, of which the last is the most strongly developed. The abdomen has only the caudal fork, of which the two branches are small and lobe-like. The testes and ovaries do not project between the lamellæ of the carapace. The male genital apparatus has no mucous gland. They are all marine animals. The females often carry the

eggs and embryos about between the valves of the shell. *Cythere lutea* O. Fr. Müller, North Seas and Mediterranean. *C. viridis* O. Fr. Müller, North Seas.

Cypris O. Fr. Müller. With median eye, but no heart. The shell valves are light but strong, the anterior antennæ have usually seven joints and are beset with long setæ. The antenna of the second pair is simple and pediform, with usually six joints. There are two pairs of legs, of which the posterior smaller pair is bent upwards towards the dorsal surface. The caudal fork is very narrow and elongated, and is provided with hooked setæ at the point. The testes and ovaries project between the lamellæ of the shell. The male genital apparatus has a peculiar mucous gland. Most of them inhabit fresh water. *Cypris fusca* Str., *C. pubera* O. Fr. Müller, *C. fuscata* Jur., and others. *Notodromus monachus* O. Fr. Müller.

Order 3.—COPEPODA.*

Entomostraca with elongated, usually well segmented body, without shell-forming reduplication of the skin, with biramous swimming feet; the abdomen is without appendages.

The group of the *Copepoda* includes a number of very different forms. The non-parasitic members of the groups are distinguished by a constant number of segments and paired appendages. The numerous parasitic forms differ in various degrees from those which lead an independent life; in extreme cases some of them are so modified, that without a knowledge of their development and the peculiarities of their structure, they would rather be taken for parasitic Worms than for Arthropods. The characteristic swimming feet are, however, usually retained, though often reduced in number, as rudimentary or modified appendages. When they are absent, the developmental history gives a certain indication of the Copepod nature.

Appendages.—The head seems as a rule to fuse with the first thoracic segment; and the cephalothorax so formed bears two pairs of antennæ, a pair of mandibles, the same number of maxillæ, and four maxillipeds, which last are only the external and internal branches of a single pair of appendages (fig. 341); and finally the first pair of swimming feet, which are not unfrequently modified in form. Then come four free thoracic segments, each with a pair of swimming feet, of which the last pair is frequently reduced and in the male may be modified to assist in copulation. Finally, the fifth pair of feet and

* O. Fr. Müller, "Entomostraca seu Insecta testacea, quæ in aquis Daniæ et Norvegiæ reperit, descripsit," Lipsiæ, 1785. Jurine, "Histoire des Monocles," Genève, 1820. W. Lilljeborg, "Crustacea ex ordinibus tribus: Cladocera, Ostracoda et Copepoda, in Scania occurrentibus," Lund., 1853. C. Claus, "Zur Morphologie der Copepoden," Würzb. naturwiss. Zeitschr., 1860. C. Claus, "Die freilebenden Copepoden," Leipzig, 1863.

the corresponding thoracic segment may be entirely absent. The abdomen as well as the thorax consists of five segments, but is without appendages and ends in a caudal fork, the branches of which are furnished at their points with several long caudal setæ (fig. 339). In the female, the two first abdominal segments usually unite to form a double genital segment, on which the genital openings are placed. The abdomen, especially in the parasitic forms, very frequently undergoes a considerable reduction.

FIG. 339.—Female of *Cyclops coronatus*, seen from the dorsal surface. *D*, intestine; *OvS*, ovisacs; *A'*, *A''*, antennæ.

FIG. 340.—An antenna of the male of *Cyclops serrulatus*. *Sf*, olfactory hairs; *M*, muscles.

The anterior antennæ, which are usually many-jointed, bear olfactory hairs, but serve in the free-swimming forms for locomotion, and in the male as prehensile arms for catching and holding the female during copulation (fig. 340). The posterior antennæ are always shorter, and not unfrequently bifurcated and adapted for clinging to surrounding objects. With regard to the oral appendages

(fig. 341), two toothed, usually palped mandibles are placed beneath the upper lip. These function in the free-living Copepoda as masticatory organs, but in the parasitic forms are usually transformed into pointed styliform rods, which are used for piercing. In this case they are frequently placed in a suction tube formed by the junction of the upper and under lips. The two jaws which follow the mandibles are weaker biting plates, and in the parasitic *Copepoda* are reduced to small palp-like protuberances. The maxil-

FIG. 341.—Mouth parts of *Cyclops*. *M*, Mandibles; *Mr*, maxilla; *Kf'*, internal; *Kf''*, external maxilliped.

lipeds, on the contrary, are much longer; they are used to procure food and, especially in the parasitic forms, to attach the body. The thoracic swimming feet consist of a two-jointed basal portion, and two three-jointed setigerous swimming rami, which are comparable to broad swimming plates. In the *Argulidae* these rami are much elongated, and by their numerous joints approximate to the legs of the *Cirripedia*.

Nervous System.—In all cases there is a brain giving off sensory nerves, and also a ventral cord, which either develops some ganglia in its course or is concentrated to a common subœsophageal ganglionic mass. Of *sense organs* the median frontal eye, divided into three parts (*Cyclops eye*), is pretty generally present. The *tactile* sense is specially localized in the setæ of the anterior antennæ, but is probably also present in many other parts of the body. Olfactory hairs are present as delicate appendages of the anterior antennæ, principally in the male sex.

The alimentary canal is divided into a short narrow œsophagus, a wide stomach which often has two blind diverticula near its commencement, and a narrow rectum which opens on the dorsal surface of the last abdominal segment. The surface of the intestine often seems to perform the function of a urinary organ. We find, however, at the same time a shell gland in the cephalo-thorax at the sides of the maxillipeds. In all cases the whole surface of the body performs

the *respiratory* function. *Circulatory* organs are either replaced by the regular oscillations of the intestinal canal (*Cyclops*, *Achtheres*), or there is present in the anterior part of the thorax above the intestine (*Calanidæ*) a short saccular heart, which may even be continued into a cephalic artery (*Calanella*) (fig. 53).

Generative organs.—The *Copepoda* are of separate sexes. Both kinds of genital organs lie in the cephalothorax and in the thoracic segments, and open right and left on the basal segment of the abdomen. Sexual differences in the form and structure of the different parts of the body are almost uniformly found. These lead

FIG. 342.—Metamorphosis of *Cyclops*. *a*, Nauplius larva of *Cyclops serrulatus* after hatching. *b*, Older stage strongly magnified. *c*, Very young *Cyclops* form. *SD*, antennal glands; *Ol*, upper lip; *Mf*, mandibular foot; *Md*, mandible; *Mx*, maxilla, *Mxf*, maxilliped; *F*, *F'*, first and second swimming feet; *Hc*, urinary concretions; *D*, intestine; *Ad*, rectum; *A*, anus; *G*, rudimentary genital organs.

in certain parasitic *Copepoda* (*Chondracanthidæ*, *Lernæopodidæ*) to an extremely striking dimorphism. The males are smaller and move with greater facility; the anterior antennæ and the last pair of feet become accessory copulatory organs, the former serving to hold the female, the latter to affix the spermatophores. The spermatophores are formed in the vas deferens by a mucous secretion which surrounds the seminal mass and hardens to a tough membrane. The females are larger than the males and often move

more clumsily; they carry the eggs about with them in sacs, placed to the right and left on the abdomen. Many of them possess a cement gland at the end of the oviduct; the secretion of this gland passes out with the eggs and gives rise to the stiff covering of the ovisacs. During copulation, which is only an external approximation of the two sexes, the male fastens one or more spermatophores on to the genital segment of the female, and, indeed, on to special openings through which the spermatozoa pass into the receptaculum seminis,

and fertilize the ova either within the body of the mother, or as they pass out into the developing ovisacs.

Development takes place by means of a complicated metamorphosis, which, in many parasitic forms, is a retrograde one. The larvæ, when hatched, have the Nauplius form, with an unpaired frontal eye and three pairs of appendages. Hooked setæ on the second and third pairs of appendages serve to conduct the food into the mouth, which is covered by a large upper lip (fig. 342, *a*). The posterior region of the body is destitute of appendages, and terminates with two setæ at the sides of the anus; it corresponds to the thorax and abdomen, which are as yet undifferentiated.

The alterations undergone by the young larvæ in the course of their further growth are connected with a number of successive moults, and consist principally in an elongation of the body and the appearance of

FIG. 343.—Metanauplius of *Cyclopsine*. *O*, eye; *G*, rudimentary genital organs; *SD*, antennal gland; *A'*, *A''*, antennæ; *Md*, mandible; *Mx*, maxilla; *Mf*, maxilliped.

fresh appendages. Even in the next larval stage (fig 342, *b*), a fourth pair of appendages, the future maxillæ, makes its appearance behind the three original pairs, which develop into the antennæ and mandibles. In a later stage three fresh pairs of appendages are formed. Of these the first corresponds to the maxillipeds, while the two last pairs represent the first rudiments of the anterior swimming feet. In this stage (*Metanauplius*) (fig.

343), the larva still resembles a Nauplius, and it is only after another moult that it is transformed into the first *Cyclops*-like form. It then resembles the adult animal in the structure of the antennæ and mouth parts, although the number of the appendages and the body rings is smaller (fig. 342, c). The two last pairs of appendages already have the form of short biramous swimming feet, and the rudiments of the third and fourth pairs of swimming feet have made their appearance as projections beset with setæ. The body consists in this stage of the oval cephalothorax; the second, third and fourth thoracic segments; and an elongated terminal portion, which gives rise to the last thoracic segment, and to all the abdominal segments by a progressive segmentation, and already terminates in the caudal fork.

FIG. 344.—*Achtheres percarum*.—a, Nauplius form. b, Larva in the youngest *Cyclops* stage; *Kf*, *Kf'*, maxillipeds. c, Female seen from the ventral side. *Ov*, Ovaries; *KD*, cement glands. d, The smaller male seen from the side; *Mxf'*, *Mxf''*, maxillipeds.

Many forms of parasitic *Copepoda*, for example *Lernanthropus* and *Chondracanthus*, do not get beyond this stage of body segmentation, and obtain neither the swimming feet of the third and fourth pairs, nor a fifth thoracic segment separate from the stump-like abdomen; others, for example *Achtheres*, by the loss of the two anterior pairs of swimming feet, sink back to a still lower stage (fig. 344).

All the non-parasitic and many of the parasitic *Copepoda* pass in the successive moults through a larger or smaller number of developmental stages, in which the still undeveloped segments and appendages make their appearance, and the appendages already

present undergo further segmentation. Many parasitic *Copepoda*, however, pass over the series of Nauplius forms, and the larva, as soon as hatched, undergoes a moult, and appears at once in the youngest Cyclops form, with antennæ adapted for adhering and mouth parts for piercing (fig. 344). From this stage they undergo

a retrogressive metamorphosis, in which they become attached to a host, lose more or less completely the segmentation of the body which grows irregular in shape, cast off their swimming feet, and even lose the eye, which was originally present (*Lernæopoda*). The males, however, in such cases often remain small and dwarfed, and adhere (frequently more than one) firmly to the body of the female in the region of the genital opening (fig. 345).

In the *Lernæa* (fig. 346) such pigmy males were for a long time vainly sought for upon the very peculiarly shaped body of the large female (fig. 346, *c*, *d*) which carries egg tubes. At last it was discovered that the small cyclops-like males (fig. 346, *a*), lead an independent life, and swim about freely by means of their four pairs of swimming feet; and that the females (fig. 436, *b*), in the copulatory stage resemble the males, and that it is only after copulation that they (the females) become parasitic and undergo the considerable

FIG. 345.—The two sexual animals of *Chondra canthus gibbosus* magnified about six diameters. *a*, Female seen from the side; *b*, from the ventral surface with adhering male; *c*, male strongly magnified. *An'*, Anterior antennæ; *An''*, antennæ for attachment; *F'*, *F''*, the two pairs of feet; *A*, eye; *Ov*, egg-tubes; *Oe*, œsophagus; *D*, intestine; *M*, mouth parts; *T*, testis; *Vd*, vas deferens; *Sp*, spermatophore.

increase in size and modification of form which characterises the female with egg-tubes.

1. Sub-order: Eucepoda.

Copepoda with swimming feet, the rami of which are two or three jointed. They have biting or piercing and sucking mouth parts.

1. *Gnathostomata*. For the most part non-parasitic; oral apparatus adapted for mastication; fully segmented body.

Fam. *Cyclopidae*. Mostly fresh-water animals, without a heart, and with a simple eye. The second pair of antennæ are four-jointed and never biramous. The feet of the fifth pair are rudimentary in both sexes. The male employs the anterior antennæ for prehension. *Cyclops coronatus* Cls., *Canthocamptus minutus* Cls., *Harpacticus chelifer* O. Fr. Müll., North Sea.

Fam. *Calanidae*. The anterior antennæ are very long, only one of them is modified for prehension. The posterior antennæ are biramous. Heart always present. The feet of the fifth pair are, in the male, modified to assist in copulation. *Cetochilus septentrionalis* Goods., *Diaptomus castor* Jur. *Irenæus Patersonii* Templ.

Fam. *Notodelphyidae*. Structure of body like that of the *Cyclopidae*. The posterior antennæ modified for attachment. The two last thoracic segments are fused in the female and form a brood cavity for the reception of the eggs. They live in the branchial cavity of Ascidians. *Notodelphys agilis* Thor.

2. *Parasita** (*Siphonostomata*). Mouth parts adapted for piercing and sucking, usually with incomplete segmentation of the body and reduced abdomen.

The posterior antennæ and maxillipeds end with hooks for attachment. Some of

FIG. 346.—*Lernæa branchialis*. a, Male (about 2 to 3 mm. long). Oc, Eye; G, brain; T, testis; M, stomach; Fⁱ to Fⁱⁱ, the four pairs of swimming feet; Sp, spermatophore sac. b, Female (5 to 6 mm. long at the time of copulation). A', A'', the two pairs of antennæ; D, intestine; R, proboscis; Mx^f, maxilliped. c, Female of *Lernæa branchialis* after copulation undergoing metamorphosis; d, the same with egg sacs, natural size.

* Besides Steenstrup and Lütken l.c. compare A.v. Nordmann, "Mikrographische Beiträge zur Naturgeschichte der wirbellosen Thiere," Berlin, 1832. H. Burmeister, "Beschreibung einiger neuen und wenig bekannten Schmarot-

them still swim freely, but most of them live on the gills, in the pharynx, and on the outer skin of fishes. Some live within the tissues of their host (*Penella*), and nourish themselves on the blood and juices of the latter.

Fam. **Corycæidæ**. Anterior antennæ short, few jointed, and similar in both sexes. The posterior antennæ unbranched, with clasping hooks, usually different according to the sex. Mouth parts often arranged for piercing. Median eye and lateral eyes often present. They live partly as temporary parasites. *Corycæus elongatus* Cls., *Sapphirina fulgens* Thomps.

Fam. **Chondracanthidæ**. Body elongated, often without distinct segmentation, and furnished with pointed outgrowths. Abdomen stump-like. The two anterior pair of swimming feet are represented by bifid lobes, the others are wanting. There is no suctorial proboscis, the mandibles are sickle-shaped. The pear-shaped males are small and dwarfed, and attached, often in pairs, to the body of the female. *Chondracanthus gibbosus* Kr. (on *Lophius*). *Ch. cornutus* O. Fr. Müll., on flat fish (*Pleuronectidæ*) (fig. 345).

Fam. **Caligidæ**. Body flat, with shield-like *cephalothorax*, and very large genital segment which in the female is especially swollen. Abdomen, on the contrary, is small and more or less reduced. There is a suctorial tube and styliform mandibles. Four paired biramous swimming feet enable the animal to swim rapidly. They live on the gills and the skin of marine fish, and the females have long string-like egg tubes. *Caligus rapax* Edw., *Cecrops Latreillii* Leach.

Fam. **Lernæidæ**. The body of the female vermiform or rod-shaped; unsegmented, with outgrowths and processes on the head. Mouth parts piercing with suctorial tube. There are four pairs of small swimming feet. The females become attached to fishes, in which the anterior part of their body is buried. *Lernæocera cyprinacea* L., *Penella sagitta* L., *Lernæa branchialis* L. (fig. 346).

Fam. **Lernæopodidæ**. Body separated into head and thorax, abdomen rudimentary. Mouth parts piercing with suctorial tube. The external maxillipeds attain a considerable size, and in the female unite at their points so as to form a single organ of attachment, by means of which the animal adheres permanently. Swimming feet completely absent. The males, which are more or less dwarfed, have large free clasping feet, and are, like the females, without swimming feet. *Achtheres percarum* Nordm. (fig. 344). *Anchorella uncinata* O. Fr. Müll. (on species of *Gadus*).

2. Sub-order: Branchiura.*

Carp-lice. With large compound eyes, and long protrusible spine in front of the suctorial tube of the mouth; with four pairs of elongated biramous swimming feet.

zerkrebse," *Nova acta Ac. Cæs. Leop.*, Tom XVII., 1835. C. Claus, "Ueber den Bau und die Entwicklung von *Achtheres percarum*," *Zeitschr für wiss. Zool.*, 1861. C. Claus, "Beobachtungen über *Lernæocera*, etc., Marburg, 1868.

* Jurine, "Mémoire sur l'Argule foliacé," *Annales du Muséum d'hist. nat.*, Tom. VII., 1806. Fr. Leydig, "Ueber *Argulus foliaceus*," *Zeitschr für wiss. Zool.*, Tom II., 1850. E. Cornalia, "Sopra una nuova specie di crostacei sifonostomi," Milano, 1860. C. Claus, "Ueber die Entwicklung, Organization und systematische Stellung der Arguliden," *Zeitschr für wiss. Zool.*, Tom XXV., 1875.

The *Branchiura* are often placed near the *Caligidæ*, but they differ from them and from the true *Copepoda* in several essential particulars. In the general body form they certainly resemble the *Caligidæ* except in the hind part of the body, which is split into two plates (caudal fins). Their internal structure, however, and the structure of the appendages distinguish them from the above-mentioned parasitic *Crustacea*. A large suctorial tube projects above the mouth, and in it are concealed finely serrated mandibles and styloform maxillæ. A little above this proboscis there is inserted a long cylindrical tube, which terminates in a retractile styloform spine, and contains the ducts of a pair of glandular tubes said to be poison glands. Powerful organs of attachment are placed on each side of and beneath the mouth; they consist of two parts—(1) of an anterior pair of appendages which correspond to the anterior maxillipeds and are in *Argulus* modified into large sucking discs, the hook-bearing terminal portion being reduced; and (2) of a posterior pair, which corresponds to the second pair of maxillipeds, and is provided with numerous spines on its broad basal portion, a tactile protuberance and two curved terminal claws at its extremity.

FIG. 347.—Young male of *Argulus foliaceus*. *A'*, Anterior antennæ; *Sg*, sucker (anterior maxilliped); *Kf*, maxilliped; *Sf*, swimming feet, *R*, rostrum; *St*, spine; *D*, intestine; *T*, testes.

Next to these come the four paired swimming feet of the thoracic region, which, with the exception of the last, are, as a rule, covered by the sides of the cephalo-thoracic shield. Each of these consists of a large many-jointed basal portion, and two much narrower rami, which are beset with long swimming setæ and in their form and setigerous investment are not unlike the biramous appendages of the *Cirripedia*, being like them derived from the Copepod-like feet of the larva (fig. 347).

The internal organization recalls that of the *Phyllopoda*. The **nervous system** is distinguished by the great size of the cerebral ganglion, and by the ventral chain composed of six closely approximated ganglia. In addition to two large compound lateral eyes, there is present an unpaired tri-lobed median eye. The **alimentary canal** consists of a short arched ascending œsophagus, a wide stomach with two lateral ramified appendages, and a rectum which runs directly backwards and opens to the exterior in the median indentation of the caudal fin above the two plates, which correspond to the caudal fork. There are two lateral slit-like apertures in the heart, and a long aorta. The entire surface of the cephalothorax functions as a **respiratory organ**. There seems, however, always to be a specially strong current of blood in the caudal fin, so that this part of the body may be regarded as a sort of gill.

Reproduction.—The small, more agile male possesses peculiar copulatory appendages on the posterior swimming feet. The females do not carry their eggs about in sacs in the typical Copepod manner, but fasten them to surrounding objects. The vitelline membrane of the deposited eggs acquires a vesicular consistence. The young are hatched as larvæ, and undergo a metamorphosis.

Fam. *Argulidæ*, Carp-lice. *Argulus* O. Fr. Müll. The anterior pair of maxillipeds modified into large suckers. There is a styliform spine apparatus. *A. foliaceus* L. (Pou de poissons, Baldner) parasitic on Carps and Sticklebacks. *A. coregoni* Thor., *A. giganteus* Luc., *Gyropeltis* Hell. The maxillipeds end in a claw; styliform spine absent. *G. Kollari* Hell, parasitic on the branchiæ of *Hydrocyon*, Brazil. *G. Doradis* Corn.

Order 4.—CIRRIPEDIA.*

Fixed, and for the most part hermaphrodite Crustacea with indistinctly segmented body enclosed by a reduplication of the skin, and a calcareous valved shell. As a rule, there are six pairs of biramous thoracic appendages.

On account of the resemblance of their shell to that of the mussels, the *Cirripedia* were held to be Molluscs until Thompson and Burmeister, by the discovery of their larvæ, satisfactorily proved that they belong to the *Entomostraca*. They are enclosed in a mussel-

* Compare S. V. Thompson, "Zoological researches," Tom. I., 1829. H. Burmeister, "Beiträge zur Naturgeschichte der Rankenfüssler." 1832. Ch. Darwin, "A monograph of the Sub-Class Cirripedia," 2 vol., London, 1851-1854. A. Krohn, "Beobachtungen über die Entwicklung der Cirripeden," *Archiv für Naturgesch* 1860. C. Claus, "Die Cypris-ähnliche Larve der Cirripeden, etc," Marburg, 1869. R. Kossmann, "Suctoria und Lepadina," Würzburg, 1873.

like shell composed of several (4, 5 or more) pieces. These pieces, which originate by the deposition of calcareous matter in the chitinous covering of a large reduplication of the skin (mantle), are distinguished as *scuta*, *terga*, and *carina*. The animal is invariably fixed by the anterior end of the head, which in the *Lepadidæ* (fig. 348, *a*) may be drawn out into a long stalk projecting freely from the shell. In the *Balanidæ*, which are without the stalk (fig. 348, *b*), the body is surrounded by an external calcareous tube, usually composed of six pieces; the aperture of the tube is closed by a sort of operculum formed of calcareous plates lying inside (fig. 348, *b*). In

FIG. 348 —*a*, *Lepas* after removal of the right shell. *A'*, Anterior antennæ at the end of the stalk; *C*, carina; *Te*, tergum; *Sc*, scutum; *Mk*, oral cone; *F*, caudal fork; *P*, cirrus or penis; *M*, muscle. *b*, *Balanus tintinnabulum* (after Ch. Darwin), one-half of the shell has been removed; *Tu*, Section of the outer shell; *Ov*, ovary; *Od*, oviduct; *Oe*, opening of oviduct; *Ad*, adductor muscle; *Sc*, scutum; *Te*, tergum; *A'*, anterior antennæ.

both cases the attachment is effected principally by the hardening of the secretion of the so-called cement gland, which opens on the penultimate joint of the small and delicate anterior antennæ; this joint being dilated to form a sort of sucker. The body, which is surrounded by the mantle and its shell-plates, lies with its hinder region stretched upwards so that the appendages, which are used to cause currents in the water, may be protruded from the slit-like space left on the ventral side between the paired scuta and terga.

Appendages and external features.—A head with antennæ and

jaws can be distinguished from the region of the body (thorax) bearing the biramous appendages, but there is no distinct boundary between these two regions. The anus is situated at the extremity of the small stump-like abdomen, which succeeds the thorax and is often only indicated by two caudal appendages. Posterior antennæ are invariably absent, while the anterior pair persists, even in the adult, as small organs of attachment. The oral apparatus is situated on a ventral prominence of the cephalic region, and consists of an upper lip with palps, two mandibles and four maxillæ, of which the two last unite to form a sort of under lip. On the thorax there are

FIG. 349.—The organization of *Lepas*, after removal of the integument. *Cd*, Cement gland and duct; *L*, liver; *T*, testis; *Vd*, vas deferens; *Ov*, ovary; *Od*, oviduct; *Cf*, thoracic appendages. Other letters as in fig. 348.

usually six pairs of many-jointed biramous appendages, the elongated cirriform rami of which are richly beset with hairs and setæ and serve to set up currents in the water in which the particles of food are brought to the animal. The stump-shaped abdomen bears an elongated cirrus, which is bent towards the ventral surface between the thoracic appendages, and constitutes the male copulatory organ. There are numerous and very peculiar variations in the shape of the whole body. Not only may the deposition of calcareous matter in the mantle be wanting, and the biramous thoracic appendages be reduced in number or even absent, but the mouth parts and the appendages may also be lost (*Peltogastridæ*), and the body may be reduced to the form of an unsegmented tube, sac, or lobed disc.

Nervous system and sense organs.—The Cirripedia possess a paired cerebral ganglion and a ventral chain of ganglia, of which there are usually five pairs, but which are sometimes fused to a common ganglion mass (*Balanidæ*). There is a double eye, which, although rudimentary, corresponds to the unpaired Nauplius eye.

An alimentary canal is absent only in the *Rhizocephala*. In the

Lepadidæ and the *Balanidæ*, the alimentary canal consists of a narrow œsophagus, a saccular dilated stomach provided with several cæcal (hepatic) diverticula, an elongated chyle-forming intestine, and a short rectum, which is only sometimes clearly marked off from the intestine (fig. 349). The *Rhizocephala* (fig. 354, *a*), which are without an alimentary canal, possess root-like processes of the parenchyma, which ramify in the viscera, especially the liver of Decapods, and absorb from them endosmotically the nutritive juices (as in *Anelasma*).

Special glandular organs, the so-called cement glands (peculiar to the *Cirripedia*), open on the sucker of the persistent (anterior) antennæ; the animal is fixed by their secretion, and the *Rhizocephala* alone seem to be entirely without them.

A heart and vascular system seem to be wanting in all cases. The tubes which are present on several thoracic appendages of many *Lepadidæ* are regarded as branchiæ, as are also two plicated lamellæ on the interior of the mantle of the *Balanidæ*.

Generative organs.—The Cirripedia are, with a few exceptions, hermaphrodite. The testes are branched glandular tubes, and lie at the sides of the alimentary canal (fig. 349, *T*). The vasa deferentia which dilate into vesiculæ seminales reach to the base of the cirriform penis, in which they unite to form a common ductus ejaculatorius opening at the point of the penis (*Vd*). The ovaries in the *Balanidæ* lie in the basal part of the body cavity (fig. 348, *Ov*); in the *Lepadidæ* (fig. 349) they are moved into the prolongation of the head, which is known as the stalk. The oviducts, according to

FIG. 350.—*Aleippe lampas* (after Ch. Darwin.) *a*, Male, very strongly magnified; *A'*, antennæ; *T*, testis; *Vs*, seminal vesicle; *D*, redundancy of the skin; *O*, eye; *P*, penis. *b*, Longitudinal section through female; *F*, maxilliped; *Cf*, the three pairs of legs; *Ov*, ovary.

FIG. 351.—*a* Later Nauplius larva. *A*, anus; *Ol*, proboscis with mouth; *H*, frontal horns; *D*, intestine; *A'*, *A''*, 1st and 2nd antennæ; *Mdf*, mandibular foot (third pair of appendages). *b*, Metanauplius larva of *Balanus* before the moult. Beneath the skin are the rudiments of the lateral eyes (*O*) and all the appendages *F'* to *F''* of the Cypris stage; *Ff*, frontal filament; *O*, unpaired eye; *Dr*, gland cells of the anterior horns; *A'*, the antennæ with suckorial disc; *Mx* rudiment of maxilla.

Krohn, open on a prominence on the basal joint of the anterior pair of thoracic appendages. The eggs accumulate in the cavity between the mantle and the body in large thin-walled flattened sacs, which, in the *Lepadidæ*, are attached to a fold of the mantle and are packed together on the dorsal surface of the animal.

In spite of the hermaphroditism, there are, according to Darwin, in certain genera (*Ibla*, *Scalpellum*) very simply organised dwarfed males of peculiar form, the so-called *complemental males*, which are attached like parasites to the body of the hermaphrodite. There are also diœcious Cirripedes with a strongly marked dimorphism of the sexes. This is the case with *Scalpel-*

Ium ornatum and *Ibla Cumingii*; also with the remarkable genera *Cryptophialus* and *Alcippe* (fig. 350). The males of these forms are not only small and dwarfed, but also, according to Darwin, have neither mouth, digestive canal, nor thoracic appendages. As a rule, two or sometimes more attach themselves to the body of the female.

Development.—The eggs, while still within the brood-pouch, undergo an irregular segmentation. The clear cells arrange themselves around the food yolk in the form of a blastoderm, the ventral side of which soon becomes considerably thickened in consequence of the appearance of the mesodermic layer. The larvæ leave the egg as Nauplii (fig. 351, *a*, *b*), of oval or pear-shaped form, with unpaired frontal eye, lateral frontal horns, and three pairs of appendages, of which the anterior is simple, the two next biramous and closely beset with swimming setæ.

After several moults, the larva, which has grown to a considerable size, enters on a new stage of development, the so-called Cypris stage (pupa) (fig. 352). The reduplication of the skin has the form of a bivalve mussel-like shell, through the gaping ventral edges of which the appendages can be protruded. While the form of the shell recalls that of the *Ostracoda*, the structure of the body, so far as the segmentation and form of the appendages are concerned, approximates to that of the *Copepoda*. The anterior appendage of the Nauplius larva has given rise to a four-jointed antenna, the penultimate joint of which has become large and disc-shaped and contains the opening of the cement gland, while the terminal joint bears in addition to tactile setæ one or two delicate lancet-shaped olfactory hairs. The frontal horns are transformed into two conical prominences near the anterior margin. Of the two pairs of biramous appendages, those which correspond to the second pair of antennæ are cast off, while

FIG. 352.—Median section through a pupa of *Lepas*. *A'* Attaching antenna; *C*, carina; *Te*, tergum; *Sc*, scutum; *Ov*, ovary; *G*, cerebral ganglion; *Gg*, ganglionic chain; *D*, alimentary canal; *Cd*, cement gland; *Mk*, oral cone; *Ab*, abdomen; *P*, rudiment of the penis; *M*, muscle.

the posterior pair becomes the rudiment of the anterior jaws (mandibles) of the oral cone, which is still closed and on which the first rudiments of the maxillæ and under lip are already visible. The oral cone is followed by the thoracic region with six pairs of biramous Copepod-like swimming feet, and a minute three-jointed abdomen, which terminates in two caudal appendages and caudal setæ. The pupa has a large pair of compound eyes at the sides of the unpaired eye-spot, and swims about by means of its swimming feet. It appears not to take in food. The material necessary for its further changes is stored up principally in the cephalic and dorsal regions in the form of a largely-developed fat body.

FIG. 353.—Young *Lepas* after disappearance of the two horny valves of the shell and the straightening of the anterior part of the head (stalk), which in the pupa stage is bent. Letters as in fig. 349.

After swimming about for a longer or shorter time, the pupa fixes itself by the suctorial disc of its bent antennæ to some foreign body. The parts of the adult Cirripede are now visible beneath the skin, and the cement gland begins to secrete a cement, which hardens and so brings about the permanent attachment of the young animal. In the *Lepadidæ* the region of the head above and between the antennæ grows so much that it projects from the pupal integument, beneath which the calcareous pieces of the shell of the Cirripede can be seen, and after the moulting of the chitinous skin of the pupa constitutes the fleshy peduncle by which the animal is attached, and into which the rudiments of the ovaries project (fig. 353). The paired eyes of the free-swimming Cypris larva disappear, while the unpaired pigment spot remains.

The mouth parts become fully differentiated, and the biramous swimming feet become short, many-jointed cirriform appendages.

The Cirripedia are marine animals. They attach themselves to various foreign objects. They are found fixed, usually in groups, to logs of wood, rocks, mussel shells, Crustacea, the skin of whales, etc. Some, as *Lithotrya*, *Alcippe*, and the *Cryptopialidæ*, are able to bore into Lammellibranch shells and Corals, while the *Rhizocephala* are parasitic on Crustacea. In the *Rhizocephala* the body is saccular,

and the animal loses all its appendages and its alimentary canal, and extracts the juices of its host (*Decapoda*) by means of root-like processes (fig. 354).

1. **Pedunculata.** There is a peduncle and six pairs of biramous feet; the mantle has usually carina, scuta, and terga.

Fam. **Lepadidæ.** Peduncle well marked, and not provided with calcareous plates. There is a membranous mantle, which, as a rule, is provided with five shell plates, of which the scuta and terga lie behind one another (fig. 348, *a*). *Lepas* L. (*Anatifa* Brug.), *L. fascicularis* Ellis, (*vitrea* Lam.) Found from the Northern Seas to the South Sea. *L. anatifera* L., cosmopolitan. *Conchoderma*

FIG. 354.—*a*, *Sacculina purpurea* (after Fr. Müller). *Oe*, Aperture of the mantle sac; *W*, root-like processes; *K*, genital aperture. *b*, Nauplius larva of *Sacculina*. *A'*, *A''*, *Mdf*, appendages. *c*, Pupa of *Lernæodiscus porcellanæ* (after Fr. Müller). *F*, The six pairs of legs; *Ab*, abdomen; *A'*, attaching antennæ; *O*, eye.

Olf. (*Otione*, *Cineras* Leach.), *C. virgata* Spengl., frequently attached to ships. *C. aurita* L., *Anelasma* Darwin. The stalk is provided with root-like processes, which grow into the skin of *Squalidæ*. *A. squalicola* Lovén.

Fam. **Pollicipedidæ.** Peduncle not sharply distinct, scaly or hairy. The shell plates very strong, numerous. The scuta and terga lie close to one another. There are sometimes complemental males. *Pollicipes cornucopia* Leach., Ocean and Mediterranean. *Scalpellum vulgare* Leach., North Sea and Mediterranean. *Sc. ornatum* Gray, South Africa. *Ibla quadrivalvis* Cuv., South Australia. *J. Cumingii* Darw., Philippines.

2. **Operculata.** The peduncle is absent or rudimentary. The body is surrounded by an external ring of plates at the extremity of which the scuta and terga form an operculum, which is usually freely movable and provided with depressor muscles (fig. 348, b).

Fam. **Balanidæ.** Scuta and terga freely movable and articulating with one another. The gills are formed each of a fold. *Balanus tintinnabulum* L. Widely distributed and found in a fossil form. *B. improvisus* Darw. Found in brackish water.

Fam. **Coronulidæ.** Scuta and terga freely movable, but not articulating with one another. The two gills formed each of two folds. *Tubicinella trachealis* Shaw., South Sea. *Coronula balenaris* L., Antarctic Ocean. *C. diadema* L., Arctic Ocean.

3. **Abdominalia.** The irregularly segmented body is enclosed in a flask-shaped mantle, and bears on its terminal portion three pairs of cirriform feet. Mouth parts and alimentary canal completely developed. The sexes are separate. They live as parasites buried in the calcareous shell of *Cirripedia* and *Mollusca*.

Fam. **Alciippidæ.** With four pairs of feet, of which the first pair is palpiform, and the two last are uniramous and composed of few elongated joints. The sexes are separate. The female bores into Mollusc shells. The male is dwarfed, and is without mouth, stomach, or feet. *Alcippe lampas* Hanc., bores into the columella of the shells of *Fusus* and *Buccinum*. Found on the coast of England.

Fam. **Cryptophialidæ.** They have three pairs of feet at the posterior end of the body. *Cryptophialus* Darw., sexes separate. *Cr. minutus* Darw., in the shell of *Concholepas Peruviana*, found on the west coast of South America. *Kochlorine hamata* Noll, lives in excavations in the shell of *Haliotis*.

4. **Apoda.** The body is segmented, and is composed of eleven rings. There is no special reduplication of the mantle. The shape resembles that of a maggot. The attaching antennæ are elongated to the form of a band. The mouth is adapted for sucking, and has mandibles and maxillæ. Feet absent. The digestive canal is rudimentary. They live parasitically in the mantle of other *Cirripedia*. They are hermaphrodite.

Fam. **Proteolepadidæ** with the single genus *Proteolepas* Darw., *Pr. biveneta* Darw., West Indies.

5. **Rhizocephala* (Suctorio).** Body tubular or saccular, without segmentation or appendages; with narrow, short peduncle for attachment, from which branched, root-like filaments arise. The

* W. Lilljeborg, "Les genres Liriope et Peltogaster," *Nova acta reg. soc. scien. Upsal.*, Ser. 3, vol. iii., 1860. Fr. Müller, "Die Rhizocephalen," *Archiv für Naturgesch.*, 1862 and 1863. R. Kossmann, "Beiträge zur Anatomie der schmarotzenden Rankenfüssler," *Verh. der med.-phys. Gesellsch.*, Würzburg, Neue Folge, Tom. IV.

latter pierce the body of the host, and carry nourishment to the parasite. Mantle saccular, and without calcareous plates, with narrow aperture which can be closed. Mouth and alimentary canal absent. The testes are usually paired, lie between the ovaries, and open into the brood-pouch. The *Rhizocephala* live principally as parasites on the abdomen of the *Decapoda*, and wind their root-like filaments around the viscera of the latter.

Fam. *Peltogastridæ*. *Peltogaster paguri* Rathke. *Sacculina carvini* Thomps., *Lernæodiscus porcellanæ* Fr. Müll., Brazil.

II.—MALACOSTRACA.

The *Malacostraca* differ from the *Entomostraca* in possessing a constant number of segments and paired appendages. The boundary between the head and thorax cannot be absolutely fixed on account of the varying number of anterior pairs of legs which are modified to form jaws. These regions are composed of thirteen segments altogether, and bear the same number of pairs of appendages, while the abdomen, which is always distinct, includes six segments and the same number of paired limbs and terminates with an anal plate (*telson*) derived from the terminal portion of the body.

Amongst the living *Malacostraca* there is, however, a single group of forms (*Nebalia*) (fig. 355, *a*, *b*), which differ in having a larger number of abdominal segments. They have, in addition to the six abdominal segments with appendages, two segments without appendages, and an elongated Phyllopod-like caudal fork. This remarkable form was for a long time regarded as a Phyllopod, and in many of its characters represents a connecting link between the *Phyllopoda* and the *Malacostraca*. The structure and segmentation of the head and thorax resembles that of the *Malacostraca*, but the terminal region of the abdomen does not present the special form of a caudal plate or telson. In *Nebalia* we probably have to do with an offshoot of the Phyllopod-like ancestors of the *Malacostraca*, which has persisted to the present time.

The head includes in all cases, behind the mandibular segment on which two paragnathi form a kind of underlip, the segments of two pairs of maxillæ. The latter preserve more or less the characters of Phyllopod feet. The head, therefore, consists of five segments, each with its pair of appendages, viz., two pairs of antennæ, one pair of mandibles, and two pairs of maxillæ. It is followed by the thorax,

which is composed of eight segments. The eight pairs of thoracic appendages may have an exactly similar shape, and possess two separate and many-jointed rami. This form of thoracic appendage is characteristic of the Schizopoda; in *Nebalia** the thoracic appen-

FIG. 355.—*Nebalia Geoffroyi*, strongly magnified. *a*, Female; *b*, male; *R*, rostrum; *O*, stalked eye; *M*, crop; *D*, intestine; *S*, shell *G*, vas deferens.

* *Nebalia* is best placed in a special group, *Leptostraca*, between the *Entomostraca* and *Malacostraca*. The palæozoic fossil genera *Hymenocaris*, *Peltocaris*, etc., would have to be placed in such a group.

dages closely resemble the typical Phyllopod limb. As a rule, however, some of the anterior thoracic legs take part in preparing the food and have a form intermediate between maxillæ and thoracic legs. Such are called *foot-jaws* or *maxillipeds*. In the *Arthrostraca* the anterior pair of thoracic appendages only are so modified, and the segment bearing them joins the head; the thorax is, therefore, in this group composed of seven segments, each with its pair of appendages. In other groups of *Malacostraca* the next or two next pairs of thoracic legs have the form of maxillipeds, so that there is no sharp division between the head and thorax. The latter is, at least partially, covered by a shield-like reduplication of the skin, which morphologically corresponds to the Phyllopod shell and forms a more or less extensive carapace, which fuses with the back of the thorax, and under which the posterior, rarely all the thoracic segments may remain separate as free rings.

Order 1.—ARTHROSTRACA.*

Malacostraca with lateral sessile eyes, usually with seven, more rarely with six or fewer separate thoracic segments, and the same number of pairs of legs. Without a reduplication of the skin.

The head bears four antennæ, the two mandibles, four maxillæ, and a pair of maxillipeds; in all six pairs of appendages. A small bilobed plate, distinguished as the under-lip, behind the pair of mandibles, marks the boundary of the *primary* region of the head. The two pairs of maxillæ as well as the maxillipeds are secondary cephalic appendages derived from the thoracic region of the body.

Behind the head there are usually seven free thoracic rings with the same number of pairs of appendages, which are adapted for creeping or swimming. The number of distinct thoracic segments is in rare cases reduced to six (*Tanais*) or five (*Anceus*), the anterior or the two anterior segments of the thorax becoming intimately connected with the head. In the latter case a more or less extensive cephalothoracic carapace is formed. The abdomen which follows the thorax includes, as a rule, six segments bearing limbs, and a simple or split plate without appendages and representing the terminal segment. The number of the abdominal segments and appendages may, however, be reduced (*Isopoda*), and the entire abdomen may

* Besides the works of Latreille, M. Edwards, Dana, and others, compare Spence Bate and J. O. Westwood, "A History of the British sessile-eyed Crustacea," Tom. I. and II., London, 1863-1868. G. O. Sars, "Histoire naturelle des Crustacés d'eau douce de Norvège," Christiania, 1867.

even be reduced to an unsegmented stump-shaped appendage (*Læmodipoda*).

The **nervous system** consists of a cerebral ganglion and a ventral ganglionic chain, which is most distinctly composed of two lateral halves. In the *Isopoda* there is also an unpaired visceral nerve. The two eyes are always sessile, compound eyes, with smooth or faceted cornea; they are never stalked. Delicate olfactory fibres are often present on the anterior antennæ, and are especially numerous in the male sex.

The **alimentary canal** begins with a short œsophagus, which passes upwards to open into a wide crop, supported by firm horny bands and often armed with strong chitinous plates. The crop leads into a long intestine provided with two or three pairs of tubular hepatic glands. The rectum, which may possess one or two tubular appendages (probably urinary), opens at the posterior end of the body.

The **antennal gland** opens on the basal segment of the posterior antenna, often upon a conical protuberance.

Vascular system.—A heart is always present as the central organ of the circulation. It may either have the form of a tube extending along the whole length of the thorax (*Amphipoda*); or it may be saccular and placed in the abdomen (*Isopoda*). In the first case the gills are placed on the thoracic feet as tubular appendages; in the latter, on the other hand, they are placed on the abdomen. From the heart the blood passes through an anterior and posterior aorta, and usually through lateral arteries. The vessels conduct the blood into the body cavity, whence it returns in regular streams to the lateral paired slits of the heart.

Generative organs.—The *Arthrostraca* are of separate sexes. The males are frequently distinguished from the females by the modification of certain parts of the appendages to form prehensile organs, by a greater development of olfactory hairs on the anterior antennæ, and by the position of the sexual and copulatory organs. It is rare to find a strongly marked dimorphism of the sexes (*Bopyrus*, *Praniza*). The generative organs open either at the posterior part of the thorax or at the base of the abdomen; the female always on the antepenultimate pair, the male on the last pair of the thoracic appendages or between the first of the abdomen (*Isopoda*). The ovaries are two simple or branched tubes with the same number of oviducts. The testes similarly seem to be composed of one (*Amphipoda*) or more (3) pairs of tubes (*Isopoda*), the efferent ducts of which (vasa deferentia) either remain separate or unite to form a copulatory

organ. Appendages of the legs may also be present as additional aids to copulation. The mature ova are, as a rule, carried about by the female in brood pouches formed by the lamellar appendages of the thoracic feet (oostegites). Development as a rule takes place without metamorphosis, but the form and appendages of the young animal not unfrequently differ from those of the adult animal (*Phronima*). The segments and the appendages may even be incomplete in number after birth (*Isopoda*).

Fossil *Arthrostraca* are found in the Oolite (*Archæoniscus*). *Prosoponiscus* occurs in the Permian, *Amphipeltis* in the Devonian.

1. Sub order.—Amphipoda.*

Arthrostraca with laterally compressed body, with gills on the thoracic feet and an elongated abdomen, of which the three anterior segments bear the swimming feet, while the three posterior bear posteriorly directed feet adapted for springing (fig. 356).

The *Amphipoda* are small animals, being only in rare cases several inches long (*Lysianassa magellanica*). They move in the water principally by springing and by swim-

FIG. 356.—*Gammarus neglectus* (after G. O. Sars), with eggs between the brood lamellæ (oostegites) on the thorax. A', A'', the two antennæ; Kf, maxilliped; F to F', the seven pairs of thoracic appendages; Sf', the first swimming foot of the abdomen.

ming. The head, which is sometimes small (*Crevettina*, fig. 356), sometimes large and then much swollen (*Hyperina*, fig. 357), is sharply distinct from the thorax and is fused with the first of the seven thoracic segments only in the aberrant group of the *Læmodipoda*.

The two pairs of antennæ usually consist of a short strong shaft

* Besides the older works of De Geer, Rösel, M. Edwards, etc., compare C. Spence Bate, "On the Morphology of some Amphipoda of the Division Hyperina," *Ann. of Nat. Hist.*, Ser. 2, vol. xix., 1857. C. Spence Bate, "On the nidification of Crustacea," *Ann. of Nat. Hist.*, Ser. 3, vol. i. C. Spence Bate, "Catalogue of the specimens of Amphipodous Crustacea in the collection of the British Museum," London, 1862. E. van Beneden et Em Bessels, "Mémoire sur la formation du Blastoderme chez les Amphipodes, etc," Bruxelles, 1868. C. Claus, "Der Organismus der Phronimiden, *Arbeiten aus dem Zool. Institut. der Universität Wien*, Tom II., 1879.

and a long multiarticulate flagellum, which, however, may be more or less rudimentary. The anterior antennæ, which are always longer in the male, often bear a short accessory flagellum and present numerous modifications in their special form. In the *Hyperina* they are very short in the female; while in the male they are of considerable length and are closely beset with olfactory hairs. The posterior antennæ are frequently longer than the anterior: in the male *Typhidæ* they are folded in a zigzag fashion, and in the *Corophiidae*

a, 357.—*Phronima sedentaria*, a, female; b, male. O, eyes; A', A'', the two pairs of antennæ; Kf, jaws; D, intestine; H, heart and aorta; K, gills; Ov, ovary; N, nervous system; Dr, glands in the chela of the fifth pair of legs; G, genital opening.

are modified to form strong pediform appendages. In the female, on the contrary, they may be degenerated and represented only by the basal joint (*Phronima*) (fig. 357, a and b).

The mandibles are powerful biting plates with a sharp, usually toothed edge and a lower masticating process. They usually possess a three-jointed palp, which is occasionally reduced. The anterior bi-

lobed maxillæ also have as a rule a short, two-jointed palp, while the maxillæ of the second pair are reduced to two lamellæ of considerable size attached to a common base. The maxillipeds fuse to form a sort of underlip, which is either tri-lobed (*Hyperina*) or bears upon a common basal portion an internal and external pair of lamellæ, of which the latter may be considered as the basal joint of a large multiarticulate and frequently pediform palp (*Creveltina* and *Læmodipoda*).

Delicate lamellæ or tubes, which are attached to the coxal joints of the thoracic legs, function as gills; the active movements of the abdominal swimming feet cause a constant renewal of the water around them. In the female there are in addition to the gills lamellar plates (*oostegites*), which are applied together under the thorax to form a brood-pouch.

The males are distinguished from the females not only by the absence of the oostegites, but chiefly by the stronger development of the prehensile hooks on the anterior thoracic feet and the different formation of the antennæ.

The eggs pass into the brood-pouch and there develop. The yolk sometimes (*G. locusta* and other marine species) undergoes a complete segmentation. Sometimes (*G. pulex*), after a superficial segmentation, a peripheral cell-layer is separated, which develops into a delicate blastoderm beneath the egg membrane. A ventral primitive streak is then formed, and on the dorsal side, beneath a differentiation which has been erroneously taken for a micropyle, a peculiar globular organ makes its appearance; this is the first rudiment of the cervical gland (*dorsal organ*), which is confined to embryonic life. The appendages are developed from before backwards on the ventrally flexed body of the embryo. The young animals usually possess at hatching all their appendages and in all essential points have the structure of the adult animal, but the number of joints of the antennæ and the special form of the legs still present differences. In the *Hyperina* alone the just hatched young may be without abdominal feet and differ so much in their form from the adult that they may be said to undergo a metamorphosis.

The *Amphipoda* for the most part live in fresh and salt water and lead an independent life (the presence of Arctic species in the Swedish and Norwegian seas is very interesting). Some, however, live in tubes (*Cerapus*), others in holes gnawed in wood (*Chelura*). The large size of the deep-sea forms is of special interest; amongst these a *Gammarid*, allied to the genus *Iphimedia*, and *Cystosoma Neptuni* (*Hyperidæ*) become several inches in length. The *Hyperina*

live principally in transparent marine animals, especially in *Medusæ*, and may, as the female *Phronima sedentaria*, take up their abode with their entire brood in transparent *Pyrosoma*, whose internal parts they eat up. The *Cyamidæ* among the *Læmodipoda* are parasitic on the skin of whales.

Tribe 1.—*Læmodipoda*.

Amphipoda with cervically placed anterior legs and rudimentary apodal abdomen.

The anterior thoracic segment is more or less closely fused with the head and the anterior pair of legs shifted on to the neck. The maxillipeds are modified to form a quadripartite under-lip with long palps. The branchiæ are usually confined to the third and fourth thoracic segments, the legs of which are often rudimentary or are altogether wanting. The feet end with hooks for attachment. The abdomen is small and reduced to a short protuberance destitute of appendages.

Caprella linearis L. Body elongated and thin. They are parasitic on Hydroids and colonies of Bryozoa. *Cyamus ceti* L. Body broad and flat; abdomen quite rudimentary; parasitic on the skin of Cetacea.

Tribe 2.—*Crevettina*.

Amphipoda with small head, small eyes, and multiarticulate pediform maxillipeds.

Both pairs of antennæ are long and multiarticulate; in the male they are larger than in the female. The upper or anterior antennæ are usually, as in *Gammarus*, the longer; their shaft is composed of several joints and bears a small accessory flagellum as well as the principal one. The contrary may, however, occur, as in *Corophium*, where the posterior antennæ are elongated and pediform. The maxillipeds in all cases fuse together at their base and form a large under-lip, usually with four lamellæ and two jointed pediform palps. The coxal joints of the thoracic legs have the form of broad and large *epimeral* plates. The abdomen has always the full number of segments. The three posterior pairs of abdominal feet (*uropoda*) are well developed and often much elongated. This group, which includes an astonishing variety of forms, is principally distributed in the colder seas.

Fam. *Corophiidæ*. The body is not laterally compressed. The posterior antennæ are more or less pediform. The coxal joints of the legs are frequently very small. They move rather by walking. *Corophium longicorne* Fabr., dig

passages in mud. *Cerapus tubularis* Say., lives in tubes. *Podocerus variegatus* Leach., English coast. *Chelura terebrans* Phil. is allied here, gnaws, with *Limnoria lignorum*, wood-work in the sea. North Sea and Mediterranean.

Fam. **Orchestiidae**. Anterior antennæ usually short, always without accessory ramus. The posterior pair of uropoda are unbranched and are shorter than the preceding pairs. They live on the shore, especially on sandy beaches, and move by springing. *Talitrus saltator* Mont. = *T. locusta* Latr. On the sandy coasts of Europe. *Orchestia littorea* Mont., North Sea.

Fam. **Gammaridae**. The anterior antennæ often have a second ramus, which is always longer than the shaft of the posterior. The coxal plates of the four anterior pairs of legs are very broad. They move more by swimming than by springing. *Gammarus pulex* L., *G. fluvialis* Rös., *G. marinus* Leach. In the blind *Niphargus* Schiödte the crystalline cones and eye pigment are wanting. *N. puteanus* Koch., in deep springs and lakes (Lake of Geneva). *Lysianassa Costæ* Edw., Mediterranean. *L. atlantica* Edw. *L. magellanica* Lillj.

Tribe 3.—Hyperina.

Amphipoda with large swollen head and large eyes, usually divided into frontal and lateral eyes. They have a pair of rudimentary maxillipeds functioning as underlip.

The antennæ are sometimes short and rudimentary, sometimes of considerable size, and in the male are elongated into a multiarticulate flagellum (*Hyperidae*). The posterior antennæ may in the female be reduced to the basal joint enclosing the glandular tube (*Phromina*); in the male, on the contrary, they are folded in a zigzag, after the manner of a carpenter's rule (*Platyscelineæ*). A paired auditory vesicle may be present above the brain (*Oxycephalus*, *Rhabdosoma*). The maxillipeds form a small bi- or tri-lobed under-lip. The paired legs end in some cases in a powerful chela. The caudal styles are sometimes lamellar and fin-like, sometimes styliiform. Development takes place by metamorphosis. They live principally in jelly-fish, and swim very rapidly.

Fam. **Hyperidae**. Head globular, almost entirely occupied by the eyes. The two pairs of antennæ have a multiarticulate shaft; the flagellum longer in the male. The mandible has a three-jointed palp. The fifth pair of feet is generally formed like the sixth and seventh, with claw-like terminal joint. *Hyperia* (*Lestrignonus* Edw.) *medusarum* O. Fr. Müll. (*H. galba* Mont. = *H. Latreilli* Edw.) with *Lestrignonus exulans* Kr. as male, North Seas.

Fam. **Phronimidae**. Head large, with projecting rostrum and large divided eye. The anterior antennæ are short in the female, with only two or three joints, in the male with long multiarticulate flagellum and a shaft closely beset with olfactory hairs. The thoracic limbs have in some cases powerful chelæ. *Phrosina nicaensis* Edw., *Phronima sedentaria* Forsk. The female lives with its offspring in *Pyrosoma* and *Diphyidæ*, Mediterranean.

Fam. **Platyscelidae**. Both pairs of antennæ hidden beneath the head; the anterior are small; in the male with much swollen bushy shaft, and short,

slender flagellum composed of few joints. The posterior antennæ are in the male very long and folded three to four times together in a zigzag fashion ; in the female they are short and straight, sometimes quite reduced. The basal joints of the fifth and sixth pairs of legs are usually enlarged into great lamellæ, which cover the thorax. The seventh pair is generally rudimentary. *Eutyphis* (*Typhis* Risso) *ovoides* Risso (*Platyscelus serratus* Sp. Bate), Mediterranean. *Orycephalus piscator* Edw., Indian Ocean.

2. Sub-order :—Isopoda.*

FIG. 353.—*Asellus aquaticus* (after G. O. Sars). Female with brood pouch, seen from the ventral side.

Arthrostraca with usually broad, more or less arched body, with seven free thoracic rings, with lamellar legs functioning as branchiæ on the short-ringed, often reduced abdomen.

The structure of the body, which is flat in shape and covered by a hard, usually encrusted integument, presents a great agreement with that of the *Amphipoda*, to which the in many respects peculiar *Tanaidæ* are most nearly allied. The abdomen of the Isopods is, however, usually much shortened and composed of six short segments, which are often fused with one another ; it terminates with a large caudal lamella. The abdominal legs are only exceptionally (*Tanaidæ*) swimming feet ; as a rule they have the form of branchial lamellæ. The sixth pair may be fin-like or styliform. The anterior antennæ are, with a few exceptions, shorter than the posterior and external antennæ ; in rare cases (*Oniscidæ*) they become so much reduced that they are hidden beneath the cephalic carapace. In exceptional cases only (*Apseudes*)

* H. Rathke, "Untersuchungen über die Bildung und Entwicklung der Wasserschüssel," Leipzig, 1832. Lereboullet, "Sur les Crustacés de la famille des Cloportides, etc." *Mém. du Museum d'hist. nat. de Strasbourg*, Tom. IV., 1850. N. Wagner, "Recherches sur le système circulatoire et les organes de la respiration chez le Porcellion élargi," *Ann. des sc. nat.*, Ser. 5, Tom. IV., 1865. A. Dohrn, "Die Embryonalentwicklung des *Asellus aquaticus*," *Zeitschr. für wiss. Zool.*, Tom. XVII., 1867. N. Bobretzky, "Zur Embryologie des *Oniscus murarius*," *Zeitschr. für wiss. Zool.*, Tom. XXIV., 1874.

they bear two flagella. As in the *Amphipoda*, pale, plumous setæ and olfactory cones are present on the antennæ. The mouth parts are in some parasitic *Isopoda* modified for piercing and sucking. The mandibles (except in *Bopyridæ* and *Oniscidæ*) often bear a three-jointed palp. On the other hand, the two pairs of maxillæ, which are usually bi- or tri-lobed, are in general without the palpiform appendage. The maxillipeds form a sort of underlip, but present great differences in the arrangement of their parts (fig. 358).

As a rule the seven pairs of thoracic legs are adapted for walking or attachment, and in the female some of them are provided with delicate membranous plates (oostegites) which form a brood pouch. They never bear gills. The branchial function is discharged by the delicate internal rami or endopodites of the abdominal limbs (pleopods), the anterior pair of which is frequently modified to form a large operculum overlying the following pairs. In certain of the terrestrial Isopods (*Porcellio* and *Armadillo*) the opercular plates of the two anterior pairs of abdominal limbs contain a system of air spaces which appear to assist respiration. The heart, unlike that in Amphipods, lies (except in *Tanüidæ*) in the posterior thoracic segments or in the abdomen.

The sexes are (except in *Cymothoidæ*) separate, and the position and arrangement of the generative organs correspond in general with those of the *Amphipoda*. The sexes are distinguished by external sexual characters, which in some cases (*Bopyridæ*) may lead to a strongly-marked dimorphism (fig. 359, *a*, *b*). In the male three tubular testes unite on either side to form a dilated seminal vesicle, from which the vasa deferentia are given off. The latter are frequently separate along their whole length and, at the end of the last thoracic segment, each of them enters a cylindrical appendage

FIG. 359.—*Gyge branchialis* (after Cornalia and Panceri). *a*, Female seen from the ventral side; *Brl*, oostegite; *K*, branchia. *b*, Abdomen of the same strongly magnified, with adhering male.

(*Asellus*) or they unite together into a common median penis which lies at the base of the abdomen (*Oniscidae*). A pair of styliform or complicated, hook-bearing appendages of the anterior abdominal feet are to be looked upon as accessory copulatory organs; in addition to these a pair of outwardly turned chitinous rods on the inner side of the second pair of feet may also be present (*Oniscidae*). The *Cymothoidæ* are hermaphrodite* (Bullar), but the sexual organs become ripe at different times. In the young stage these animals function as males, and possess three pairs of testes, two rudimentary ovaries internal to the testes, and a paired copulatory organ into

FIG. 360.—*a*, Female of *Cymothoa Banksi* (after M. Edwards). *Brt*, oostegite. *b*, Sexual organs from a *Cymothoa astrides*, 13 mm. in length (after P. Mayer). *T*, The three testes; *Ov*, ovary; *Od*, oviduct; *Vd*, vas deferens; *P*, penis.

which the two vasa deferentia open (fig. 360). After a subsequent ecdysis and after the female glands have developed at the expense of the gradually diminishing male glands, the oostegites, which in the meantime have been developed, become free on the thoracic legs and the copulatory organs are thrown off. Henceforward the animal functions only as a female.

The embryonic development begins after the entry of the eggs into the brood pouch and is introduced by a centro-lecithal segmentation, the central part of the egg (food yolk) remaining at first unsegmented. The blastoderm soon consists of a peripheral layer of naked nucleated cells and produces by a rapid growth

of its constituent cells the ventrally placed germinal bands, at the anterior end of which the cephalic lobes are first marked off. The rudiments of the trifoliate appendages (dorsal organ) of the Isopod embryos are next formed as two prominences on the cephalic lobes. The physiological and morphological meaning of these structures has not yet been explained. Of the appendages the two pairs of antennæ

* J. Bullar, "The generative organs of the Parasitic Isopoda," *Journ. Anat. Physiol.*, 1876. P. Mayer, "Ueber den Hermaphroditismus einiger Isopoden," *Mittheil. aus der Zool. Stat. Neapel*, 1879.

are the first formed. After these have made their appearance, a new cuticle, the larval skin corresponding to the Nauplius stage, is formed (as also is the case in *Ligia* according to Fr. Müller). While the other appendages are successively developed, the caudal region of the embryo becomes bent towards the dorsal surface. Of the embryonic membranes the chorion is the first to disappear, then the cuticle of the blastoderm, and finally, when the embryo is fully developed, the Nauplius skin.

The young animals, when they become free in the brood-chamber (fig. 361), are still without the last pair of thoracic legs; in the *Tanaidæ* the abdominal feet are also wanting. They undergo not inconsiderable changes in the form of the appendages until the attainment of sexual maturity. The *Isopoda* may therefore be said to undergo a metamorphosis which is most complete in *Tanais*, *Praniza* (*Anceus*) and the *Bopyridæ*.

The *Isopoda* live some in the sea, some in fresh waters, and some on land (*Oniscidæ*). They nourish themselves on animal matters; many of them are parasitic (seldom complete endoparasites, *Entoniscus*) principally on the skin and in the buccal and branchial cavities of fishes (*Cy-mothoidæ*) or in the branchial cavity of prawns (*Bopyridæ*).

FIG. 361.—Larva of *Bopyrus virbii*, with six pairs of thoracic legs (after R. Walz). *Ul*, Under lip; *Abs*, first abdominal segment; *A', A''*, two pairs of antennæ; *Mdb*, mandible.

Tribe 1.—Anisopoda.*

Body more or less resembling that of an Amphipod. The abdomen with biramous swimming feet (Tanais), which do not function as gills, or with fin-like feet (Anceus).

Fam. *Tanaidæ*. *Tanais dubius* Kr., Brazil. Two kinds of males, "smellers and claspers." *T. gracilis* Kr., Spitzbergen.

Fam. *Pranizidæ*, *Anceidæ*. *Anceus maxillaris* Mont. (*Pr. cæruleata* Desm.), North and West coasts of Europe.

* Compare Spence Bate, "On *Praniza* and *Anceus*, etc.," *Ann. of Nat. Hist.*, Ser. 3, Vol. II., 1858. Hesse, "Mémoire sur les *Pranizes* et les *Ancées*," *Ann. d. Scien. Nat.*, Ser. IV., Tom IX., 1864. Fr. Müller, "Ueber den Bau der Scheerenasseln," *Archiv. für Naturgesch.*, Tom XXX., 1864. A. Dohrn, "Entwicklung und Organisation von *Praniza maxillaris* sowie zur Kenntniss des Baues von *Paranthura costana*," *Zeitschr. für wiss. Zool.*, Tom. XX., 1870.

Tribe 2.—Euispoda.

Body with seven free thoracic segments and as many pairs of appendages. Abdomen relatively short and broad, with abdominal feet modified to form branchial lamellæ.

Fam. **Cymothoidæ**. With biting and sucking mouth parts, broad abdomen with short segments and shield-like caudal plate. The last maxillipeds in the form of an operculum. They live partly as parasites on fish, and partly as free-living animals. *Cymothoa æstrum* Leach., *C. æstroides* Risso, Mediterranean. *Anilocera mediterranea* Leach., *Æga bicarinata* Leach., *Serolis paradoxa* Fabr.

Fam. **Sphæromidæ**. Free-living *Isopoda* with broad head and short, very convex body, which can often be rolled up in a ball towards the ventral side. *Sphæroma fossarum* Mont., in the Pontine marshes; nearly allied is the *S. granulatum* of the Mediterranean. *S. serratum* Fabr., Ocean and Mediterranean. It also lives in brackish water.

Fam. **Idoteidæ**. Free-living *Isopoda* with elongated body, biting mouth parts, and a long caudal shield formed of several segments fused together. The last pair of abdominal feet is modified to form a wing-shaped operculum for the protection of the preceding branchial feet. *Idotea entomon* L., Baltic.

Fam. **Asellidæ**. Body flattened; the last pair of abdominal feet (pleopods) are styliform (not shaped like an operculum). *Jæra albifrons* Mont., British seas. *Asellus aquaticus* L., fresh-water form. *A. cavaticus* Schiödte, in deep springs. *Limnoria terebrans* Leach. *L. lignorum*, gnaws wood-work in the sea.

Fam. **Bopyridæ**. Parasitic in the branchial chamber of prawns; the body of the female is disc-shaped, unsymmetrical, and without eyes. The males are very small and elongated, with distinctly separated segments and eyes. *Bopyrus squillarum* Batr., on *Palæmon squilla*.

Here are allied the *Entoniscidæ*, which are parasitic in the body cavity of other *Crustacea* (*Cirripedia*, *Paguridæ*, and Crabs), *Cryptoniscus planarioides* Fr. Müll., parasitic on *Sacculina purpurea* of a *Pagurus*, Brazil. *Cr. pygmæus* Rathke, parasitic on *Peltogaster*. *Entoniscus Porcellanæ* Fr. Müll., lives between the heart and the intestine of a species of *Porcellana* in Brazil.

Fam. **Oniscidæ**. Land Isopods. Only the internal lamellæ (endopodites) of the abdominal feet are modified to form delicate branchiæ, the exopodites constituting firm opercula. The two anterior abdominal feet are sometimes provided with air chambers. The mandibles are without palps. They live mostly in damp places on land. *Ligia oceanica* L., on stones and rocks on the sea coast. *Oniscus murarius* Cuv., *Porcellio scaber* Leach., *Armadillo vulgaris* Latr., *A. officinarum* Brdt.

Order 2.—THORACOSTRACA.*

Malacostraca with compound eyes which are usually placed on movable stalks, with a dorsal shield which connects all or at least the anterior thoracic segments with the head.

* Besides the larger works of Herbst, M. Edwards, Dana, and the essays of Duvernoy, Audouin and M. Edwards, Joly, Couch, etc. compare Leach,

The *Thoracostraca*, like the *Arthrostraca*, possess a cephalo-thorax composed of thirteen segments and an abdomen composed of six segments, as well as a caudal plate (telson); but the body is stouter and adapted to a more perfect locomotion and a higher grade of life. The thorax, instead of being composed of seven distinctly separate segments, is covered by a dorsal carapace which effects a firm and intimate fusion between the head and thorax. The degrees of development of this dorsal carapace are various. When most highly developed, it forms the dorsal integument of the anterior or of almost all the thoracic segments; and its lateral portions only, which have the form of wings and are bent towards the ventral surface, consist of a free reduplication.

The application of the **appendages** differs from that in the *Arthrostraca*, and, indeed, varies in the different groups of the *Thoracostraca*. The cephalothorax has thirteen pairs, and the abdomen seven. The faceted eyes are born on two movably separated stalks. These were for a long time considered as the anterior pair of appendages, while in fact they are merely lateral portions of the head which have become jointed. Both pairs of antennæ belong to the anterior region of the head. The anterior antennæ or antennules as a rule bear on a common shaft two or three *flagella*—as the peripheral multiarticulate filaments are called—and are pre-eminently sense organs. In the *Decapoda* the auditory vesicles are placed in the basal joint, and on one of the flagella there are delicate hairs and fibres, which are in connection with nerves and are to be looked on as olfactory organs. The second antennæ are attached externally to and somewhat beneath the antennules. They bear a long flagellum and in the macrurous *Decapoda* are often provided with a more or less considerable scale. A gland (the green or antennal gland) usually opens on a conical process of their basal joint.

The following three pairs of appendages function as jaws; the powerful mandibles, which are furnished with palps, lie at the side of the upper lip; further backwards are the two pairs of lobed maxillæ, in front of which and behind the mouth is the small bilobed underlip. The following eight pairs of appendages present a very

"Malacostraca podophthalma Britanniae," London, 1817—1821. V. Thompson, "On the metamorphosis of Decapodous Crustacea," *Zool. Journ.*, vol. ii., 1831, also *Isis*, 1834, 1836, 1838. H. Rathke, "Untersuchungen über die Bildung und die Entwicklung des Flusskrebses," Leipzig, 1829. Th. Bell, "A history of the British stalk-eyed Crustacea," London, 1853. Lereboullet, "Recherches d'embryologie comparée sur le développement du Brochet, de la Perche et de l'Ecrevisse," Paris. 1862. V. Hensen, "Studien über das Gehörorgan der Decapoden," Leipzig, 1863.

different form and adaptation in the various groups. As a rule, the anterior pairs are modified to assist in taking up food and are moved nearer the mouth; these are the maxillipeds, which, with regard to their structure, hold an intermediate position between jaws and feet. In the *Decapoda* (fig. 362) three pairs of appendages have the form

FIG. 362.—Male and female of *Astacus fluviatilis* seen from the ventral side. In the male the ambulatory and abdominal feet of the left side have been removed; in the female the ambulatory feet of the right side and the maxillipeds of both sides. *A'* antennules; *A''*, antennæ; *Pl*, scale of antenna; *Md*, mandible with palp; *Mx'*, *Mx''*, first and second maxillæ; *Mxf'* to *Mxf''*, the three pairs of maxillipeds; *Goe*, genital opening; *Doe*, opening of the green gland; *F'*, *F''*, first and second abdominal foot; *Ov*, eggs; *A*, anus.

of maxillipeds, so that there are only five pairs of legs left on the thorax. In the *Stomatopoda* the first five pairs of thoracic appendages are modified to form maxillipeds and there are only three pairs

of biramous swimming feet, which arise from the three posterior free segments of the thorax. The thoracic legs are either, at least in part, biramous (with swimming ramus), or as in the Decapods the exopodite is absent and the legs have the form of ambulatory appendages. They then terminate with simple claws; the anterior frequently with large chelæ. The terminal joints may however be broad plates, in which case they can be used as swimming feet. The biramous legs of the sixth abdominal segment are, as a rule, broad and fin-like and form, together with the last abdominal segment which is transformed into a large plate (telson), the *caudal fin*. The feet of the five anterior abdominal segments, on the other hand, are sometimes swimming feet (*Stomatopoda*), sometimes serve to carry the eggs, or the anterior may assist in copulation (in the male). They may however be more or less rudimentary and some of them absent.

With rare exceptions (*Mysidæ*) all the *Thoracostraca* possess gills, which are either tufted or composed of regular lancet-shaped leaves. The gills are appendages of the limbs: in the *Stomatopoda* they are attached to the abdominal feet, in the *Schizopoda* and

FIG. 363.—Cephalothorax of *Astacus fluviatilis*, after removal of the branchiostegite (after Huxley). K, Gills; R, rostrum; O, stalked eye; Mp, scaphognathite (of the second maxilla); Mxf^{III}, third maxilliped.

Decapoda to the maxillipeds and ambulatory feet. The *Cumacea* are without gills, except for a single pair on the second pair of maxillipeds. In the Decapods they are contained in a special branchial chamber beneath lateral expansions of the carapace (branchiostegite) (fig. 363).

The organs of circulation also attain a high degree of development, the highest not only among the *Crustacea*, but in general amongst all Arthropods. A heart and vessels are always present. In the *Stomatopoda* the heart has the form of an elongated tube, which extends through the thorax and abdomen, possesses numerous paired slits, and in addition to an anterior and a posterior aorta gives off to the right and left several branching arterial trunks. In the *Cumacea*, *Schizopoda* and *Decapoda* the heart has a saccular form and lies in the posterior region of the cephalo-thorax. More rarely,

as in the youngest larvæ of the *Decapoda*, only one pair of slits is present and the arterial system has but few branches. In the fully-developed *Decapoda* the number of paired slits is increased by the addition of a dorsal and a ventral pair, and the vascular system is considerably perfected. An anterior cephalic aorta supplies the brain, the antennæ and eyes. Two lateral pairs of arteries send branches to the stomach, liver and generative organs. The posterior abdominal aorta usually divides into a dorsal and a ventral artery, of which the first supplies the muscles of the tail, the latter (known as *sternal artery*) sends branches to the appendages of the thorax and abdomen (fig. 364). From the ramifications (often capillary-like) the blood flows into larger or smaller canals with connective tissue walls which may be regarded as veins, and from thence into a wide blood space situated at the base of the gills. It thence passes through

FIG. 364.—Longitudinal section through *Astacus fluviatilis* (after Huxley). *C*, Heart; *Ac*, cephalic aorta; *Aa*, abdominal aorta, the sternal artery (*Sta*) is given off close to its origin; *Km*, masticatory stomach; *D*, intestine; *L*, liver; *T*, testis; *Vd*, vas deferens; *Gö*, genital opening; *G*, brain; *N*, ganglionic cord; *Sf*, lateral plate of the caudal fin.

the gills and, having become arterial, passes into other vascular tracts (branchial veins containing arterial blood), which conduct it to a receptacle surrounding the heart, the pericardial sinus: from the latter the blood enters the heart through the slits which are provided with valves.

The **alimentary canal** consists of a short œsophagus, a wide saccular crop and an elongated intestine which opens by the anus beneath the median plate (telson) of the caudal fin. The wide crop or masticatory stomach is supported by a firm chitinous framework, to which are affixed several pairs of masticatory plates (derived from thickenings of the chitinous lining). In the *Decapoda* two round concretions of carbonate of lime (Cray-fish) may be deposited in the walls of the masticatory stomach beneath the chitinous lining; these are the so-called “eyes,” and are found in the spring and summer.

The ducts of the very numerous, multilobed hepatic cæca open into the anterior part of the elongated intestine.

A simple or looped glandular tube (the *green gland*) opens on the basal joint of the posterior antenna. A shell gland is not developed.

The **nervous system** is distinguished by the size of the brain, which is placed far forwards and gives off nerves to the eyes and antennæ. The ventral cord, which is connected with the supra-oesophageal ganglion (brain) by very long commissures, presents very different degrees of concentration. In the brachyurous Decapods this concentration reaches its highest point, all the ganglia being fused together to form one great thoracic ganglionic mass. The system of *visceral nerves* is also very highly developed.

Sense organs.—The eyes are large and faceted. Except in the

FIG. 365.—Generative organs of *Astacus*. *a*, Female; *b*, male. *Or*, ovaries; *Od*, oviduct; *Va*, vulva on the basal joint of the third pair of ambulatory legs (*F'''*); *T*, testis; *Vd*, vas deferens; *Oe*, genital openings on the basal joint of the fifth pair of ambulatory legs (*Fv*).

Cumacea, in which the eyes are sessile, they are borne on movable stalks, which morphologically are to be regarded as the lateral parts of the anterior region of the head which have been segmented off. In the larva a median simple eye, equivalent to the unpaired Entomostracan eye, may appear between the stalked faceted eyes. In exceptional cases the adult animal may have paired eyes at the sides of the thoracic appendages, and unpaired eyes between the abdominal feet (*Euphausia*). *Auditory organs* are wanting in the *Cumacea* and *Stomatopoda*. In the *Decapoda* they are present as vesicles containing otoliths in the basal joint of the anterior antenna, and in many *Schizopoda* in the lamellæ of the caudal fin. The delicate

filaments and hairs on the surface of the anterior antennæ have the value of *olfactory organs*; the antennæ function as *tactile organs*, as do also the palps of the jaws, the maxillipeds and the legs.

The **generative organs** are paired and lie in the thorax or in the abdomen (*Stomatopoda*), and, as a rule, are connected across the middle line by a median portion. The female organs consist of two ovaries and two oviducts, which open on the basal joint of the antepenultimate pair of ambulatory legs or on the sternal region between these appendages (fig. 365, *a*). The testes (fig. 365, *b*) are composed of numerous sacs and blind tubes, and, like the ovaries, are connected by a median portion; there are two vasa deferentia, often much coiled, which open on the basal joint of the last pair of ambulatory legs, more rarely on the sternum, and occasionally on a special

FIG. 366.—Crab zoea (*Thia*), after the first moult. *ZS*, Zoëa spine on the back; *Kf'*, *Kf''*, the two pairs of biramous appendages corresponding to the first and second pairs of maxillipeds.

copulatory organ (*Schizopoda*). The first, or the first and second, pair of abdominal feet act as intromittent organs. The eggs either pass into a brood-pouch formed by lamellar appendages of the thoracic legs (*Cumacea*, *Schizopoda*), or become attached by means of the cementing secretion of special glands to the hairy abdominal feet of

the female, where they remain until they are hatched (*Decapoda*).

Development.—Most of the *Thoracostraca* undergo a metamorphosis which may be more or less complicated. The *Cumacea*, some *Schizopoda* (*Mysidea*) and the fresh-water *Decapoda* (*Astacus*) leave the egg membranes with the full number of segments and appendages. All the *Stomatopoda*, on the contrary, as well as most of the *Decapoda*, are hatched as larvæ; the latter in the so-called *Zoea* form with only seven pairs of appendages in the anterior region of the body (there are two pairs of antennæ, mandibles, two pairs of maxillæ, and two pairs of maxillipeds), without the last six thoracic segments and with a long abdomen destitute of appendages (fig. 366). The two pairs of antennæ of the *Zoea* are short and destitute of flagella. The mandibles are without a palp; the maxillæ are already

lobed and used as jaws; the four anterior maxillipeds are biramous and act as biramous swimming feet; and behind them, in the macrurous Decapods, the maxilliped of the third pair also appears as a biramous swimming foot. Gills are as yet wanting, being repre-

FIG. 367.—Larva of *Penaeus* (after Fr. Müller). *a*, Nauplius form seen from the dorsal surface. *b*, Metanauplius stage seen from the left side; *Mx'*, anterior maxillæ; *Mx''*, posterior maxillæ; *Gl*, sixth and seventh pairs of appendages or first and second maxillipeds. *c*, Zoea stage; *O*, eyes.

sented by the thin surfaces of the sides of the cephalo-thoracic shield, beneath which a continual current of water flowing from behind forwards is kept up. A short heart with one or two pairs

of slits is present. The faceted eyes are of considerable size, but are not stalked. Between the faceted eyes there is in addition an unpaired simple eye, the *Entomostracan eye*. The *Zoæa* larvæ of the short-tailed *Decapoda* (Crabs) are, as a rule, armed with spinous processes. They usually have one frontal spine, a long, curved dorsal spine, and two lateral spinous processes of the cephalo-thoracic shield.

The *Zoæa*, however, is not by any means always the earliest larval stage. Passing over those cases in which the larva has the *Zoæa* form but is without the middle maxillipeds, there are *Podophthalmata* (*Pencus*), which leave the egg as Nauplii (fig. 367). Thus

FIG. 368.—*a*, *Zoæa* of *Inachus* in advanced stage with rudiments of the third maxilliped (*Kf'''*) and the five pairs of ambulatory feet (*5Bp*); *C*, heart; *L*, liver. *b*, *Megalopa* stage of *Portunus*; *Ab*, abdomen, *F'* to *F'''* first to fifth ambulatory legs.

the developmental history proves that the series of forms of *Entomostraca* and *Malacostraca* are continuous.

During the growth of the *Zoæa*, the subsequent metamorphosis of which is quite gradual and always different, the six (five) pairs of thoracic legs, which are as yet absent, sprout out beneath the cephalo-thoracic shield. The abdominal feet also make their appearance on the abdomen, and the larvæ finally enter the Schizopod-like stage, from which the adult form proceeds. The Crab *Zoæa*, however, after a later ecdysis, enters upon a new larval stage, that of the *Megalopa* (fig. 368, *b*); in this stage it already presents the characters of the *Brachyura*, but still possesses a large abdomen, which is indeed ventrally flexed, but provided with a caudal fin.

The *Thoracostraca* are for the most part marine, and feed on dead animal matter or capture living prey. Most of them are good swimmers; others, *e.g.* numerous species of crabs, walk and run and sometimes move sideways or backwards with great agility. The chelæ of the first pair of ambulatory legs (fourth thoracic appendages) constitute powerful weapons of defence. Besides the frequent ecdyses of the larval stages, the sexually adult animals cast their shell once or several times in the year (*Decapoda*). They then live with the new and still soft skin for some time in protected hiding-places. Some *Brachyura* are able to live for a long time in holes in the earth away from the sea. These land crabs undertake, usually at the breeding season, common migrations to the sea and return later to the land with their fully developed offspring (*Gecarcinus ruricola*). The most ancient fossil *Podophthalmia* hitherto known are the macrurous *Decapoda* and *Schizopoda*, from the carboniferous formations (*Palæocrangon*, *Palæocarabus*, *Pygocephalus*).

(1) Sub-order : Cumacea.*

Thoracostraca with a small cephalo-thoracic shield, (four to) five free thoracic segments, two pairs of maxillipeds, and six pairs of legs, of which at least the two anterior pairs have the biramous Schizopod form. The abdomen is elongated and composed of six segments, and bears, in the male, two, three or five pairs of swimming feet in addition to the caudal appendages.

The *Cumacea*, the systematic position of which was formerly very differently estimated, have a superficial resemblance to Decapod larvæ, which they also recall in the simplicity of their organization; while in many of their characters, such as the formation of the brood-pouch and their embryonic development, they approach the *Arthrostraca*. A cephalo-thoracic shield is always present and includes, besides the segments of the head, the anterior thoracic segments and their appendages; the four or five posterior thoracic segments, however, remain free.

The anterior antennæ are small and consist of a three-jointed basal portion, to the end of which, especially in the male, tufts of olfactory hairs are attached, and of a short flagellum and secondary flagellum

* H. Krøyer, "Fire nye Arter af slægten Cuma," *Naturh. Tidsskr.*, Tom III., 1841. H. Krøyer, "Om Cumaceernes Familie," *Naturh. Tidsskr. N. R.*, Tom III., 1846. G. O. Sars, "Beskrivelse af de paa Fregatten Josephines Exped. fundne Cumaceer," Stockholm, 1871. A. Dohrn, "Ueber den Bau und die Entwicklung der Cumaceen," *Jen. naturwiss. Zeitschr.* Tom V., 1870.

In the female the posterior antennæ are short and rudimentary, while in the adult male they, together with their multiarticulate flagellum, may be as long as the body (as in *Nebalia*). The upper-lip is usually small, while the deeply cleft under-lip is of considerable size. The mandibles are without palps, and possess a comb of bristles and a powerful masticatory process below their strongly toothed extremity. The anterior maxillæ consist of two toothed blades and a cylindrical, flagellate appendage directed backwards. The unpalped maxilla of the second pair is composed of several pairs of masticatory plates lying one above another. The two following pairs of appendages may be distinguished as maxillipeds. The anterior, which corresponds to the palped under-lip of the *Isopoda*, is five-jointed and may be recognised by the process of the basal joint; the posterior, which is also usually five-jointed, is of considerable length and the basal joint is cylindrical and elongated. They also bear the large pinnate gill and a peculiar plate. Of the remaining six pairs of thoracic appendages, the two anterior are always formed like the feet of the *Schizopoda*; they consist of a six-jointed leg, the basal joint being strongly developed and lamellar, and of a multiarticulate accessory ramus (exopodite) beset with long swimming setæ. The four last pairs of appendages are also six-jointed, but are shorter; they bear in many cases, with the invariable exception of the last pair, a larger or smaller swimming appendage as exopodite. The very narrow and elongated abdomen is, in the female, entirely without swimming feet, but bears on the large sixth segment at the sides of the caudal plate long-stalked biramous caudal styles; while in the male two, three or five pairs of swimming feet may in addition be present on the preceding segments.

Fam. *Diastylidæ*. *Diastylis Rathkii* Kr., North Sea. *D. Edwardsii* Kr. *Leucon nasicus* Kr., Norway.

(2) Sub-order: Stomatopoda.*

Elongated Thoracostraca with short cephalo-thoracic shield which does not cover the thoracic segments. There are five pair of maxillipeds and three pair of biramous thoracic feet. The swimming feet on the strongly developed abdomen bear branchial tufts.

* Besides Dana, M. Edwards and others, compare O. Fr. Müller, "Bruchstück aus der Entwicklungsgeschichte der Maulfüßer," I. and II., *Archiv für Naturgesch.*, Tom XXVIII., 1862, and Tom XXIX., 1863. C. Claus, "Die Metamorphose der Squilliden," *Abhandl. der Göttinger Societät*, 1872. C. Grobben, "Die Geschlechtsorgane von *Squilla mantis*," *Sitzungsber. der k. Akad. der Wissenschaften*, Wien, 1876.

The sub-order *Stomatopoda*, with which formerly the *Schizopoda*, the genus *Leucifer* and the *Phyllosomata* (which are now known to be the larvæ of *Scyllarus* and *Palinurus*) were united, is confined at the present day to the small and well-defined group of forms included in the *Squillidæ*.

They are *Thoracostraca* of considerable size and of elongated shape, with a broad, well-developed abdomen, which is much more extensive than the anterior part of the body and terminates in an extraordinarily large caudal fin. The cephalo-thoracic shield, which is formed of comparatively soft integument, is short and leaves at least the three large posterior thoracic segments to which the biramous swimming feet belong quite uncovered. The short segments of the maxillipeds also are not fused with the carapace.

Appendages.—The anterior part of the head with the eyes and antennæ is movable, and the ventral portions of the following segments covered by the cephalo-thoracic shield are capable of limited movements upon one another (fig. 369). The anterior

FIG. 369.—*Squilla mantis*. A', A'', antennæ; Kf, Kf'', the anterior maxillipeds on the cephalothorax; B', B'', B''', the three pairs of biramous legs.

internal antennæ consist of a long three-jointed shaft, bearing three multiarticulate flagella. The second pair of antennæ has a large scale on the outer side of the multiarticulate flagellum (fig. 369). The mandibles, which are placed far back, are provided with a slender three-jointed palp. The maxillæ are relatively small and weak. The five following pairs of pediform appendages are crowded together close to the mouth, and on this account have been appropriately described as oral feet. They all bear at their base a discoidal plate, which, in the case of the two anterior pairs, attains a considerable size. The anterior pair alone (first maxilliped) is slender and palpiform; it ends, however, in a small chela, which serves to seize the prey. The chela in this and all the other maxillipeds of the *Stomatopoda* is formed by the terminal joint turning back and biting on the penultimate joint. The maxillipeds

of the second pair are by far the largest; they are moved more or less outwards and are provided with a very large chela. The three following pairs resemble each other in size and structure, each ending in a smaller rounded chela. Accordingly there remain for locomotion only the three pairs of legs of the last three uncovered thoracic segments; they have the form of biramous swimming feet. The abdominal swimming feet, however, are much more developed and bear the branchial tufts on their external lamellæ.

The two sexes are only slightly different. The male is, however, easily to be recognised by the possession of the pair of rods at the base of the last pair of thoracic feet, and also by the slightly modified form of the first pair of abdominal feet.

FIG. 370.—Young *Alima* larva. *Af*. Abdominal feet (pleopods); *Mxf*, anterior maxillipeds; *Mxf'*, the large maxillipeds (second pair).

Metamorphosis.—The post-embryonic development consists of a complicated metamorphosis, which, unfortunately, is as yet not completely known to us. The youngest larvæ observed (about 2 mm. long) already possess all the segments of the thorax; but the abdomen, except the caudal plate, is still undeveloped. They are thus very different from the Zoæa of the *Decapoda*. Later larval stages are described as *Alima* and *Erichthus* (fig. 370).

The *Stomatopoda* are found exclusively in the warmer seas. They are excellent swimmers and live by preying on other marine animals.

Fam. *Squillidæ*. *Squilla mantis* Rond., *Sq. Desmarestii* Risso, Adriatic and Mediterranean.

(3) Sub-order: *Schizopoda*.*

Small Thoracostraca with large, usually soft cephalo-thoracic shield and eight pairs of biramous thoracic feet, which are similarly formed and frequently bear freely-projecting gills.

* G. O. Sars, "Hist. nat. des Crustacés d'eau douce de Norvège," Christiania

In their outward appearance the *Schizopoda* resemble the long-tailed Decapods, inasmuch as they possess an elongated and usually compressed body, a large cephalo-thoracic shield covering the thoracic segments more or less completely and a well-developed abdomen. In the structure of their maxillipeds and thoracic legs, however, they differ essentially from the Decapods and approach the more advanced larvæ of the prawns, which they also resemble in their simpler internal organization. Further, in all the deep sea forms the cephalo-thoracic shield leaves a greater number of the thoracic segments free (*Siriella*), and in the early larval stages all the thoracic segments are free as in *Nebalia*. A larger or smaller number of these free segments subsequently fuse on the dorsal side with the carapace (*Gnathophausia*).

Appendages.—The first three pairs of thoracic appendages (the homologues of the maxillipeds of the *Decapoda*) are biramous ambulatory legs and resemble in structure the following thoracic legs, which, by the possession of a multiarticulate setigerous exopodite, are adapted both for swimming and for producing currents in the water. The two anterior pairs, however, show a closer relation to the oral appendages by their shorter and stouter form and by the presence of processes on the basal joint (*Mysis*, *Siriella*). The principal ramus (endopodite) of the leg is always relatively slender and ends with a simple weak claw or with a multiarticulate tarsal flagellum. Rarely (*Euphausia*) the two last pairs of thoracic legs are entirely rudimentary, except as regards the largely developed branchial appendages. The abdominal legs are usually small and delicate in the female, but are strongly developed in the male. Sometimes they are of abnormal size and form (to assist in copulation), but only exceptionally (male of *Siriella*) bear gills. The appendages of the sixth segment, which is usually very much elongated, are always lamellar, biramous structures and form with the telson a powerful caudal fin (fig. 371). The inner lamella or endopodite of this pair of limbs frequently contains an **auditory vesicle**.

The differences between the males and females are so great that formerly they were placed in distinct genera. The former possess, on the anterior antennæ, a comb-shaped prominence bearing a great number of olfactory hairs; and, owing to the larger size of the

1867. G. O. Sars, "Carcinologiske Bidrag til Norges Fauna. Mysider," Christiania, 1870 and 1872. R. v. Willemoes-Suhm, "On some Atlant. Crustacea," cf. Trans. Lin. Soc., 1875.

abdominal feet, of which the anterior may, moreover, be provided with copulatory appendages, they are capable of a more rapid and perfect locomotion than the females, to which fact corresponds again the greater respiratory requirements and the possession of branchial appendages in *Siriella*.

Development.—The females bear on the two posterior (*Mysis*) or at the same time also on the median and anterior (*Lophogaster*) pairs

of thoracic limbs lamellæ, which form a brood pouch, in which, as in the *Arthrostraca*, the large eggs undergo their embryonic development. In other cases (*Euphausia*), the development proceeds by metamorphosis. The young *Euphausia* is hatched as a Nauplius larva, on which the three following pairs of appendages (maxillæ and first maxillipeds) soon appear as small prominences. The large carapace of the Nauplius, which is curved forwards round the base of the antennæ where it has a serrated edge, is the first rudiment of the cephalo-thoracic shield, and beneath it, at the sides of the unpaired eye, the rudiments of the lateral eyes are visible. The larva then, having moulted, assumes first the form of the Protozœa and then of the Zœa (described by Dana as *Calyptopis*), which is however provided with only six pairs of

FIG. 371.—*Mysis oculata*. Female with brood lamellæ (after G. O. Sars). Gb, Auditory vesicle.

appendages and a long, already fully segmented, apodal abdomen. In the numerous succeeding larval stages (*Furcilia*, *Cyrtopia*) the remaining appendages are successively developed.

Fam. **Mysidæ**. *Mysis vulgaris* Thomps., *M. flexuosa* O. Fr. Müll., *M. inermis* Raethk., Northern seas *Siriella Edwardsii* Cls.

Fam. Euphausiæ. *Euphausia splendens* Dana, Atl. Ocean. *Thysanopoda norvegica* Sars.

Fam. Lophogastridæ. *Lophogaster typicus* Sars, Norway.

(4) Sub-order : Decapoda.*

Podophthalmia with large dorsal cephalo-thoracic shield, which is usually fused with all the segments of the head and thorax. They have three (two) pairs of maxillipeds and ten (twelve) ambulatory limbs, some of which are armed with chelæ.

The head and thorax are completely covered by the dorsal carapace, the lateral expansions of which cover the basal joints of the maxillipeds and legs, forming a branchial chamber on either side, in which the gills are concealed. Only the last thoracic segment may retain its independence and be more or less movable. The shell is prolonged into a frontal spine (the rostrum) between the eyes. The firm, calcified integument of the dorsal carapace presents, especially in the larger forms, symmetrical prominences caused by the subjacent internal organs: these may be distinguished as regions and named in accordance with the internal organs.

The abdomen presents considerable differences both of size and form throughout the sub-order. In the *Macrura* it is of considerable size, possesses a hard exoskeleton, and, in addition to the five pairs of feet of which the anterior are often aborted in the female, is provided with a large swimming fin (the telson and the pair of large swimming feet of the sixth segment). In the *Brachyura* the abdomen is without a caudal fin and is reduced to a broad (female) or a narrow triangular (male) plate, which is bent up against the concave sternal surface of the thorax. The abdominal feet also are slender and styliform, and in the male are only developed on the two anterior segments.

Appendages.—The anterior antennæ in the *Brachyura* are often concealed in lateral pits; they usually arise beneath the movably articulated eye-stalks, and consist of a three-jointed basal portion bearing two or three multiarticulate flagella. The posterior antennæ

* Herbst, "Versuch einer Naturgeschichte der Krabben und Krebse," 3 Bde., Berlin, 1782-1804. Leach, "Malacostraca podophthalma Britannia," London 1817 to 1821. Th. Bell, "A history of the British stalk-eyed Crustacea," London, 1853. H. Rathke, "Untersuchungen über die Bildung und Entwicklung des Flusskrebsses," Leipzig, 1829. Spence Bate, "On the development of Decapod Crustacea," *Phil. Trans. of the Roy. Soc.*, London, 1859. C. Claus, "Zur Kenntniss der Malacostrakenlarven," *Würzb. naturwiss. Zeitschr.*, Tom II., 1861. Fr. Müller, "Die Verwandlung der Garneelen," *Archiv für Naturgesch.*, Tom XIX., 1863. Fr. Müller, "Für Darwin," Leipzig, 1864.

are usually inserted externally and somewhat ventrally to the first pair on a flat plate placed in front of the mouth (*epistom* or oral shield): they frequently possess a scale-like lamellar appendage. At their base there is always a protuberance with a pore at its end, through which the duct of the antennal gland (green gland) opens.

The mandibles vary considerably in shape in the different forms, but have, as a rule, a two or three-jointed palp, which, however, is absent in many prawns (*Carididæ*). They are either straight and strongly toothed on their thickened anterior edge (*Brachyura*), or are slender and much bent (*Crangon*), or else forked at the ends (*Palæmonidæ* and *Alpheidæ*). The anterior maxillæ always consist of two lamellæ and a palp, which is usually simple. The posterior maxillæ, on which there are usually four lamellæ (two double lamellæ) as well as palps, bear a large respiratory plate with setose edges (scaphognathite). These are followed by three pairs of maxillipeds, which, as a rule, have a flagellate appendage. There

FIG. 372.—Young form (larva) of the lobster (after G. O. Sars). *R*, rostrum; *A'*, *A''*, antennæ; *K'''*, third maxilliped; *F'* anterior ambulatory leg.

remain, therefore, only five pairs of thoracic appendages for use as legs; of these the two last are sometimes reduced or may even be entirely absent (*Leucifer*) as the result of retrogressive changes. The thoracic segments to which the ambulatory legs belong are, as a rule, all or all but the last fused together and form on the ventral side a continuous plate, which in all the *Brachyura* is broad. The legs consist of seven joints, which correspond to those of the *Arthrostraca*, and frequently end with a chela or prehensile hand.

Development.—The greater number of marine *Decapoda* leave the egg membranes in the zœa form; in *Homarus*, amongst the *Macrura*, the metamorphosis is much reduced and the just-hatched young possesses all the thoracic legs, which are, however, provided with external swimming rami, but it is still without the abdominal feet (fig. 372).

Embryonic development.—In addition to the classical researches of Rathke* on the crayfish, more recent works, especially those of

* Besides Rathke l. c. and Lereboullet l. c., and a Russian paper of Bobretzky,

Bobretzky (prawns and cray-fish) and Reichenbach (cray-fish) have yielded important results. The segmentation seems (in all cases?) to be superficial (centrolecithal), that is, to be confined to the peripheral yolk (formative yolk). This divides successively into two, four, eight, and an increasing number of segmentation cells, while the central granular food yolk, which is rich in oil globules, remains unsegmented. The young of *Astacus*, when hatched, resemble the adult animal, excepting that the caudal fin is still rudimentary.

I.—MACRURA.

The abdomen is strongly developed and is at least as long as the anterior part of the body; there are four or five pairs of abdominal feet and a broad, well-developed caudal fin. The antennules bear two or three flagella, the antennæ have one simple flagellum and frequently bear a scale at the base. The maxillipeds of the third pair are long and pediform and do not completely cover the preceding ones. The *Zoæa* larva, when hatched, is elongated and has usually three pair of biramous feet.

Fam. *Carididæ*. Prawns. Body laterally compressed, with a thin shell, which is often provided with a median ridge and prolonged into a saw-like frontal process. The posterior (external) antennæ are inserted beneath the anterior (internal) and have a large scale projecting over the stalk. The long and slender anterior pairs of ambulatory legs frequently end in chelæ. They live in shoals near the coast. Some genera (*Penæus*) possess a rudimentary swimming ramus. *Palæmon squilla* L., *Crangon vulgaris* Fabr., *Pontonia tyrrhena* Risso, lives between the shells of bivalves. *Sergestes atlanticus* Edw.

Fam. *Astacidæ*. Tolerably large, usually with a hard shell. The cephalo-thorax is slightly compressed, the abdomen flattened. The antennæ are attached near the antennules, and bear a small or quite reduced scale at their base. The first pair of ambulatory feet ends with large chelæ, as do in many cases the weaker and smaller second and third pairs. Some soft-skinned forms bury themselves in the mud or sand. *Astacus fluviatilis* Rond., Crayfish. *Homarus vulgaris* Bel., Lobster. *Nephrops norvegicus* L., *Gebia* Leach., *Thalassinia* Latr., *Callinassa subterranea* Mont., buries itself in sand on the sea-shore.

Fam. *Loricata*. With very hard, rough armour, and large broad abdomen. The antennules end with two short flagella; all five pairs of ambulatory feet with simple claws. The larvæ are described as species of *Phyllosoma*. *Palinurus quadricornis* Latr. *Scyllarus latus* Latr.

Fam. *Galatheidæ*. With broad, rather large abdomen, and well-developed caudal fin. The first pair of legs is chelate, the last is weak and reduced. *Galathea strigosa* L.

Fam. *Hippidæ*. Cephalo-thoracic shield long; end of the abdomen curved. The first pair of legs usually with a finger-shaped terminal joint; the last is

Kiew, 1873, compare H. Reichenbach, "Die Embryonalanlage und erste Entwicklung des Flusskrebses," *Zeitschr. für wiss. Zool.*, Tom XXIX, 1877.

weak. *Hippa eremita* L., lives buried in the sea sand, Brazil. *Albunea symnista* Fabr., Mediterranean.

Fam. **Paguridæ**. Hermit crabs. Abdomen long, usually covered with a soft skin and distorted, with narrow anal fin and rudimentary abdominal feet. The first pair of feet ends with powerful chelæ, the two last are reduced. Some of them seek shelter in empty snail shells, to protect their soft-skinned abdominal region. *Pagurus Bernhardus* L., *Cænobita rugosa* Edw., *Birgus latro* Herbst, said to climb palm-trees.

II.—BRACHYURA.

With pits for the reception of the short internal (anterior) antennæ and so-called orbits, *i.e.*, cavities for the reception of the stalked eyes. Abdomen short and reduced, without caudal fin, curved round against the excavated ventral surface of the thorax; in the male narrow and pointed, with only one, more rarely two pairs of abdominal feet; in the female broad, with four pairs of abdominal feet. In the female each oviduct dilates to form a bursa copulatrix. The third pair of maxillipeds have broad flat joints and completely cover the anterior mouth parts. The just-hatched *Zoea* larvæ of stout shape, with only two pairs of biramous feet and a dorsal spine; later they assume the *Megalopa* form. Many Brachyura live on land.

Fam. **Notopoda**. Transitional between the *Brachyura* and *Macrura*. The two or four posterior thoracic feet are articulated higher up than the four or three posterior pairs, and shifted on to the back. The first pair of feet has large chelæ, the last is often modified to swimming feet. *Porcellana platycheles* Penn., *Dromia vulgaris* Edw., *Lithodes*. Latr.

Fam. **Oxystomata**. With rounded cephalo-thorax. The frontal region does not project. The buccal frame is triangular. The male genital openings are on the basal joint of the last pair of thoracic legs. *Calappa granulata* L., *Ilia nucleus* Herbst, Mediterranean.

Fam. **Oxyrhyncha**. Cephalo-thorax usually triangular, with projecting pointed rostrum. There are nine gills on either side. The male genital opening is on the basal joint of the last pair of thoracic legs. The thoracic ganglia are united into one mass. They do not swim but crawl. *Inachus scorpio* Fabr., *Maja squinado* Rond., *Pisa armata* Latr., *Stenorhynchus* Lam.

Fam. **Cyclometopa**. With broad, short cephalo-thorax, rounded anteriorly. Without projecting frontal rostrum. There are nine gills on either side. The male genital opening is on the basal joint of the last pair of thoracic legs. Some of them are good swimmers. *Cancer pagurus* L., *Xantho rivulosus* Risso, Mediterranean. *Carcinus mænas* L., *Portunus puber* L.

Fam. **Catometopa, Quadrilatera**. Cephalo-thorax quadrilateral. Frontal region is curved downwards. There are fewer than nine gills. The male genital openings usually lie on the sternum. Some of them live for a long time away from the water. Some live in holes in the earth, as land crabs. *Pinnotheres pisum* L., in the shells of *Mytilus*. *P. veterum* Bosc., in the shells of *Pinna*; known to the ancients, who thought that there was a relation of mutual assistance between the crab and the mollusk. *Ocypoda cursor* Bel.,

Gelasimus foreepts Latr., *Grapsus varius* Latr., *Gecarcinus ruricola* L., Land Crabs. Water is retained for a long time in the branchial cavities, owing to the presence of secondary spaces around the branchial plates, which are thus prevented from sticking together. They live in holes in the earth in the Antilles.

III.—GIGANTOSTRACA.

The **Xiphosura** or **Pæcilopoda**, represented by the living genus *Limulus* and the orders of the fossil **Merostomata**, may be united under this head, as opposed to the *Entomostraca* and *Malacostraca*.

They are principally characterised by the possession of a single pair of appendages placed in front of the mouth and innervated from the cerebral ganglion, also by the presence of four or five pairs of legs, which are placed round the mouth and whose basal joints are modified to form large mandible-like masticatory organs. Behind the last pair of legs there is a simple or cleft prominence, forming a sort of underlip. The region of the body which bears these appendages is to be considered as an unsegmented cephalo-thorax; it is shield-shaped and may be drawn out into projecting wing-shaped lateral portions. On its upper surface two small median frontal eyes as well as two large lateral eyes can be distinguished. Following the cephalo-thorax there is an abdomen, which is usually elongated and composed of a greater number of segments. The abdomen tapers posteriorly and terminates in a telson, which may be flat or drawn out into the form of a spine.

Order 1.—MEROSTOMATA.*

Gigantostraca with five pairs of appendages on the cephalo-thorax which is relatively short; with an elongated apodal abdomen, usually composed of twelve segments and ending in a flat or styliform telson.

The powerful body of the *Eurypteridæ* (included with the *Pæcilopoda* by Woodward), as the most important family of the *Merostomata* is named after the genus *Eurypterus*, consists of a cephalo-thoracic shield with median ocelli as well as large projecting marginal eyes, also of an abdomen with numerous (usually twelve) segments which become longer posteriorly, and of a caudal shield, which is prolonged into a spine. Round the mouth on the underside of the cephalo-thorax

* Woodward, "Monograph of the Brit. fossil Crustacea belonging to the order of Merostomata." P. I., & II., *Palæont. Soc. of London*, 1866-1869. Woodward, "On some points in the structure of the Xiphosura, having reference to their relationship with the Eurypteridæ," *Quarterly Journ. Geol. Soc. of London*, 1867 and 1871.

there are five pairs of long spiny legs, of which the last is much the largest and ends in a broad swimming-fin. Some of the anterior appendages may be armed with a chela. The resemblance of the true *Eurypteridæ* (in the general shape of their body) to the *Scorpionidæ* is very striking, while the genus *Hemiaspis* presents affinities to the *Pæcilopoda*. The most important forms are: *Eurypterus pygmaeus* Salt., Devonian strata, *Pterygotus anglicus* Ag., four feet long, from the upper Silurian (fig. 373).

FIG. 373.—*Eurypterus remipes* after Nieszkowski. *a*, Dorsal view; *b*, ventral view; *O*, eyes; *St*, caudal spine; *H*, hypostome.

Order 2.—XIPHOSURA.*

Gigantostraca whose body is divided into three parts, which are movably articulated together; a large shield-shaped cephalo-thorax, an abdomen with five pairs of lamellar feet and a long movable caudal spine.

The large body of these Crustacea is covered with a strong chiti-

* C. Gegenbaur, "Anatomische Untersuchung eines *Limulus*, mit besonderer Berücksichtigung der Gewebe," *Abhandl. der naturforsch. Gesellschaft zu Halle*, IV., 1858. Packard, "The Development of *Limulus Polyphemus*," *Soc. of Nat. Hist.*, 1870. A. M. Edwards, "Recherches sur l'anatomie des *Limules*," *Ann. sc. nat.* V^e Sér. Tom. XVII., 1872-1873. [E. R. Lankester, "*Limulus* an Arachnid," *Quart. Journ. Mic. Soc.*, vol. xxi.]

nous armour and is divided into an arched cephalo-thorax and a flat, almost hexagonal abdomen, which ends in a movable sword-like caudal spine. The cephalo-thorax (fig. 374) forms by far the larger part of the body; it bears on its arched dorsal surface two large compound eyes, and further forwards, nearer the middle line, two smaller simple eyes; while on its ventral surface there are six pairs of appendages, of which the anterior pair is slender and may, on account of its position in front of the mouth, be regarded as a pair of antennæ, although it ends, like the others, with a chela. The latter are placed to the right and left of the mouth, and their coxal joints serve as organs for the mastication of the food. At the end of the cephalo-thorax there is a pair of lamellar appendages, which are connected in the middle line and form a kind of operculum for the branchial appendages of the abdomen. It seems of interest that the form of this branchial operculum in the Asiatic and American species presents constant differences, in that the median portion in the former is undivided, and in the latter consists of two joints. The shield-shaped abdomen which, by means of a transverse joint, is movable on the cephalic shield in a dorso-ventral direction, is armed on either side with movable spines, and bears on its ventral surface five pairs of lamellar feet, which are almost completely covered by the operculum. These abdominal feet assist both in swimming and in respiration, since the respiratory lamellæ are placed on them (fig. 374, *a*, *b*).

The internal organization attains a relatively high development in correspondence with the large size of the body. In the

nervous system the following parts can be distinguished:—a broad cesophageal ring, the anterior part of which constitutes the brain and gives off the optic nerves, while from the lateral parts the

FIG. 374.—*a* *Limulus moluccanus*, seen from the dorsal side (after Huxley). *O*, eyes; *St*, caudal spine. *b*, *L. rotundicauda* (after M. Edwards), seen from the ventral side. *A* Antennæ; *B*, the feet with their coxal jaws; *K*, gills; *Op*, operculum.

six pairs of nerves to the antennæ and legs take their origin; a subœsophageal ganglionic mass with three transverse commissures; and a double ganglionic cord, which gives off branches to the ventral feet and ends with a double ganglion in the abdomen. The **alimentary canal** consists of œsophagus, masticatory stomach, and a straight intestine communicating with a liver and opening by the anus, which is placed immediately in front of the base of the caudal spine.

The **heart** is elongated and tubular, and is pierced by eight pairs of slits, which can be closed with valves; it is also provided with arteries, which, after a short course, pass into lacunar blood paths. From the base of the gills, two spaces, returning the blood, extend to the pericardial sinus.

Five pairs of appendages of the abdominal feet function as **gills**.

FIG. 375.—Embryo of *Limulus* in the Trilobite stage (after A. Dohrn).

These are composed of a very large number of delicate lamellæ, lying one on another like the leaves of a book.

Generative organs.—The branched *ovaries* unite to form two oviducts, which open by separate openings on the under side of the operculum (first pair of abdominal limbs); in the male the openings of the two seminal ducts are placed in the same position. In the male, the anterior thoracic feet end in simple claws.

Development.—It is known that the young leave the egg without the caudal spine and often without the three posterior pairs of gill-bearing feet. This stage has been suitably named the Trilobite stage, on account of the resemblance which the larva presents to a Trilobite (fig. 375). On the cephalic shield there is a median keel-like ridge, which is also found on the abdominal segments. The last abdominal segment includes between its lateral portions the short rudiment of the caudal spine. In the next stage the segmentation of the abdomen becomes less obvious (the caudal shield becomes consolidated) and the caudal spine developed.

The adult animals reach a length of several feet, and live exclusively in the warm seas, in the Indian Archipelago and on the east coast of America. They exist at a depth of two to six fathoms and move about in the mud by the alternating bending and straightening of the cephalic and abdominal shields and the caudal spine. Their food consists chiefly of Nereids. They are found in a

fossil state, especially in the Sohlenhofen lithographic slate, but also in older formations as far back as the Uebergangsgebirge (Cambrian, Silurian, etc.) formation.

Limulus moluccanus Latr., East Indies. *L. polyphemus* L., East Coast of North America.

TRILOBITA.*

In connection with the *Merostomata* and the *Xiphosura*, the *Trilobites* may be considered. Their systematic position cannot as yet be defined with certainty. They lived only in the most ancient periods of the earth's history, and their fossil remains are found in great numbers and are excellently preserved; but, unfortunately, the conditions under which they were fossilised were such that the under side of the body, and, consequently, the structure of the appendages, that is the very characters which would enable us to decide their affinities, remain unknown to us. We may probably infer from this absence of any trace of appendages* in the fossils, that the legs were soft and delicate; but Burmeister's conclusion that they resembled the legs of the *Phyllopoda* is not justified.

The body, which is frequently found rolled up, is covered with a thick shell, which is divided by two parallel longitudinal furrows into an elevated median portion (*rhachis*) and two lateral portions (*pleura*): it rarely attains any considerable size. There is an

FIG. 376.—Diagram of *Dalmatites* (after Pictet). *Gl*, Glabella; *Sf*, great suture (ocular suture); *O*, eyes; *Ge*, separable gena (cheeks); *Rh*, rhachis (tergum); *Pl*, pleuron; *Pg*, pygidium.

* Burmeister, "Die Organisation der Trilobiten," etc., Berlin, 1843. Beyrich, "Untersuchungen über Trilobiten," Berlin, 1845, 1846. J. Barrande, "Système silurien du centre de la Bohême," Prague, 1852. S. W. Salter, "A monograph of the British Trilobites," London, 1864-1866.

* Portions of appendages have been recently observed on the ventral surface of an *Asaphus* ("Notes on some Specimens of Lower Silurian Trilobites," by E. Billings; also "Note on the Palpus and other appendages of *Asaphus*," etc., by H. Woodward, *Quart. Journ. of the Geolog. Soc.*, London, 1870), which are said to point to the affinity of *Trilobites* with the *Isopoda*.

anterior arched, semicircular region, which may be regarded as head or perhaps as cephalo-thorax, and a number of sharply distinct segments, which belong partly to the thorax and partly to the abdomen and are terminated by a larger shield-shaped caudal portion, the *pygidium* (fig. 376).

At the edge of the pygidium, the armour of the upper surface is folded round on to the ventral side and leaves only the middle part of the latter uncovered. The lateral regions of the head, the median part of which especially projects as the "*glabellum*," bear usually upon two protuberances large compound faceted eyes, and are often prolonged into two very long backwardly directed spines; they are also folded inwards on to the ventral surface. With the exception of a plate (hypostoma) comparable to the under-lip of *Apus*, no trace of mouth parts has been observed for certain on the ventral surface of the head. The number of thoracic (trunk) segments varies considerably, but is tolerably definite for the adults of each species. Their lateral portions are likewise folded inwards on to the ventral surface, and present variously shaped wing-like processes and long pointed spines.

The Trilobites lived in the sea, probably in shoals in shallow water near the coast. Their fossils are amongst the most ancient remains of animal life, and are found principally in Bohemia, Russia, Sweden etc., in the lowest strata of the Uebergangsgebirge (Cambrian, Silurian, etc.) They have been divided into numerous families according to the structure of the head (especially of the glabellum), the form of the pygidium and the number of segments. The most important genera are *Calymene Blumenbachii* Brogn; *Olenus gibbosus* Wahlb., *Ellipsocephalus Hoffii* Schlotth.

Class II.—ARACHNIDA.*

Air-breathing Arthropoda with fused head and thorax, with two pairs of jaws, four pairs of ambulatory legs and apodal abdomen.

The Arachnida include animals of extraordinarily different form. The head and thorax are almost invariably fused to form a short cephalo-thorax; but the condition of the abdomen presents very great variations.

* C. A. Walckenaer et P. Gervais, "Histoire naturelle des Insectes Aptères," 3 Vols., Paris, 1837-1844. Hahn und Koch, "Die Arachniden, getreu nach der Natur abgebildet und beschrieben," Nürnberg, 1831-1849. E. Blanchard, "Organisation du règne animal. Arachnides," Paris, 1860.

In the Spiders (*Araneida*) the abdomen is swollen and is joined to the cephalo-thorax by a short stalk. In the *Scorpionidæ*, on the contrary, the long abdomen is joined to the cephalo-thorax by its whole breadth, and is divided into a broad segmented præ-abdomen and a narrow, very movable post-abdomen, which is also segmented. In the Mites (*Acarina*) the abdomen is unsegmented and fused with the cephalo-thorax. In the *Pentastomida* the entire body is elongated, ringed and vermiform, with four (two pairs of) hooks in place of the appendages; these animals are known as *Linguatulida*, and might be placed, on account of their parasitism, amongst the intestinal worms.

The marked reduction of the cephalic region, which is without true antennæ and possesses only two pair of oral appendages, is characteristic of the Arachnida. The anterior pair of cephalic appendages (chelicerae), which are used as jaws, have been regarded as modified antennæ; but it is perhaps more natural to regard them as morphologically equivalent to the mandibles of Crustaceans and Insects. These anterior jaws or chelicerae are either chelate, in which case the claw-like terminal joint can be moved against a process of the preceding joint (Scorpions, many Acarina), or subchelate, when the last joint is folded down upon the next like the blade of a pocket-knife upon the handle (Spiders).

The chelicerae may also have the form of stylets, which are enclosed in a tube formed by the second pair of jaws (Mites). The latter, which constitute the second pair of appendages of the head or the pedipalpi, consist of a stout basal joint and a palp, which has frequently the form and segmentation of a leg. This either ends with or without a claw or with a chela (Scorpions). In the true Spiders there is an unpaired plate, the lower lip, between the basal joints of the two pedipalpi and belonging to the same segment as the latter. The four following pairs of appendages of the thorax are ambulatory legs. The first of them is sometimes modified in form and elongated like a palp; its basal joint may function as a jaw. The legs consist of six or seven joints, which, in the higher forms, have been called by the same names as the analogous regions of the Insect leg.

The internal organization of the *Arachnida* shows hardly fewer differences than does that of the *Crustacea*. The nervous system may have the form of a common ganglionic mass around the œsophagus (Mites), and may even possess only a simple commissure above the œsophagus (*Pentastomida*). As a rule, however, there is a distinct separation between brain and ventral cord, the latter showing

very different grades of development. Visceral nerves have been shown to exist in the Spiders and Scorpions. The **sense organs** are, as a rule, not so highly developed as in the *Crustacea*, and, putting on one side the tactile function of the extremities, are confined to eyes. The eyes are simple and immovable, and never possess a faceted cornea; they are from two to twelve in number, and are symmetrically arranged on the anterior surface of the cephalo-thoracic shield. Auditory organs have not yet been discovered, but there are tactile and olfactory organs.

The **alimentary canal** runs straight from the mouth to the hind end of the body, and is divided into a narrow œsophagus and a wide intestine, which is, as a rule, provided with lateral cæca. The intestine is, in the Spiders and Scorpions, divided into an anterior dilated portion—the so-called stomach—and the intestine proper. The glandular appendages of the digestive canal are **salivary glands**; in Spiders and Scorpions, a **liver**, composed of a number of branched canals; and, with a few exceptions, **Malpighian tubes**, which function as *urinary organs* and open into the hind end of the intestine.

The organs of **circulation** and **respiration** also show very different degrees of development and are only absent in the lowest Mites. The heart lies in the abdomen, and is a long, many-chambered dorsal vessel with lateral slits through which the blood enters. It is frequently continued into an anterior and posterior aorta, and in Scorpions gives off in addition lateral branching arteries. The organs of **respiration** are internal air chambers, which have the form either of ramified tubes (*tracheæ*), or of hollow lamellæ (*fan-tracheæ*, *lungs*) placed upon one another in great number like the leaves of a book and connected together by trabeculæ so as to have the form of a sac. The air chambers are always kept open by a firm internal chitinous membrane, so that the air can enter by the paired openings (*stigmata*) of the tracheæ or lungs at the beginning of the abdomen, and be distributed to the finest ramifications. The chitinous lining may become thickened so as to give rise to a spiral fibre.

Generative organs.—With the exception of the hermaphrodite Tardigrada, all the *Arachnida* are of separate sexes. The males are frequently distinguished by external characteristics, as for example by their smaller size, by the possession of organs of attachment (Mites), or by the modification of certain appendages. Their generative organs consist of paired testicular tubes, and the vasa deferentia often receive the contents of accessory glands before opening to the exterior by a single or double aperture at the base (anterior end) of

the abdomen. Special copulatory organs in the region of the genital openings are, as a rule, wanting, but appendages far removed from the genital openings (*e.g.*, pedipalpi of Spiders) often serve to transfer the sperm from the male to the female. The female sexual organs are also paired, usually racemose glands, with two oviducts, which usually dilate to a receptaculum seminis before their single or double opening at the beginning of the abdomen. They are also connected with accessory glands. Rarely (*Phalangium*) there is a long protrusible ovipositor.

Only a few of the *Arachnida* are viviparous (Scorpions and some Mites); the greater number lay eggs, which they sometimes carry about with them in sacs till the young are hatched. As a rule, the just-hatched young have the form of the adult; but in most Mites two or more rarely four legs are wanting, and appear only with the succeeding moults. The development of the *Pygnogonida* *Pentastomida* and *Hydrachnea* (water-mites) (which latter pass through a pupa-like inactive stage) consists of a complicated metamorphosis.

Almost all *Arachnida* live on animals, a few on vegetable juices. The lowest forms are parasitic. The larger and more highly organised forms prey on living animals, principally on Insects and Spiders, and are usually furnished with poison weapons, with which they kill their prey. Many of them, by means of the secretion of spinning glands, spin webs, in which their prey becomes entangled. Most of them remain during the daytime beneath stones and in hiding-places, and come out to catch their prey only in the evening and at night.

Order 1.—LINGUATULIDA, PENTASTOMIDA.*

Parasitic Arachnida with ringed, elongated, vermiform body, with two pairs of hooks in the neighbourhood of the jawless mouth.

The vermiform ringed body of these parasites, which were for a long time taken for intestinal worms, is to be regarded as being principally formed of the extremely enlarged and elongated abdomen, the cephalo-thorax being much reduced; an interpretation which the form of the body of the *Dermatophili* seems to support. In the adult, jaws are completely wanting, but there are four curved hooks (two on each side of the mouth, fig. 377), which can be protruded from pouches in the skin and are attached to special chitinous rods. These may correspond to the terminal claws of the two posterior pairs of legs, since the two pairs of legs of the larva, which are to

* R. Leuckart, "Bau und Entwicklungsgeschichte der Pentastomiden," Leipzig und Heidelberg, 1860.

be regarded as the anterior appendages, are lost in the course of development. The **nervous system** is confined to a simple subœsophageal nervous mass, with œsophageal ring and giving off numerous nervous trunks. **Eyes** and organs of **respiration** and **circulation** are wanting. The **alimentary tract** is a simple canal in the middle of the body, which opens by an anus at the posterior end. Special cutaneous glands are present in great numbers and strongly developed. **Male** and **female** are distinguished by considerable differences in size and by the different position of the genital openings. While the genital opening of the surprisingly small male lies not far behind the mouth, that of the female is situated near the anus, at the hinder end of the body.

The *Linguatulida*, when sexually adult, inhabit the air chambers of warm-blooded animals and *Amphibia*. The developmental history of *Pentastomum tenioides*, which lives in the nasal cavities and in the frontal sinuses of dogs and wolves, is known from the researches of Leuckart. The embryos of this species, while still enveloped in the egg-membranes, pass out the nasal mucus on to plants, and thence into the stomach of Rabbits and Hares, more rarely into that of Man. When freed from the egg-membranes, they pierce the walls of the in-

FIG. 377.—*Pentastomum denticulatum*. Young form of *P. tenioides*. O, Mouth; Hf, the four hooks; D, intestine; A, anus.

FIG. 378.—Young forms of *Pentastomum tenioides* (after R. Leuckart). a, Egg with embryo. b, Embryo with two pairs of hooked feet, Hf' and Hf''. c, Larva from liver of rabbit. G, Ganglion; D, intestine; Hd, skin glands. d, Older larva. O, mouth; A, anus; Gd, genital glands.

testine and reach the liver. There they surround themselves with a cyst, in which they pass through a series of changes of form, accompanied, as in insect larvæ, by repeated ecdyses (fig. 378). When six months have elapsed, they have attained a considerable size and have acquired the four oral hooks, as well as a number of finely serrated superficial rings. They have now reached the stage formerly described as *P. denticulatum* (fig. 377), in which they break through their capsules and begin a fresh migration. They traverse the liver, and if present in great numbers, occasion the death of their host. In other cases, on the other hand, they soon become enveloped in

FIG. 379.—Ripe male of *Atax Bonzi*, seen from the dorsal surface (after E. Claparède). *Kt*, Pedipalpus; *G*, brain; *Oc*, eyes; *T*, testis; *N*, Y-shaped gland; *D*, intestine; *A*, anus; *Hd*, cutaneous glands.

another cyst. If they now pass with the flesh of the Hare or Rabbit into the buccal cavity of the Dog, they penetrate into the neighbouring air-chambers, and in two or three months become sexually mature.

Pentastomum tanioides Rud., 80-85 mm., Male only 18-20 mm. long. *P. multicinctum* Harl., in the liver of *Naja haje*. *P. constrictum* v. Sieb. Encysted in the liver of negroes in Egypt.

Order 2.—ACARINA,* MITES.

Arachnida with stout body. The abdomen is unsegmented and

* O. Fr. Müller, "Hydrachnæ," etc., 1781. A. Dugès, "Recherches sur

fused with the thorax. The oral apparatus is adapted for biting or piercing and sucking. Respiration, as a rule, by means of tracheæ.

The body of the *Acarina* is generally small and possesses a stout and unsegmented form. The head, thorax, and abdomen are fused into a common mass (fig. 379). The form of the oral apparatus varies exceedingly, and may be adapted either for biting or for piercing and sucking. The chelicerae are accordingly sometimes retractile styles, and are sometimes furnished with claws or chelæ. In the first case, the bases of the pedipalpi form a sheath which surrounds the styliform chelicerae and serves as a suctional rostrum, while the peripheral part of the pedipalpus or palp frequently

projects laterally, and ends with a claw or chela. The structure of the four pairs of legs is not less various, inasmuch as they may serve for crawling, attachment, running and swimming. They usually end with two claws, sometimes in parasitic forms with stalked suctional discs.

The nervous system is reduced to a common ganglionic mass representing the brain and ventral cord. Eyes may be absent or may be present, as one or two pairs of simple eyes.

The alimentary canal is frequently provided with salivary glands, and gives off on

either side a number of blind saccular diverticula which may be forked (fig. 380).

Heart and blood vessels are invariably absent, but respiratory organs are frequently present in the form of tracheæ, which arise

FIG. 380—Anatomy of *Ixodes Ricinus* (after Al. Pagenstecher). G, Brain; SpD, salivary gland; Dg, ducts of salivary gland; D, diverticula of intestine; A, anus; N, urinary organ; Tr, bundles of tracheæ; St, stigma.

l'ordre des Acariens en général et les familles des Trombidies, Hydrachnés en part," *Ann. des Sc. Nat.*, II. Ser., Tom. I. and II. H. Nicolet, "Histoire naturelle des Acariens, etc. Oribatides." *Archives du musée d'hist. nat.*, Tom VII. O. Fürstenberg, "Die Krätzmilben des Menschen und der Thiere," Leipzig, 1861. Al. Pagenstecher, "Beiträge zur Anatomie der Milben," I. and II., Leipzig, 1860-1861. E. Claparède, "Studien an Acariden," *Zeitschr. für wiss. Zool.*, Tom XVIII., 1868. P. Mégnin, "Les parasites et les maladies apasitaires, 1880.

in tufts from a pair of stigmata, placed, as a rule, before or behind the last pair of legs (fig. 380, *St*).

The common **generative opening** is placed as a rule far away from the anus, and may be situated anteriorly between the last pair of legs (fig. 381, *a*, *b*). There may be a special copulatory opening, as in

FIG. 381.—*a*, Male; *b*, female genital organs of *Argas* (after Al. Pagenstecher). *T*, Testes; *Vd*, seminal duct; *Dr*, prostate gland; *Go*, genital opening; *Ov*, ovaries; *Od*, oviduct; *U*, uterus; *Dr*, glandular appendages.

the itch-mites (*Sarcoptidæ*), through which the sperm passes into the receptaculum. The males are often distinguished not only by their

FIG. 382.—Larva of a *Hydrachna*. *b*, Its pupa. *Kf*, chelicera; *Kt*, pedipalpus; *Oc*, eyes; *B*, legs.

appendages, which are more powerful and of a slightly different form, but also by the possession of posterior suctional pits, and sometimes also by the manner of nourishment and mode of life. The *Acarina* are, with the exception of the viviparous

Oribatidæ, oviparous. The young are usually hatched with only three pairs of legs, and undergo a metamorphosis, which in the *Hydrachnidæ* is distinguished by several larval and pupal stages (fig. 382 *a, b*). Very many Mites are parasitic on animals and plants, others are predacious and live some on land and others in water.

Fam. Dermatophili. Small elongated mites with long vermiform, transversely ringed abdomen, with suctorial proboscis, styliform jaws, and four pairs of short, two-jointed stump-like feet. The only known genus, *Demodex* (*Simonea*), lives in the hair follicles of domestic animals (Dog, Cat, Sheep, Cow, Horse), and as *D. folliculorum* Sim. in the hair follicles of Man, where they may give rise to comedones (fig. 384).

Fam. Sarcoptidæ. Itch mites. Body microscopic in size, stout, and with a soft skin, with chitinous rods for the support of the appendages.

There are no eyes. The oral apparatus consists of a suctorial cone with chelate chelicerae and short laterally-placed pedipalpi. The legs are short and stump-shaped, and some or all of them have stalked suctorial discs. The males often have suckers and processes at the posterior end of the body. The females have a special vulva and receptaculum seminis. They live upon or in the skin of Vertebrates, and occasion the itch and mange. *Sarcoptes scabiei* Dug. (fig. 385), itch mite. With numerous pointed tubercles, spines and hairs on the dorsal surface. Legs five-jointed, the two anterior terminate with stalked sucker; the last pair of legs in the male ends not, as in the female, in a bristle, but in a stalked sucker (fig. 385). The females only bore deep passages in the epidermis, at the end of which they live, and produce by their pricking the skin disease known as the itch. The young,

FIG. 383.—Female of *Phytopus vitis*, from the leaf of the vine (after H. Landois). *Or*, Ovaries; *A*, anus; *Go*, genital opening; *B'''*, *B''*, third and fourth pair of legs.

FIG. 384 — *Demodex folliculorum* (after Ménégnin), strongly magnified; *Kt*, pedipalpus.

when hatched, possess only three pairs of legs and undergo several moults. The domestic animals are infected by different species of *Sarcoptidæ*, which may be temporarily transferred to man. *Dermatodectes communis* Fürst. *Symbiotes equi* Gerl. (fig. 386).

Fam. Tyroglyphidæ. Cheese-mites. Of more elongated form, with conical proboscis, chelate chelicerae, and three-jointed pedipalpi. The five-jointed legs are tolerably long, and have lobes for attachment and claws. Large suckers, especially in the male, are often present at the sides of the anus. They live on animal and vegetable matters. *Tyroglyphus siro* Gerv. *Rhizoglyphus*

Robini Clap., on roots. *Glyciphagus fecularum* Guér., on potatoes. *Hypopus* Dug., according to Mégnin and Robin, contains larval forms, which attach themselves to insects by their suckers.

Fam. Ixodidæ. Ticks. Larger usually blood-sucking mites, with strong dorsal shield and large, protrusible toothed chelicerae. The pedipalpi are three- or four-jointed and club-shaped; their bases are joined together to form a

FIG. 385.—*Sarcoptes scabiei* (after Gudden). *a*, Male from the ventral side. *b*, Female from the ventral side. *c*, Female from the dorsal surface. *d*, Larva. *Kf*, Chelicerae; *B'''*, third pair of legs.

proboscis, bearing recurved hooks (fig. 387). The slender legs end with two claws. Two simple eyes are often present. Respiration by tracheæ. The Ticks live on the underwood in forests. The females crawl on to Mammalia and Man, suck blood, and become much swollen out. The young, when hatched, have three pairs of legs. In tropical countries the Ticks are of considerable size, and are amongst the most troublesome parasites. *Ixodes ricinus* L. *I. reduvius*,

FIG. 386.—*Symbiotes equi* = *Chorioptes spathiferus*, from ventral side (after Mégnin). *a*, Male; *HG*, sucker; *b*, young female in copulatory stage; *c*, female ready to lay.

FIG. 387.—Oral apparatus of *Ixodes* (after Al. Pagenstecher). *R*, Proboscis; *Kf*, chelicera; *Kt*, pedipalpus; *B'* first pair of legs.

Deg., *Argas reflexus*, Latr., on Pigeons, occasionally on Man. *A. persicus* Fisch. Notorious for its bite.

Fam. **Gamasidæ**. Beetle-mites. Chelicerae chelate. Pedipalpi five-jointed. The legs end with two claws and a sucker. Tracheae are present. Some of them lead a free life and are predacious, some are parasitic on Beetles and on the skin of Birds and Mammals. *Gamasus coleopratorum* L., *Dermanyssus avium*, Dug., *Pteroptus vespertilionis* Herm.

Fam. **Hydrachnidæ**. Water-mites. Body globular, often brightly coloured. Chelicerae usually with a claw-like terminal joint. They have swimming legs, and two or four simple eyes. There are tracheae. The larvæ, when hatched, adhere with their large suetorial cone to aquatic Insects, on the blood of which they live. *Hydrachna cruenta*, O. Fr. Müll. *Atax Bonzi* Clap., in the mantle cavity of the *Unios*. *Limnochares holosericeus* Latr.

Fam. **Trombidiidæ** (fig. 388). Body brightly coloured and covered with hairs; the pedipalpus has a claw and a lobe-like appendage. Eyes present. Respiration by tracheae. The hexapodous young live as parasites on *Insecta*

FIG. 388.—*Trombidium holosericeum* (after Mégnin).

FIG. 389.—*Pygnogonum littorale*, (règne animal) AB, pair of legs used for carrying the eggs.

and *Arachnida*, sometimes on *Mammalia*, and on Man, in whom they (as *Leptus autumnalis*) produce a transitory affection of the skin. *Trombidium holosericeum* L. *Erythraeus parietinus* Herm. *Tetranychus telarius* L. Spinning mite.

Fam. **Oribatidæ**. Chelicerae retractile and chelate. Pedipalpus five-jointed, with toothed biting plate on its basal joint. Ocelli absent. *Oribates alatus* Herm., under moss.

Fam. **Bdellidæ**. The cephalic region is elongated to form a proboscis, and is distinct from the rest of the body. The chelicerae are chelate. The pedipalpi are long and thin. The animals creep about on damp ground. *Bdella longicornis* L.

PYGNOGONIDA.*

Milne Edwards and Kröyer placed the *Pygnogonida* among the *Crustacea*; latterly, however, they have been generally placed between

* A. Dohrn, "Die Pantopoden des Golfes von Neapel und der angrenzenden Meeresabsehnitte," Eine Monographie, Leipzig, 1881.

the Mites and Spiders amongst the *Arachnida*, although they possess a greater number of appendages than either, inasmuch as the males have an accessory pair of legs, used in carrying the eggs (fig. 389, *A B*). They are small animals with a conical suctorial proboscis and rudimentary abdomen (reduced to a tubercle); and they live in the sea, and crawl slowly about amongst the sea-weeds. There are four pairs of very long, many-jointed legs, which contain tubular diverticula of the stomach and the sexual glands. There are no tracheæ. On the other hand, there is a well-developed heart with an aorta

FIG. 300.—*Ammothea pygnogonoides* (règne animal). *Da*, prolongations of alimentary canal into the legs.

and several lateral ostia. Above the brain lie four small simple eyes. There is a considerable ventral chain, composed of several ganglia. The eggs are carried about on the accessory pair of legs on the thorax of the male (fig. 389) till the larvæ are hatched.

Pygnogonum littorale O. Fr. Müller, North Sea. *Phorichilidium* Edw., *Ammothea* Leach, *A. pygnogonoides* Quatr. (fig. 390).

TARDIGRADA.*

The *Tardigrada* constitute a second group, which is often separated as a distinct order. They are small mite-like *Arachnida*, and may

* Doyère, "Mémoire sur les Tardigrades," *Ann. des Sc. Nat.*, II^e Sér., Tom. XIV., XVII., XVIII. C. A. S. Schultze, "Macrobiosus Hufelandii, etc," Berolini 1834. C. S. Schultze, "Echiniscus Bellermanni," Berolini, 1840. Dujardin,

be defined as *hermaphrodite Arachnida with suctorial mouth parts, and short stumpy legs, without heart or respiratory organs.*

The body of these small, slowly-creeping aquatic animals is elongated and vermiform, and prolonged at the anterior extremity into a suctorial tube, from which two styliform jaws can be protruded. The four pairs of legs are short tubercles terminated by several claws (fig. 391); the last pair is placed at the extreme end of the body. The **nervous system** consists of four ganglia connected by long commissures. The first of these ganglia corresponds to the brain and gives off nerves to two simple eyes and to two sensory papillæ. **Circulatory** and **respiratory** organs are entirely absent. The **alimentary canal** consists of a muscular pharynx and a stomach beset with short cæcal diverticula. The ducts of two salivary glands of considerable size open into the suctorial proboscis (fig. 391). The *Tardigrada* are hermaphrodite, and possess a pair of **testes** and an unpaired **ovarian sac** which open together into the cloacal termination of the intestine. They usually lay large eggs at the time of moulting, which remain enclosed in the old cast-off skin till the young animals are hatched. Development takes place without metamorphosis. The animals live in moss and algæ in the gutters of roofs, and also on the sea-beach, and it is specially worthy of remark that, like the *Rotifera*, they can, by the addition of moisture, be called back to life after a long period of desiccation.

Macrobiotus Hufelandii S. Sch., *Milnesium tardigradum* Doy., *Echiniscus Bellermanni* S. Sch.

"Sur les Tardigrades et sur une espèce à longs pieds vivant dans l'eau de mer," *Ann. des Sc. nat.* Sér. III., Tom XV. Also the works of Kaufmann, Greeff and Max. S. Schultze.

FIG. 391.—*Macrobiotus Schultzei* (after Greeff),
O, Mouth; Vm, pharynx; Md, stomach;
Spd, salivary glands; Ov, ovary; T, testes;
Vs, vesicula seminalis.

Order 3.—ARANEIDA * (SPIDERS).

Arachnida with poison glands in the subchelate chelicerae; with pediform pedipalpi and stalked unsegmented abdomen. They have four or six spinning mammillae, and two or four pulmonary sacs.

The peculiar shape of the true spiders is due to the swollen and unsegmented abdomen, the base of which is constricted to form the stalk by which it is united to the rest of the body (fig. 392). The large subchelate chelicerae, which project beyond the front of the head, consist of a powerful basal portion grooved on the inner side, and a claw-shaped terminal joint at the point of which the duct of a

FIG. 392.—*Dysdera erythrina* from the ventral side (règne animal). *Kf*, chelicera; *Kt*, pedipalpus; *K*, basal joint (jaw) of pedipalpus; *P*, lungs; *St*, stigma of lungs; *St*, posterior stigma leading into the tracheae; *G*, genital opening; *Sp*, spinning mammillae.

poison gland opens (fig. 393). At the moment of the bite the secretion of this gland flows into the wound, and in the case of small animals causes an almost instantaneous death. The pedipalpus bears on its broad coxal joint, which constitutes a kind of biting-blade (fig. 392 *K*), a many-jointed palp, the terminal region of which is peculiarly modified in the male and functions as a copulatory organ. The mouth is bounded on the under side by an unpaired plate, forming a sort of lower lip. The four pairs of usually long legs, whose form and size vary according to the manner

FIG. 393.—Poison gland and terminal joint of chelicera of *Mygale* (règne animal). *K*, claw; *Gd*, poison-gland; *B*, poison vesicle.

of life, end with two toothed claws, to which a small claw (*Tk*) and several accessory claws may be added (fig. 394). The abdomen in the female is always larger and more swollen than in the male; at the base (anterior part) of its ventral surface is placed the unpaired sexual opening, at the sides of which are the two slit-like apertures of the lung sacs. There is often

a second pair of stigmata behind these openings leading either into the

* Besides the works of C. A. Walckenaer, Treviranus, C. J. Sundevall, T. Thorell, Menge, Koch, Dugès, Lebert, etc., compare. E. Claparède, "Recherches sur l'évolution des Araignées," Genève, 1862; E. Claparède, "Études sur la circulation du sang chez les Arachnides du genre *Lycosa*," Genève, 1863; F. Plateau, "Recherches sur la structure de l'appareil digestif et sur les phénomènes de la digestion chez les Arachnides dipneumones," Bruxelles, 1877.

posterior lung sacs (*Mygalidæ*) or into a system of tracheæ (*Argyro-neta*, *Dysdera*). The anus is placed ventrally at the end of the

abdomen, and is surrounded by four or six wart-like protuberances (fig. 395, *Spw*), the spinning or arachnidial mammillæ, from which the secretion of the spinning glands passes out. In front

FIG. 394.—a, Leg of the fourth pair of *Amaurobius ferox*. Ca, Calamistrum. b, End of foot of *Philæus chrysops* with two claws and pencil consisting of spatulate hairs (S). c, End of foot of *Epeira diadema*; K, web-claws; Tk, ambulatory claw; Gb, toothed bristles (accessory claws) (after O. Hermann).

of these protuberances there often lies a peculiar structure called the *cribellum*, with a covering of very fine hairs (fig. 395, *Cr*). The spinning glands (fig. 396) are tubes of various shapes; they open by fine pores on the surface of the spinning papillæ, and secrete a viscid material, which in the air hardens to a fine thread and is woven by the aid of the claws on the feet into the well-known spider's web.

Nervous system (fig. 367).—Besides the brain, with the nerves to the eyes and chelicerae, there is a single, usually star-shaped ganglionic mass in the thorax, from which nerves pass to the pedipalpi and legs, and also to the abdomen. Visceral nerves have also been observed on the alimentary canal.

As a rule there are eight, or more rarely six simple eyes, which are disposed in two curved lines or more in a quadrate on the

FIG. 395.—Spinning organ of *Amaurobius ferox* (after O. Hermann). Cr, Cribellum; Spw, spinning mammillæ.

FIG. 396.—Lungs (P), spinning glands (Spd) and generative organs (Vd) of a male *Pholcus phalangista* (règne animal). R, Rectum with Malpighian vessels opening into it.

dorsal surface of the cephalic region behind the frontal margin. Their arrangement is very regular, and is characteristic for the different genera (figs. 398 and 399).

FIG. 397.—*Mygale* from the ventral side, part of the skin is turned aside (règne animal). *K*, Chelicera; *Bg*, thoracic ganglionic mass; *P*, *P'*, lungs; *F*, lamellæ of the lungs; *St*, *St'*, stigmata; *Ov*, ovary; *Sw*, spinning papillæ.

FIG. 398.—Anterior part of the cephalo-thorax of *Mygale* with the eyes (*O*) (règne animal).

FIG. 399.—Arrangement of the eyes in different spiders (after Lebert). *a*, *Epeira*; *b*, *Tegenaria*; *c*, *Dolomedes*; *d*, *Salticus*.

FIG. 400.—Alimentary canal of *Mygale* (règne animal). *G*, Cerebral ganglion; *Ms*, diverticula of stomach; *L*, hepatic ducts; *N*, Malpighian vessels; *R*, rectum.

The alimentary canal (fig. 400) begins beneath the upper lip with an ascending pharyngeal portion of the œsophagus, into which a saccular pharyngeal gland opens (salivary gland). The narrow œsophagus, before passing into the midgut or intestine, is dilated to form a suctorial stomach, which is furnished with powerful muscles arising from the dorsal part of the cephalo-thorax. The midgut is divided into an anterior part, lying within the cephalo-thoracic region and provided with two anterior and four lateral pairs of cæca, and into a narrower abdominal small intestine, into which the ducts of the branched hepatic tubes pour their secretion. The latter

appears to have a digestive function similar to that of the pancreatic secretion, inasmuch as it dissolves albumens and transforms amyloid substances into sugar. The short rectum receives two branched urinary (Malpighian) canals, and dilates in front of the anal opening to the form of a vesicle (fig. 400).

FIG. 401.—Heart and vascular trunks of *Lycosa*, in lateral and dorsal view (after Claparède). *P*, Lungs; *C*, heart; *Ao*, aorta; *O*, eyes.

The vascular system is not less highly developed (fig. 401). The blood flows from the pulsating dorsal vessel placed in the abdomen, through an anterior aorta into the cephalo-thorax, and thence into lateral arteries, supplying the legs, jaws, brain, and eyes. The blood returns from these organs into the abdomen, bathes the so-called lungs, which are composed of numerous flattened tubes, and then returns to the dorsal vessel through three pairs of lateral slits.

The ovaries (fig. 397) are two racemose glands surrounded by the liver; the short oviducts unite to form a single vagina, which is usually connected with two long receptacula seminis and opens on the ventral surface of the anterior part of the abdomen between the anterior stigmata. The testes consist of two long coiled canals with a common terminal duct, which likewise opens at the base of the abdomen (fig. 402).

FIG. 402.—Sexual organs of a *Tegenaria* (*Philoica*) *domestica*, with the abdomen in outline (after Bertkau). *T*, Testis; *Vd* vas deferens; *St*. stigma.

FIG. 403.—Terminal part of the pedipalpus of *Segestria* (♂) with the receptacle of the spermatozoa (after Bertkau).

The males are distinguished from the females by the smaller size of the abdomen. The females are always oviparous, and frequently carry their eggs about in special webs (*Theridium*, *Dolomedes*). In the male the pedipalpus is modified to form a copulatory organ; the thickened and excavated terminal joint is spoon-shaped, and possesses a vesicular copulatory appendage with a spirally-twisted fibre (fig. 403). Before copulation the male fills this appendage with sperm, and at the moment of coitus introduces the terminal fibre into the female genital opening (fig. 404). Sometimes the two sexes live peacefully near each other on neighbouring webs, or even for a time on the same web; in other cases the female, which is the stronger animal, lies in wait for the male in the same way as she does for all animals weaker than herself, and does not spare him even during or after copulation; the male, therefore, only approaches her with the greatest caution.

Development.

—The segmentation of the ovum is centrolecithal (fig. 107). The embryos possess, in addition to the thoracic appendages, the rudiments of abdominal

FIG. 404.—Male and female of *Linyphia*, during copulation (after O. Herman).

FIG. 405.—Spider embryo (after Balfour). *AF*, Rudiments of abdominal feet.

(fig. 405). The young, when hatched, already possess the form and appendages of the adult. They are not, however, sufficiently developed before the first moult to spin or to capture prey. It is only after the moult that they become capable of performing these functions, leave the web of the egg membranes, and begin to spin threads and to capture small insects. The threads which we find floating in the air in great numbers in autumn and are known as *gossamer* threads are the work of young Spiders, which raise themselves in the air by their means, and pass the winter in sheltered places.

The habits of spiders are so remarkable that they have for a long time excited the interest of observers. All spiders are predacious, and suck the juices of other insects; nevertheless, the manner in which they get possession of their prey varies much, and often

indicates the possession of highly-developed instincts. The so-called vagrant spiders do not, as a rule, form nets to catch their prey, but use the secretion of the spinning glands only to line their hiding-places and to make their ovisacs. They catch their prey either by running after it (fig. 406, *a*), or by springing on it (fig. 406, *b*). Other Spiders (fig. 406, *c*) are indeed able to run quickly, but they render the task of catching prey easier by making webs and nets, on which they move about with great dexterity, while other animals, especially insects, become very easily entangled. The webs themselves are of various kinds, and constructed with more or less skill;

a

Fig. 406.

c *Dolomedes mirabilis* ♀*d* *Tegenaria domestica* ♀ *Salticus scenicus*

♀

Thomisus citreus

they are either delicate and thin and formed of irregularly arranged threads, or they are of a felt-like quality and extended horizontally or again, they may have the form of vertically placed wheel-shaped nets; in this case they consist of concentric and radial threads, which are arranged with wonderful regularity, the radial threads meeting in a central point. Tubular or funnel-shaped hiding-places for the spider are often found near the webs. Most spiders rest in the daytime, and go out for prey in the dusk or in the night-time. Many vagrant spiders, however, hunt in the day-time, even when the sun is shining.

1. **Tetrapneumones.** With four lungs and usually with four spinning mammillæ.

Fam. **Mygalidæ.** Large spiders thickly covered with hairs, with four lungs and four spinning mammillæ, of which two are very small. They do not construct true webs, but prepare long tubes in the earth, or line their hiding-places (in clefts in trees or in holes in the earth) with a thick web; they lie in wait for their prey (at the entrance of their homes), or they may catch it in the open by springing. The claw joints of the chelicerae are bent downwards. *Mygale aricularia* L., the large Bird Spider of South America, lives in a tubular web between stones and in crevices in the bark of trees. *Cteniza cæmentaria* Latr. The trap-door spider in South Europe, lives in tubular holes in the earth, the entrance to which is closed with an operculum, as with a sort of trap-door. *Atypus Sulzeri* Latr., in Central Germany, with six spinning mammillæ.

2. **Dipneumones.** With two lungs and six spinning mammillæ.

Fam. **Saltigradæ.** Springing spiders (fig. 406, *b*) with a large arched cephalo-thorax and eight eyes of unequal size, which are grouped almost in a square. The anterior legs with stout femoral joints serve with the following legs for making the leaps by which these animals catch their prey. They do not construct webs, but spin fine saccular structures in which they remain at night, and later on keep guard over their egg-sacs. *Salticus cupreus*, *formicarius* Koch. *Myrmecia* Latr., in Brazil, resemble ants in form.

Fam. **Citigradæ = Lycosidæ.** Wolf-spiders. With long oval cephalo-thorax, which is narrow anteriorly, but is strongly arched. There are eight eyes, which are usually arranged in three transverse rows. They run about with their long strong legs in pursuit of their prey. By day they are usually concealed beneath stones, in hiding-places, which they line with their webs. The females frequently sit on their egg-sacs, or carry them about on the abdomen, and usually protect the young for some time after they are hatched. *Dolomedes mirabilis* Walk. (fig. 406, *a*). *Lycosa saccata* L., *tarantula* L., the Tarantula Spider of Spain and Italy. It lives in holes in the ground, and its bite, according to the erroneous popular belief, occasions the dancing madness.

Fam. **Laterigradæ = Thomisidæ.** Crab-spiders. With rounded cephalo-thorax and flattened abdomen. The two anterior pairs of legs are longer than the following legs. They only spin isolated threads. They hunt insects beneath leaves running sideways and backwards. *Micrommata smaragdina* Fabr., *Thomisus citreus* Geoffr. (fig. 406, *d*).

Fam. **Tubitelæ.** Tube spinners. With six or eight eyes arranged in two transverse rows, which are usually curved. The two middle pairs of legs are the shortest, the hindmost pair often the longest. They spin for the capture of their prey horizontal webs with tubes in which they lie in wait. *Tegenaria domestica* L. (fig. 406, *c*) (Winkelspinne). Others, as *Agelena labyrinthica* L., construct funnel-shaped webs or, as *Clubiona holosericea* L., saccular receptacles. *Argyroneta aquatica* L., water spiders, with longer anterior pair of legs. The body has a silvery appearance, owing to the numerous air-bubbles which adhere to the hairs with which it is covered. It spins a bell-shaped watertight web, which it fills with air like a diving-bell and attaches to water-plants.

Fam. **Inæquitelæ.** Web spinners. With eight unequally large eyes arranged

in two transverse rows, and long anterior legs. They construct irregular webs, the threads of which cross one another in all directions, and live on their webs. *Theridium sisypium* Clerck., *Pholcus phalangioides* Walck.

Fam. **Orbitelæ**. Wheel spinners. Head and thorax separated by a furrow ; abdomen swollen to a globular form. The eight eyes are arranged rather irregularly in two rows, and the anterior legs are longer than the following legs. The legs of the third pair are the shortest. They spin perpendicularly hanging wheel-shaped webs with concentric and radial threads, and lie in wait in the middle point or in a remote hiding-place, which they surround with a web. *Epeira diadema* L., cross spiders.

FIG. 407.—*Phalangium opilio* ♂ (*cornutum*) (règne animal).

FIG. 408.—Male and female generative organs of *Phalangium opilio* (after Krohn). T, Testis; Vd, vasa deferentia; P, penis with accessory glands; R, retractor muscles; Ov, ovary; U, uterus; Op, ovipositor.

Order 4.—PHALANGIIDA.*

Arachnida with four pairs of long, slender legs, with chelate chelicerae and segmented abdomen joined by its whole breadth to the cephalo-thorax. They have no spinning glands, and breathe by tracheae.

* Meade, "Monograph of the British species of Phalangiidae," *Ann. of nat. hist.* 2^d. Ser. XV., 1845. A. Tulk, "Upon the anatomy of *Phalangium opilio*," *Ann. of nat. hist.*, XII. A. Krohn, "Zur näheren Kenntniss der männlichen Zeugungsorgane von *Phalangium*," *Archiv für Naturgesch.*, 1865.

The *Phalangiida* (fig. 407) resemble the true spiders in their general appearance, but differ from them by possessing chelate chelicerae which are bent downwards, by the form of the abdomen, the tracheal respiration, and the absence of spinning glands. The Pedipalpi are either filiform or pediform, and are armed with claws. The abdomen consists, as a rule, of six or more rarely eight or nine segments, and is joined to the cephalo-thorax by its whole breadth.

The **nervous system** is divided into a brain and a thoracic ganglionic mass, whence arise two visceral nerves which form ganglia in their course on either side. There are two or four simple **eyes**. The organs of **respiration**, which in all cases consist of tracheae branching within the body, open by a single pair of stigmata, usually beneath the coxa of the last pair of legs. The **heart** consists of a long dorsal vessel divided into three chambers. The **stomach** is provided with a number of caeca, of which the last extend as far as the anus. The **male** as well as the **female** genital opening lies between the posterior pair of legs. In the male a long tubular copulatory organ, and in the female a long ovipositor can be protruded from the opening (fig. 408). The production of ova as well of spermatozoa in the testis, as was observed by Krohn and Treviranus in almost all males, is remarkable.

The *Phalangiidae* usually conceal themselves during the day and go out at night to capture prey. The South American species are very numerous, and of very strange form.

Fam. Phalangiidae. With characters of the order. *Phalangium opilio* L. (fig. 407). *Gonyleptus horridus* Kirb. To this group also belongs *Cyphophthalmus duricorius* Jos., and the genus *Gibocellum* Steck.

Order 5.—PEDIPALPI * (SCORPION-SPIDERS).

Arachnida of considerable size; jaws provided with claws, and the anterior pair of the legs elongated, resembling antennae. The abdomen has eleven or twelve segments, and is clearly marked off from the rest of the body.

The Scorpion-spiders (fig. 409) are allied both to the Spiders and the Scorpions. The abdomen, which is always separated from the cephalo-thorax by a constricted portion, is divided into a considerable number of segments, but presents no distinction into a broad præ-abdomen and a thin styliform post-abdomen as in the Scorpions.

* H. Lucas, "Essai sur une monographie du genre Thelyphonus," *Magas. de Zool.*, 1835. J. v. d. Hoeven, "Bijdragen tot de kennis van het geslacht Phrynus," *Tijdschr. voor nat. Geschied.* IX., 1842.

In the genus *Thelyphonus*, however, which is most closely allied to the Scorpions, the three last segments of the abdomen are narrowed to the form of a short tube, the end of which is prolonged into a long-jointed appendage. The chelicerae are always provided with claws, and probably, as in the spiders, contain a poison gland, since the bite of these animals is much feared. The Pedipalpi, on the other hand, are sometimes of considerable strength and armed with a claw and several spines (*Phrynus*). Sometimes (*Thelyphonus*) they are, as in the Scorpions, chelate. The legs of the anterior pair are always very long and thin, and end with a flagelliform ringed portion. There are eight eyes, of which the two largest are placed

FIG. 409.—*Phrynus reniformis* (règne animal). *Kt*, Pedipalpi; *Gb*, flagelliform anterior leg.

in the middle of the cephalo-thoracic shield, while the three smaller pairs are situated on each side behind the frontal margin. They breathe by means of four lung sacs, composed of a very large number of lamellar tubes. The slit-like openings of the lung sacs lie on either side of the posterior margin of the second and third abdominal segments. In the structure of the alimentary canal they resemble the Scorpions, in that of the nervous system the Spiders. The genus *Phrynus* is viviparous. All the *Pedipalpi* live in the tropics of the Old and New World.

Fam. *Phrynidae*. With the characters of the order. *Phrynus* Oliv. The large broad pedipalpi are armed with a number of spines and end with a claw. The masticating blades are free. The abdomen is flat and relatively short, and has

eleven segments and no jointed anal filament. *Ph. reniformis* Latr., in Brazil. *Thelyphonus* Latr. The chelicerae are short and end in a chela, their masticating blades fuse in the middle line. The elongated twelve-ringed abdomen with segmented anal filament. *T. caudatus* Fabr., in Java.

Order 6.—SCORPIONIDEA* (SCORPIONS).

Arachnida with chelate chelicerae, and elongated, pediform chelate pedipalpi, with a præ-abdomen composed of seven segments, and an elongated post-abdomen of six segments, with poison spine at the hind end; with four pairs of lungs.

FIG. 410.—Cephalo-thorax and præ-abdomen of *Scorpio africanus* (règne animal). *Kf*, Chelicerae; *Kt*, pedipalpi; *K*, pectines; *St*, stigmata.

The Scorpions have a certain resemblance to the *Decapod* Crustacea in their powerful chelate pedipalpi and firm armour (fig. 410). The stout cephalo-thorax is joined to an elongated abdomen, which is divided into a cylindrical præ-abdomen, composed of seven segments, and a very narrow six-segmented post-abdomen, which is curved dorsalwards. The post-abdomen ends with a curved poison spine, which is provided with two poison glands. The chelicerae are three-jointed and chelate; the pedipalpi end with a swollen terminal chela, while the basal joint serves with its broad grinding surface as a jaw. The four pairs of legs are strongly developed and end with double claws.

In their internal organization the Scorpions reach the highest

* P. Gervais, "Remarques sur la famille des Scorpions et description de plusieurs espèces nouvelles, etc." *Arch. du musée d'hist. nat.*, IV. Newport, "On the structure, relations, and development of the nervous and circulatory Systems in Myriapoda and macrourous Arachnida," *Phil. Trans.* 1843. L. Dufour, "Histoire anatomique et physiologique des Scorpions," *Mém. près à l'acad. des sciences*, XIV., 1856. E. Metschnikoff, "Embryologie des Scorpions," *Zeitschr für wiss., Zool.*, 1870.

grade of all the *Arachnida*. The **nervous system** is composed of a bilobed brain, a large oval ganglionic mass in the thorax, and seven to eight smaller ganglionic swellings in the abdomen, of which the last four belong to the post-abdomen. The visceral nervous system is represented by a small ganglion, which is placed at the beginning of the œsophagus, connected with the brain by fibres and gives off nerves to the alimentary canal. The principal organs of sense are the **simple eyes**. Of these there are from three to six pairs, which are so distributed that the largest pair is situated on the middle of the cephalo-thorax, and the others right and left at the sides of the frontal region.

The **alimentary canal** is a narrow straight tube, which is surrounded in the præ-abdomen by the large multilobed liver, and opens on the penultimate ring of the abdomen. Two Malpighian vessels function as excretory organs.

The **circulation** is the most complicated in the whole class, but, as in the *Decapoda*, special blood sinuses of the body cavity are inserted into the vascular system. The elongated dorsal-vessel, which is divided into eight chambers and is attached by alary muscles, is surrounded by a pericardial sinus, from which it receives the blood through eight pairs of slit-like openings, which are capable of being closed. From the heart the blood

is driven through an anterior and posterior artery, and through lateral arteries to the organs. The finer ends of the arteries seem to be connected with the commencing veins by capillaries. From the veins the blood is collected in a receptacle on the ventral surface. Thence the blood passes to the respiratory organs, whence it passes by special veins into the pericardial sinus, and so back to the heart. **Respiration** is effected by means of four pairs of lung sacs, which open to the exterior by four pairs of stigmata on the third to the sixth abdominal segments and are composed of a relatively small number of flat tubes.

The male and female **generative organs** open on the ventral face of the first abdominal segment [the median opening being covered

FIG. 411.—Embryo of a Scorpion (after E. Metschnikoff). *Kf*, Chelicerae; *Kt*, pedipalpi; *B¹* to *B⁴*, the four pairs of thoracic legs. There are rudimentary limbs on the abdomen.

by a small valve-like flap, the genital operculum]; on the second abdominal segment are attached two peculiar comb-shaped structures, known as pectines. The latter are probably the remains of the appendages of the segment, and serve as tactile organs. The males are distinguished from the females by their broader chelæ and longer post-abdomen.

The females are viviparous. The development of the ovum takes place in the ovary, and the embryos have the rudiments of appendages on the præ-abdomen (fig. 411).

The Scorpions live in warm countries, and leave their hiding-places at dusk. When they run, the post-abdomen is bent upwards over the back. They seize their prey, *i.e.*, principally spiders and large insects, with their large chelate pedipalps, and sting them to death with their caudal poison-spine. Some species attain a very considerable size, and their sting may even prove fatal to man.

FIG. 412.—*Obisium trombidoides* (règne animal). Kt, Pedipalpus.

Fam. **Scorpionidæ**. *Scorpio europæus* Schr., of small size and with only six eyes, in Italy. *Androctonus occitanus* Am., *Buthus afer* L.

Order 7.—PSEUDOSCORPIONIDEA.*

Arachnida of small size and resembling scorpions, but without caudal spine or poison gland. They breathe by means of tracheæ.

The Pseudoscorpions are far smaller and more simply organised than the scorpions. They bear much the same relation to the true scorpions that the mites do to the spiders. In their form and the structure of their chelicerae and chelate pedipalpi they resemble the scorpions. On the other hand, the hind end of the segmented abdomen does not become narrow so as to form a post-abdomen, and is without a caudal spine and poison gland (fig. 412). They all possess spinning glands, the openings of which lie near the genital openings on the second abdominal ring. They possess only two or four ocelli, and respire by means of tracheæ, which open by two pairs of stigmata on the two first abdominal rings. They live beneath the bark of trees, in moss, between the leaves of old books,

* W. E. Leach, "On the characters of Scorpionidea with description of the British species of Chelifer and Obisium," *Zool. Miscell.* III. A. Menge, "Ueber die Scheerenspinnen," *Neueste Schriften der naturforsch. Gesellschaft zu Danzig* V., 1855. L. Koch, "Uebersichtliche Darstellung der europ. Chernetiden," Nürnberg, 1873.

etc.; they run rapidly laterally and backwards, and live on mites and small insects.

Fam. **Chernetidæ**. *Chelifer cancroides* L. Book-scorpion with two eyes. *Obisium ischnosceles* Herm., with four eyes. *Chthonius trombidoides* Latr. (fig. 412).

Order 8.—SOLIFUGÆ.*

Spider-like animals with separated head and thorax, with elongated, segmented abdomen; sub-chelate chelicerae and pediform pedipalpi. Respiration is effected by means of tracheae.

The *Solifugæ* approach insects in the segmentation of the body. The cephalo-thorax is divided into two regions of which the anterior is comparable to the insect head, the posterior (composed of three segments) to the insect thorax. The long cylindrical abdominal region, which is composed of nine to ten segments, is quite distinct (fig. 413). The body is closely covered with hairs. The oral apparatus consists of powerful chelicerae, which end in a large vertically placed chela, the lower arm of which can be moved perpendicularly against the upper. The pedipalpi serve as ambulatory legs, but are without claws, which are found only on the three posterior pairs of legs. The latter arise from the three free thoracic rings, and bear peculiar cutaneous lamellæ at their base. The anterior pair of legs belongs to the head and may be considered as a second pair of pedipalpi (maxillary palps). The *Solifugæ* possess two large projecting simple eyes, and respire like insects by

FIG. 413.—*Galeodes arancoides* (règne animal).

* L. Dufour, "Anatomie, physiologie et histoire naturelle des Galéodes," *Comptes rendus d'acad. des sciences*, XLVI. 1858. Th. Hutton, "Observations on the habits of a large species of Galeodes," *Ann. and Mag. of Nat. Hist.*, XII., 1843.

means of tracheæ, which open to the exterior by four slit-like openings between the first and second pair of thoracic appendages and on the ventral surface of the abdomen. They live in warm, sandy localities, especially of the Old World. They are nocturnal in their habits, and are feared on account of their bite.

Fam. Solpugidæ. *Solpuga* (*Galeodes*) *araneoides* Pall., found on the steppes of the Volga and in South Russia. Other larger species are found in Africa, and some forms are known in America.

Class III.—ONYCHOPHORA * (PROTOTRACHEATA).

Tracheata with elongated vermiform body, two antennæ, and short paired imperfectly-jointed legs armed with claws.

FIG. 414.—*Peripatus capensis* (after Moseley).

The *Onychophora*, which are represented by the single genus *Peripatus*, have a moderately elongated body, which is provided with paired legs (from fourteen to more than thirty pairs), each armed with two small claws (fig. 414). The head is distinct, and bears a

FIG. 415.—Head of a *Peripatus* embryo (after Moseley). *An*, Antennæ; *K*, jaws, anterior to which are the ectoderm thickenings, which will form the brain.

pair of antennæ and two simple eyes. On its under surface the mouth is placed beneath a large projecting suctorial lip, and is furnished with a pair of jaws armed with chitinous claws. On each side of the mouth short, indistinctly jointed oral papillæ are attached to the sides of the head. The **nervous system** is distinguished by the remarkable separation of its two halves. The paired cerebral ganglion

gives off two nerve trunks, which indeed approach each other closely

* E. Grube, "Ueber den Bau des *Peripatus Edwardsii*," *Müller's Archiv.*, 1853. Moseley, "On the Structure and Development of *Peripatus capensis*," *Phil. Trans.*, 1875. [F. M. Balfour, "On the Structure and Development of *Peripatus Capensis*," *Quart. Journ. of Mic. Science*, 1883.]

beneath the œsophagus, but, soon diverging, remain widely separate for the rest of their course. They are without ganglionic swellings; are connected together in their whole length by fine transverse commissures, and finally unite with each other over the rectum at the end of the body (fig. 416). The **alimentary canal** begins with a muscular pharynx, and runs in a straight course. The anus is terminal. A dorsal longitudinal vessel probably functions as **heart**.

[A pair of elongated unbranched glandular tubes, the salivary glands, open into the buccal cavity.] Moseley discovered a well-developed **tracheal system**, the stigmata of which are distributed over the whole surface of the body. The tracheal trunks are delicate tubes, which are distributed upon the viscera in fine tufts. Long slime glands (considered as testes by Grube) open on the oral papillæ; they produce an exceedingly sticky fluid, which the animal ejects when irritated. The *Onychophora* are, according to Moseley, of separate sexes. The **ovaries** are united to form one structure placed in the middle line on the dorsal side of the intestine, near the hind end of the body. There are two long oviducts, which function as uterus and open by a common aperture on the

ventral surface close to the hind end of the body (fig. 416). The **testes** are paired and egg-shaped, and lie towards the hind end of the body. The vasa deferentia are coiled and unite to form a common duct, which opens at the same place as do the female organs (fig 417). The eggs develop in the uterus.

FIG. 416.—Anatomy of a female *Peripatus* (after Moseley). F, Antennæ; G, brain with the ventral nerve cords (Vc); Ph, pharynx; D, intestine; A, anus; Sd, slime gland; Ov, ovaries; Od, oviduct; U, uterus.

[Segmental organs or nephridia, resembling those of Annelids, are found one pair in each segment. They open externally at the base of the legs and internally into the body cavity. The body cavity is divided into four parts by three septa—(1) into a dorsal section containing the dorsal vessel, (2) a main central division containing the alimentary canal, slime glands and generative organs; and (3) two lateral compartments, which are continued into the legs and contain the salivary glands, segmental organs and ventral nerve cords.]

The animals live in damp places beneath decaying wood. [They are viviparous; in *Peripatus* Capensis the period of gestation is eleven or twelve months, the young being born in April and May.]

FIG. 417.—Hind end of a male *Peripatus* (after Moseley). T, Testes; Pr, prostate gland; Vd, vasa deferentia; De, ductus ejaculatorius; R, rectum; Vc, ventral nerve trunks.

Fam. *Peripatidæ*. *Peripatus* Edwardsii Blanch., *P. capensis* Gr.

Class IV.—MYRIAPODA.*

Tracheata with separated head and numerous fairly similar segments. They have one pair of antennæ, three pairs of jaws, and numerous pairs of legs.

The Myriapoda of all the *Arthropoda* present the greatest resemblance to the Annelids, in the serial similarity of the segments, in the possession of an elongated, sometimes cylindrical, sometimes flattened body, and in the mode of locomotion. In fact, they bear much the same relation to the Annelids that the Snakes do to the

vermiform fishes amongst the Vertebrata.

* J. F. Brandt, "Recueil des mémoires relatifs à l'ordre des Insectes Myriapodes," St. Petersburg, 1841. G. Newport, "On the organs of reproduction and the development of the Myriapoda," *Phil. Trans.*, 1841. Koch, "System der Myriapoden, Regensburg, 1847. M. Fabre, "Recherches sur l'anatomie des organes reproducteurs et sur développement des Myriapodes," *Ann. des. Sc. Nat.*, IV. Sér., Tom. III. Fr. Meinert, "Danmarks Chilognather," *Naturh. Tidsskrift*, 3 R., Tom. V.; and "Scolopendrer og Lithobier," *Ibid.*, Tom. V. 1868. Latzel, "Die Myriapoden der österreichisch-ungarischen Monarchie" I., "Die Chilopoden," Wien, 1880. Erich Haase, "Schlesiens Chilopoden," Breslau, 1880, 1881.

The head of the Myriapods corresponds closely with that of the Insects, and, like the latter, bears a pair of antennæ, the eyes, and two or in the *Chilopoda* three pairs of jaws. The antennæ are placed on the frontal region, and are usually filiform or setiform. The strongly-toothed mandibles resemble those of Insects, and, like the latter, are without palps. The maxillæ in the Chilognatha have the form of a complicated lobed oral valve (fig. 427 b), the parts of which were formerly supposed to represent two pairs of maxillæ fused together; while in the *Chilopoda* they consist of a single blade bearing a short palp (fig. 425). In rare cases the mouth parts are transformed into a suctorial apparatus (*Polyzonium*).

The body is composed of similar and distinctly separated segments, the number of which varies considerably in different species, but is usually constant for the same species. The segments bear paired appendages, and a strong dorsal and ventral plate (tergum and sternum) may often be distinguished. Although the segments of the body are so much alike that it is impossible to fix a limit between thorax and abdomen, still certain features of the internal organisation, especially the fusion of the three first ganglia of the ventral chain, show that we must regard the three anterior body segments at least of the *Chilognatha* as constituting a thorax. In the *Chilognatha* a single pair of legs is attached to each of the first three to five body segments; each of the following segments, on the other hand, bears

FIG. 418. — *Scolopenira morsitans*.

FIG. 419. — *Iulus terrestris* (after C. L. Koch).

almost invariably two pairs, so that they may be regarded as double segments, formed by the fusion of two somites. The legs may be attached to the sides of the somites (*Chilopoda*), or nearer the middle line of the ventral surface (*Chilognatha*), and are usually short with from six to seven joints, and terminate with claws (figs. 418 and 419).

In their internal structure the Myriapods closely resemble the

Insects. The **nervous system** is distinguished by the great elongation of the ventral ganglionic cord, which runs along the whole length of the body and is swollen in each segment to form a ganglion. According to Newport, there is a system of paired and unpaired visceral nerves, like those of Insects. **Eyes** are only rarely wanting, and are usually present as ocelli which are sometimes closely packed together, or rarely (*Scutigera*) as peculiarly-formed faceted eyes.

The **alimentary canal**, with rare exceptions (*Glomeris*), takes a straight course through the entire length of the body, and opens by the anus in the last segment. The following parts can be distin-

FIG. 420.—Head and anterior segments of *Scolopendra* (after Newport). *G*, brain; *O*, eyes; *A*, antennæ; *Kf*, maxilliped (poison-claw); *C*, heart; *M*, alary muscles of the heart; *Ar*, arteries.

guished:—a narrow *oesophagus* beginning with the buccal cavity and, as in Insects, receiving the contents of two to six tubular salivary glands; a wide, very long *mesenteron*, the surface of which is closely beset with short hepatic tubes projecting into the body cavity; a *hind gut*, which receives two or four Malpighian tubules, the latter being coiled round the intestine; and finally a short and wide rectum.

The central organ of the circulation is a long pulsating **dorsal vessel**, which extends through all the segments of the body (fig. 420). It is divided into a great number of chambers, which correspond to the segmentation and, in *Scolopendra*, are attached to

the dorsal wall by alary muscles to the right and left (fig. 420, *M*). The blood passes from the body cavity through lateral paired slits into the chambers of the heart, and is thence driven, partly through paired lateral arteries and partly through an anterior cephalic aorta which divides into three branches, to the organs of the body cavity, from which a blood sinus, embracing the ventral ganglionic chain, is separated off.

All *Myriapods* breathe by means of **tracheæ**. These, as in Insects, receive the air from the exterior through paired slits, which are found in almost every segment (sometimes beneath the basal joints

of the limbs, sometimes in the connecting membranes between the sterna and terga); and they give off bunches of tracheæ, which branch and are distributed to all the organs.

Generative organs.—The *Myriapoda* are dioecious. The ovaries and testes usually have the form of long unpaired tubes, while their ducts are often paired and are always connected with accessory glands, and in the female are sometimes provided with a double receptaculum seminis (fig. 421). The genital openings lie on either side on the coxal joints of the second pair of legs, or behind this pair of appendages (*Chilognatha*), or, as in the *Chilopoda*, there is an unpaired genital opening at the posterior end of the body (fig. 422).

In the male sex amongst the *Chilognatha* there are often external copulatory organs* on the 7th segment, remote from the genital openings. These become full of sperm before copulation, and during the coitus introduce it into the female genital opening.

Development.—The females are usually larger than the males, and lay

* Besides Fabre l.c., compare Voges, "Beiträge zur Kenntniss der Juliden," *Zeitschr. für wiss. Zool.*, Tom XXXI., 1878.

FIG. 421.—Generative organs of *Glomeris marginata* (after Fabre). T, Testis; Ov, ovaries; Od, Oviduct.

FIG. 422.—Generative organs of *Scolopendra complanata* (after Fabre). T, Testis; Vd, vas deferens; Dr, accessory glands; Sb, loop of the vesicula seminalis; Ov, ovary.

their eggs in earth. The just-hatched young often pass through a metamorphosis, having at first only three or seven pairs of legs in addition to the antennæ, and a few somites without limbs (fig. 423). The young animals undergo numerous moults, and

FIG. 423.—Embryo of *Strongylosoma* (after E. Metschnikoff).

gradually increase in size; the extremities sprout out on the somites, which are already present. New somites are constricted off from the terminal one until the full number is completed; the number of ocelli and of the joints of the antennæ is increased, and the

resemblance to the sexual animal is gradually perfected. In other cases (*Scolopendra*, *Geophilidæ*) the embryo already possesses the full number of appendages.

Order 1.—CHILOPODA.*

Myriapoda of usually flattened form, with long many-jointed antennæ, and mouth parts adapted for predatory habits, with only one pair of appendages to each segment.

FIG. 424.—*Lithobius forficatus* (after C. L. Koch). *Kf*, Poison claws.

The body is long and usually flattened. The chitinous exoskeleton is hardened on the dorsal and ventral surface of each somite, constituting the tergal and sternal plates, while on the sides of the somites it remains soft. In certain forms some of the terga develop to large shields, which over-lap the smaller terga of the intermediate somites (fig. 424). The number of legs is never greater than that of the separate segments, a single pair only being developed on each segment. The antennæ are long and many-jointed, and are inserted beneath the frontal margin. The eyes are simple

or aggregated ocelli, except in the genus *Scutigera* which has faceted

* Newport, "Monograph of the Class Myriapoda, order Chilopoda," *Linnean Transactions*, XIX.

eyes. There are always two pairs of jaws (fig. 425); the mandibles (*Md*) and one pair of maxillæ (*Mx'*), the latter bearing a short palp. In addition, the first pair of (thoracic) legs (*Mx''*) forms a kind of underlip which often bears two long palps. The next pair of legs always approaches the head as a kind of maxilliped, and forms by the growing together of its basal parts a considerable median plate, on the right and left of which great four-jointed poison claws (*Mf*) project. The remaining appendages arise from the sides of the body segments, the last pair being frequently elongated so as to project backwards far behind the last segment.

The generative organs open by a single aperture at the hind end of the body. There is no male copulatory apparatus. The young, when hatched, have seven pairs (*Lithobius*) or the entire number of appendages (*Scolopendra*). The Chilopoda feed entirely on animals, which they bite with the poison claws and kill by the secretion of the poison gland which flows into the wound. Certain tropical species of large size are able to inflict wounds which are dangerous even to man.

FIG. 425.—Oral apparatus of *Scolopendra mutica* (after Stein). *Ob*, Upper lip; *Md*, mandibles; *Mx'*, maxilla; *Mx''*, first pair of legs or second maxillæ; *Mf*, poison claws (maxilliped); *Ta*, palp.

FIG. 426.—Mouth parts of *Geophilus* (Carus, *Icones*). *K*, Maxillæ; *Mf*, maxilliped.

Some of the terga are greatly developed, and partially over-lap those of

Fam. **Scolopendridæ**. Antennæ long and thin with a relatively small number of joints, only a few ocelli. The segments of the body are sometimes equal, sometimes unequal. *Scolopendra* (with nine pairs of stigmata) *gigantea* L., found in the East Indies. *Sc. morsitans*, from South Europe. *Geophilus subterraneus, electricus* L.

Fam. **Lithobiidæ**. With long, many-jointed antennæ and numerous ocelli.

the intermediate segments. *Lithobius forficatus* L., with fifteen pairs of legs.

Fam. *Scutigera*dæ. The antennæ are at least as long as the body. The legs are long, their length increasing from before backwards. Facetted eyes instead of ocelli. With a small number of free terga. *Scutigera coleoptrata* L., South Germany and Italy.

Order 2.—CHILOGNATHA.

The shape of the body is cylindrical or subcylindrical. There is a four-lobed plate behind the mandibles, and two pairs of legs on each segment (the anterior segments excepted). The genital openings are on the coxal joint of the second pair of legs.

The body of the *Chilognatha* is, as a rule, cylindrical or subcylindrical. The segments have the form of complete rings, or are provided with special dorsal plates. In many cases (*Julidæ*) the body is much elongated; in others (*Glomeris*) it is short, like that of a wood-louse (fig. 427). The antennæ are short, and consist only

FIG. 427.—a, *Glomeris marginata* (after C. L. Koch). b, Maxillæ (inferior buccal plate) of *Julus terrestris*.

of seven joints, of which the last may abort. The mandibles are provided with broad masticating surfaces, which serve to crush the

vegetable matters on which the animals feed, and with an upper movably articulated pointed tooth. The maxillæ are united so as to form an inferior buccal plate, the sides of which bear two rudimentary hook-shaped blades (fig. 427, b), while the middle portion appears to represent the underlip. The eyes, which as a rule consist of aggregated simple eyes, are situated above and external to the antennæ. The anterior thoracic legs are as a rule directed forwards towards the mouth. The three thoracic segments, and sometimes the next two or three segments, bear a single pair of legs. All the others, except the seventh in the male, bear two pairs. *Stigmata* are present in all the segments, and are more or less hidden beneath the coxal joints of the limbs. The rows of pores (*foramina repugnatoria*) on either side of the back, which are often taken for rows of stigmata, are the openings of cutaneous glands, and secrete a corrosive fluid for the protection of the animal. The generative organs open on the coxal joint of the second pair of legs, and in the male sex there is also a paired copulatory organ present on the seventh

segment of the body, at some distance from the genital openings. In *Glomeris*, this copulatory organ seems to be replaced by two accessory pairs of appendages on the anal segment. The young possess at first only three pairs of legs, and the metamorphosis would therefore seem to be more complete than in the Chilopods.

The Chilognatha live in damp places, beneath stones on the ground, and feed on vegetable and dead animal matters. Many of them roll themselves up into a ball like the woodlice or into a spiral.

Fam. *Polyzonidæ*. With small head and subcylindrical body which can be rolled up into a spiral, and suctorial mouth parts. *Polyzonium germanicum* Brdt.

Fam. *Julidæ*. The head is large and free. The eyes are mostly aggregated together; with cylindrical body, which can be rolled up in a spiral; without broad dorsal plates. The limbs meet together in the middle ventral line. *Julus sabulosus* L.

Fam. *Polydesmidæ*. With large free head and laterally extended dorsal plates. The number of somites is small. *Polydesmus complanatus* Deg., *Polyxenus lagurus* L., with twelve pairs of legs. *Pauropus Huxleyi* Lubb.

Fam. *Glomeridæ*. The body is short and broad, and can be rolled up into a ball. There are only twelve to thirteen segments, which possess dorsal plates. The last ring of the body is shield-like. They remind one of the genus *Armadillo*. *Glomeris marginata* Leach., with seventeen pairs of legs; in the male there are in addition two pairs of genital appendages at the hinder end of the body. *Sphærotherium elongatum* Brdt.

Class V.—HEXAPODA *=INSECTA.

Tracheata with two antennæ on the head, and with three pairs of legs and usually two pairs of wings on the thorax, which latter is composed of three segments; the abdomen has nine or ten segments.

FIG. 428.—Head, thorax and abdomen of an *Acridium* seen from the side. St, Stigmata; T, tympanic organ.

* J. Swammerdam, "Historia Insectorum generalis," Utrecht, 1669. J. Swammerdam, "Bijbel der natuure," 1737-1738. Réaumur, "Memoires pour servir à l'histoire des Insectes," 12 vols., Paris, 1734-1742. Ch. Bonnet, "Traité d'Insectologie," 2 vols., Paris, 1740. A. Rösel von Rosenhof, "Insectenbelustigung," Nürnberg, 1746 to 1761. Ch. de Geer, "Mémoires pour servir à l'histoire des Insectes," 8 vols., 1752 to 1776. H. Burmeister, "Handbuch der Entomologie," Halle, 1832.

The separation of the body into the three regions known as head, thorax and abdomen is more distinctly marked in Insects than in any other of the *Articulata*. The number of somites and appendages appears to be constant; the head, with its four pairs of appendages, being composed of four segments, the thorax of three, the abdomen usually of nine or ten (eleven) (*Orthoptera*) (fig. 428). The anterior abdominal segment, however, not unfrequently takes part in the formation of the thorax.

FIG. 429.—Different forms of antennæ (after Bar-meister). *a*, bristle-like antenna of *Locusta*; *b*, filiform antenna of *Curabius*; *c*, moniliform antenna of *Tenebrio*; *d*, dentate of *Elater*; *e*, pectinate antenna of *Ctenicera*; *f*, crooked antenna of *Apis*; *g*, club-shaped of *Silpha*; *h*, knobbed of *Necrophorus*; *i*, lamellated of *Melolontha*; *k*, antenna with bristle from *Sargus*.

The head, which is almost always sharply marked off from the thorax, is formed of an unsegmented capsule, in which different regions may be distinguished. These regions have been named, face, forehead, cheeks, throat, skull, etc. after the parts of the Vertebrate head. The upper side of the head bears the eyes laterally, and the antennæ, while on the under part the three pairs of oral appendages are inserted round the mouth. The anterior appendages, the antennæ, are in Insects formed of a simple row of segments, but vary much in form and size. They usually arise from the frontal region, and serve not only as tactile organs, but also as organs of smell. We can

distinguish between *regular* antennæ (where all the joints are alike) and *irregular* antennæ (fig. 429). The first may be bristle-like, filiform, moniliform, dentate, or pectinate; the irregular antennæ, in which the second joint and terminal joints are especially liable to modification, are most frequently club-shaped, knobbed.

lobed, or crooked. In the last case the first or second joint is elongated forming the shaft, to which the distal and shorter joints are attached at an angle as the flagellum (*Apis*).

The following structures enter into the formation of the mouth parts:—the upper lip (*labrum*), the upper jaws (*mandibles*), the first pair of maxillæ or lower jaws, the second pair of maxillæ or lower lip (*labium*). The upper lip is a plate, which is usually movably articulated to the cephalic shield and covers the mouth from above. Beneath the upper lip to the right and left are the mandibles or upper jaws, in the form of two *palpless* biting plates; they are unjointed, and therefore more powerful as masticatory organs. The first pair of maxillæ or lower jaws have a more complicated structure. They are composed of several joints, and are, therefore, adapted for less powerful but more varied movements in aid of the masticatory process.

The maxillæ of the first pair (fig. 430) are made up of the following parts:—a short basal joint (*cardo*, *C'*), a longer second joint or shaft (*stipes*, *St*)

FIG. 430.—Mouth parts of a *Blatta* (after Savigny). *a*, Head seen from the front: *Oc*, ocelli; *Mxt*, maxillary palp; *Lt*, labial palp. *b*, Upper lip (*labrum*, *Lr*). *c*, Mandible (*Md*). *d*, 1st maxilla: *C*, *Cardo*; *St*, *stipes*; *L. in*, *lobus internus*; *L. ex*, *Lobus externus*. *e*, 2nd maxillæ or labium (lower lip), clearly composed of two halves.

with an external scale (*squama palpigera*), to which is attached a many-jointed palp (*palpus maxillaris*, *Mxt.*). Two blades, an internal and external, are attached to the distal end of the second joint [and known respectively as *lacinia* and *galea*] (*lobus externus*, *internus*, *L. in*, *L. ex*). The maxillæ of the second pair arise from the throat, and are partially fused together across the middle line so as to form the unpaired lower lip or *labium*. It is rarely the case that all the parts of the first maxillæ are discernible in the labium, the fusion being generally accompanied by the reduction and disappearance of certain parts. There are, however, cases in which all the elements of the first maxillæ can be shown to exist (*Orthop-*

tera, fig. 430). While the labium is usually reduced to a simple plate with two lateral palps (*palpi labiales*), in the *Orthoptera* we can distinguish a proximal piece (*submentum*), fixed to the throat, from a second piece, bearing the two palps (*mentum*), at the point of which there is a piece, the tongue (*glossa*) (fig. 430, *e*, *L. in*), and sometimes secondary pieces, the *paraglossæ* (*L. ex*). The submentum evidently corresponds to the fused basal joints (*cardo*), the mentum to the fused shafts (*stipes*), the simple or bifid glossa to the lobus internus, and the paraglossæ to the lobus externus of the first maxillæ. Median projections on the internal surface of the upper and lower lips are distinguished as *epipharynx* and *hypopharynx* respectively.

FIG. 431.—Mouth parts of *Anthophora retusa* (after Newport) *A*, Antennæ; *Oc*, ocelli; *Md*, mandibles; *Mx*, maxillæ; *Mxt*, maxillary palp; *Lt*, labial palp; *Gl*, glossa; *Pg*, paraglossæ.

The above description refers to insects which gnaw or bite their food. When the food is fluid, the mouth parts, either in whole or part, become so remarkably modified that it required the penetration of Savigny to establish their morphological relations. The biting mouth parts found in the orders of the *Coleoptera*, the *Neuroptera* and the *Orthoptera* are most nearly allied to the mouth parts of the *Hymenoptera*, which may be described as a *licking apparatus* (fig. 431). The upper lip and mandibles agree with those of the biting apparatus, but the maxillæ and labium are more or less elongated and modified, to admit of licking and sucking up fluids.

Mouth parts adapted for *sucking* are found in the *Lepidoptera*, where the first maxillæ are united to form a sucking tube, while the other parts are more or less

aborted (fig. 432). Finally the *piercing* mouth parts of the *Diptera* and *Rhynchota* also possess a sucking apparatus, which is usually formed of the labium; but there are also styliform weapons, by means of which access is gained to the nourishing fluid, which is to be sucked up (figs. 433, 434). These weapons may be formed by the mandibles, and also by the maxillæ, and even the hypopharynx and epipharynx may be used, undergoing numerous modifications. Since the piercing part of the apparatus may be

totally aborted, or, at any rate, become functionless, it is obvious

FIG. 432.—Oral apparatus of Butterflies (after Savigny). *a*, Of *Zygaena*; *b*, of *Noctua*. *A*, Antennæ; *Oc*, eyes; *Lr*, upper lip; *Md*, mandible; *Mxt*, maxillary palps; *Mx*, maxilla (first); *Lt*, labial palps, cut away.

FIG. 433.—Mouth parts of *Nepa cinerea* (after Savigny). *Ul*, Lower lip (abium) or rostrum; *Lr*, upper lip; *Md*, mandible; *Mx*, maxilla (first).

that no sharp line can be drawn between the piercing and sucking forms of oral apparatus (fig. 434).

The next principal region of the body in Insects is the **thorax**, which is connected with the head by a slender neck. It consists of three segments, and bears three pairs of legs and usually two pairs of wings on the dorsal surface. These three segments, the *prothorax*, the *mesothorax* and the *metathorax* are rarely simple horny rings, but are usually composed of several parts united by sutures. In each segment a dorsal plate, lateral regions and a ventral plate can be distinguished. These may be termed *notum*, *pleura* and *sternum* respectively, and they may further be described, according to the segments in which they occur, as *pro-*, *meso-* and *meta-notum*, and *pro-*, *meso-*, and *meta-sternum*. The lateral regions are divided into an anterior piece (*episternum*) and a posterior (*epimerum*),

FIG. 434.—Mouth parts of *Culex memorosus* ♀ (after Becher). *Lbr*, Upper lip; *Lb*, lower lip (proboscis); *Lt*, labial palps; *Md*, mandibles; *Mx*, maxillæ (first); *H*, hypopharynx (piercing weapon).

while on the *mesonotum* there is a median triangular plate (the *scutellum*), and on the *metanotum* there is not rarely a similar but smaller shield (the *postscutellum*). The manner in which the three regions of the thorax are connected with one another varies in the different orders. In the *Coleoptera*, *Neuroptera*, *Orthoptera* and in many *Rhynchota*, the pro-thorax is freely movable, while in all other cases it is a relatively small ring and is fused with the following segments.

The three pairs of legs are articulated in excavations of the chitinous integument of the ventral surface between the sterna and pleura. The number and size of the joints of the legs seem

FIG. 435.—Different form of legs (règne animal). *a*, *Mantis* with predatory leg; *b*, leg of *Carabus* used in running; *c*, of *Acridium* used in springing; *d*, of *Gryllotalpa* used in digging; *e*, swimming leg of *Dytiscus*.

more constant in the *Insecta* than in any other group of the *Arthropoda*, so that it is possible to distinguish five regions (fig. 435). The basal joint (*coxa*), which is either spherical or cylindrical, is articulated to the thorax and permits of free movement of the limb. The *coxa* is followed by a second very short ring, constituting the *trochanter*, which is sometimes divided into two parts or in other cases is fused with the next joint. The third joint, which is conspicuous on account of its size and strength, is the long *femur*. The next joint is the likewise long but slender *tibia*, which is armed at

the point with movable spines. Finally the last joint, or *tarsus*, is less movably articulated. It is simple only in rare cases; generally it is composed of a number of joints (usually five), of which the last is terminated by movable claws, and sometimes also by lobed appendages.

Of course the special form of the legs varies according to the mode of locomotion and the special needs of each insect. Legs adapted for running, walking, burrowing, leaping, prehension can be distinguished (fig. 435). The anterior pair only is used for predatory purposes, and in such a leg the tibia and tarsus are bent backward against the femur in the same way that the blade of a pocket-knife folds back against its handle (*Mantis*, *Nepa*). The legs used in springing are the posterior pair (*Acridium*), and they are characterised by the powerful femur. Those used in digging are usually the anterior pair, and they may be recognised by the broad, shovel-like tibia (*Gryllotalpa*). In the swimming legs all the parts are flat, and closely beset with long swimming hairs (*Naucoris*). The legs used in walking may be distinguished from the ordinary running legs by the broad hairy lower surface of the tarsus (*Lamia*).

Wings are only found in the fully developed, sexually adult animals, which are relatively rarely without them. They are attached

to the dorsal surface of the meso- and meta-thorax, being articulated between the notum and pleura. The anterior wings are attached to the meso-thorax, and the posterior wings to the meta-thorax. As regards their form and structure they are thin, superficially expanded plates, consisting of two membranes firmly adhering to one another and continuously connected at the edges. They are usually delicate and transparent, and are traversed by various strongly chitinised bands, the *nervures* or *veins* or *ribs* (fig. 436).

These nervures, which have a very definite and systematically important course, consist of canals, placed between the two layers of the wing, surrounded by chitin and containing *blood*, *nerves* and especially *tracheæ*, the distribution of which corresponds with the

FIG. 436.—Wing of *Tipula* (after Fr. Brauer). *H*, Subcosta; 1, first longitudinal nervure (costa mediana); 2, radial rib (radius or sector); 3, cubital rib; 4, discooidal rib (or cubitus anticus); 5, submedian (or cubitus posticus); 6, anal rib (or postcosta); 7, axillar rib; *R*, marginal cell; *U*, submarginal cell. *D*, discooidal cell; *I*—*V*, posterior marginal cells; *VB*, anterior basal cell; *HB*, posterior basal cell; *AZ*, anal cell.

course of the nervures. The nervures, therefore, always start from the root of the wing as two or three principal stems, and distribute their branches more especially to the upper half. The first (fig. 436) of the main trunks which runs beneath the upper margin of the wing is called the *costa*, and often ends in a horny dilatation. Beneath the *costa* there is a second main stem, the *radius*, and behind this a third, the *cubitus*, which rarely remains simple, but usually bifurcates before the middle of its course into branches, which are often further divided so that a more or less complicated network is formed in the upper half of the wing. The spaces of this network may be distinguished as *marginal spaces* or *radial cells*, and as *sub-marginal spaces* or *cubital cells*. Not rarely there may also be present one or more lower nervures (anal, axillar nervures).

The form and structure of the wings present various modifications. The anterior wings may become coriaceous by the stronger chitination of their substance, as for instance in the *Orthoptera* and *Rhynchota*; or, as in the *Coleoptera*, they may have a firm horny structure (*tegmina* or *elytra*), and be used less for flight than as a protection of the back, the skin of which is soft. The anterior wings in the *Rhynchota* group of the *Hemiptera* are mostly horny and only membranous at the tip, while the posterior wings are membranous. When both pairs of wings are of a membranous structure, their surface is either thickly covered with scales, *Lepidoptera* and *Phryganidæ* (group of *Neuroptera*), or remains naked and is marked out into a number of very conspicuous spaces, which may not unfrequently have the form of a close net-like mesh-work, as in the *Neuroptera*. In general the two pairs of wings differ in size. Those insects which have coriaceous anterior wings and half or whole wing covers, have much larger posterior wings, while in the insects with membranous wings the anterior wings are, as a rule, the largest. In many of the *Neuroptera*, the wings are pretty nearly the same size, while in the *Diptera* the posterior wings are aborted and reduced to small knobs (*halteres*). Finally we find in all the orders of insects examples of a complete absence of wings either in both sexes, or in the female sex alone.

The third region of the body, which contains most of the vegetative organs, as well as the organs of reproduction, is the elongated and well-segmented **abdomen**. In the adult insect this region is destitute of appendages, although very often in larval life, and as an exception in the sexually adult animal (*Japyx*), short appendages are present. The abdominal segments are very definitely separated

from one another by soft connecting membranes. They are composed of simple dorsal and ventral plates, which are also connected laterally by soft membranes. This structure of the abdomen, which contains the respiratory and genital organs, permits of its being dilated and contracted (respiratory movements, distension of the ovary). Very often the posterior segments have a special structure, owing to the various appendages which are connected with the processes of copulation and of deposition of the eggs. The anus is usually placed on the last abdominal ring, while the generative opening which is separate from the anal aperture opens on the ventral surface of the preceding segment (fig. 437). Terminal appendages, such as jointed filaments, etc., are present on the anal segment. The *appendices genitales*, forming the genital armature, are, on the contrary, placed on the ventral side around the genital opening. Developed in the male as valves and in the female in the form of ovipositors, stings, etc., they arise from the imaginal discs (growths of the hypodermis), in the *Hymenoptera* and *Orthoptera* on the eighth (first pair) and ninth (second pair) segments of the abdomen (fig. 438). The ovipositors of the *Diptera*, on the other hand, are to be derived from the retracted posterior segments.

FIG. 437.—Posterior end of body of a Beetle. (*Pterostichus* ♂) (after Stein). 8, 9, Dorsal plates; 8' 9', ventral plates; St, stigma; A, anus; G, genital opening.

FIG. 438.—a, Hind end of abdomen of a young female *Locusta* with the protuberances of the ovipositor and the anal styles; C' and C'', the internal and external protuberances of the penultimate; C''', the same of the antepenultimate segment. b, slightly older stage. c, Nympha; A, anus with anal styles (after Dewitz).

Alimentary canal (figs. 439, 440).—The mouth, which is covered by the upper lip, usually leads into a narrow œsophagus, into the anterior portion of which, distinguished as the buccal

Alimentary canal (figs.

439, 440).—The mouth,

which is covered by the upper lip, usually leads into a narrow œsophagus, into the anterior portion of which, distinguished as the buccal

cavity, open one or more pairs of tubular or racemose salivary glands (*Sp*). In many of the suctorial insects, the end of the œsophagus is dilated into a sack with thin membranous walls and a short stalk, the *suctorial stomach*; in others into a more uniform dilatation, known as the *crop* (fig. 439, *Oe*). The intestine which follows the œsophagus is sometimes straight and sometimes coiled; it varies exceedingly in accordance with the mode of life. It is always at least divisible

FIG. 439.—Digestive apparatus of *Apis mellifica* (after Léon Dufour). *Sp*, Salivary glands; *Oe*, œsophagus with crop-like dilatation; *M*, chylific ventricle; *Re*, Malpighian vessels; *R*, rectum with so-called rectal glands; *G. Dr.*, poison glands.

into a longer portion, which is concerned in digestion, the mesenteron or *chylific ventricle* (*M*, *Chd*), and a terminal portion, which is concerned with the ejection of the fæces (figs. 439, 440).

The number of regions may, however, be larger. In predaceous Insects, especially in the orders of *Coleoptera* and *Neuroptera*, a masticatory stomach or proventriculus (fig. 440, *Pv*) is inserted between the crop and chylific ventricle; this is of globular form, and has powerful muscular walls. It is lined by a specially thick chitinous cuticle, which is beset with strong bands, teeth, and bristles. The chylific ventricle also, on which especially the digestive glandular layer is developed at the expense of the muscular layer, is sometimes divided into several regions, as for example in some Beetles the anterior

part has a shaggy appearance from the numerous cæca which project from it (fig. 440 *Chd*), and is sharply marked off from

the simple narrower portion which follows it. Larger caeca, too, after the manner of *hepatic glands*, may be inserted at the commencement of the chylific ventricle (*Orthoptera*).

The commencement of the hind gut or posterior portion of the alimentary canal is indicated by the opening of filiform caecal tubes, the *Malpighian vessels*. It is divided into two or more rarely three regions, which are distinguished as the *small intestine*, the *large intestine* and the *rectum*. The last region is provided with a strong layer of muscles, and contains in its walls four, six or more longitudinal ridges, the so-called *rectal glands* (fig. 439, *R*). Sometimes two glands, the so-called anal glands (*G. Dr, Ad*), open into the rectum immediately in front of the anus. Their secretion, on account of its irritating qualities and disagreeable smell, seems to serve as a protection to the animal. In exceptional cases the larva alone takes up nutriment, the sexually mature apterous form being without a mouth (*Ephemera*). Finally the stomach of the larva in a few cases ends blindly, and does not communicate with the hind gut (larvæ of *Hymenoptera*, *Pupipara*, *Ant-lion*).

The *Malpighian vessels* already mentioned, which were formerly erroneously held to be bile organs, undoubtedly function as urinary organs. Their contents, secreted by the large nucleated cells of their walls, are usually of a brownish yellow or white colour, and consist of an aggregation of small granules and concretions, which, for the most part, consist of uric acid. Crystals of *oxalate of lime* and *taurin* have also been found. The numbers and grouping of these filiform tubes, which are usually very long and wound round about the chylific ventricle, varies very much. As a rule there are four or six, or more rarely eight of them opening into the intestine, but in the *Hymenoptera* and *Orthoptera* the number is much larger; in the latter there may even be a common duct into which the tubes are united (*Gryllotalpa*).

FIG. 440.—Alimentary canal and glandular appendages of a Beetle (*Carabus*) (after L. Dufour). *Oe*, oesophagus; *Jn*, crop; *Pv*, proventriculus; *Chd*, chylific ventricle; *Mg*, Malpighian tubes; *R*, rectum; *Ad*, anal glands with vesicle.

Amongst the **secretory glands** of insects the *glandulæ odoriferæ*, the *wax-glands*, *spinning-glands* and *poison glands* are to be mentioned. Of these, the first, to which belong the anal glands which we have already mentioned (fig. 440), lie beneath the covering of the body and secrete, usually between the articulations, strongly smelling fluids. In the *bugs* there is an unpaired piriform gland in the metathorax, which pours out its secretion by an opening between the hind legs and gives rise to the notorious smell. Unicellular cutaneous glands have been shewn to exist in different parts of the body of insects, and, like the sebaceous glands of vertebrates, seem to secrete an oily liquid, which serves to lubricate the joints. Similar glandular tubes of the integument, which may be called *wax-glands*, secrete white threads and flakes, which cover the body as with a kind of powder or wool (Plant lice, etc., fig. 441). *Spinning-glands* occur

FIG. 441.—The wax glands and the prominences on which they open of an *Aphide* (*Schizoneura Lonicerae*). *a*, Pupa seen from dorsal surface; *Wh*, prominences on which the wax glands open; *b*, the unicellular wax glands (*WD*) beneath the cuticular facets (*Cf*) of the skin.

exclusively in larvæ and serve for the production of webs and cases. When these glands have the form of two or more less swollen and elongated tubes (*sericteria*) opening behind the mouth, they may be compared to a special form of salivary gland,

which they also resemble in their structure. The larva of the antlion has its spinning organs at the opposite end of the body; the wall of the rectum, which is shut off from the chylic ventricle, taking the place of the *sericteria*.

The poison glands, which are present in the female *Hymenoptera*, consist of two simple or branched tubes, the common duct of which is dilated to form a vesicular reservoir for the secreted fluid, which consists of formic acid. The end of this reservoir is connected with the *poison spine*.

Vascular system.—The blood, which is usually colourless but not

unfrequently has a green tinge, always contains amœboid blood cells and travels along definite tracts of the body cavity. The simplification of the *circulatory apparatus*, which is confined to a *dorsal vessel*, is correlated with the richly branched respiratory apparatus, the air-conducting *tracheæ*, which are distributed to all the organs and carry oxygen to the blood. The heart, which has the form of a *dorsal vessel* (fig. 442), runs in the middle line of the abdomen, and is divided by transverse constrictions into numerous (up to eight) chambers corresponding to the segments. These chambers are attached to the integument of the dorsal surface by triangular muscles (alary muscles). During the diastole of the chambers the blood streams through as many paired lateral slits into the heart, which contracts gradually from before backwards and drives the blood in the same direction. The anterior chamber is prolonged into a median aorta, which runs forward to the head. From this aorta the blood flows freely into the body cavity and returns to the heart in four principal streams, two lateral, one dorsal beneath the dorsal vessel, and one ventral above the ganglionic chain, giving off numerous branches to the extremities, etc. It is only in exceptional cases (*e.g.*, in the caudal filaments of the larvæ of *Ephemera*) that arterial vessels are found passing out from the heart.

Respiration is effected by branched *tracheæ*, which take in their supply of air through paired slit-like openings, the *stigmata*. The latter are usually situated in the membranes connecting the sterna and terga (fig. 428), and the exchange of air is determined by the distinct respiratory movements of the abdomen. The number of stigmata is very various, but there are rarely more than nine or fewer

FIG. 442.—Longitudinal section through the body of *Sphinx liquetii* (after Newport). *Mx*, maxillæ forming the proboscis; *t*, palp; *At*, antenna; *Gs*, brain; *Gi*, subœsophageal ganglion; *N*, thoracic and abdominal ganglia; *V*, œsophagus; *V'*, suctorial stomach; *M*, mesenteron; *Vm*, Malpighian tubes; *H*, heart; *G*, testes; *E*, rectum; *A*, anus.

than two pairs present. They are never present on the head or on the last abdominal segment. They are least numerous in the aquatic larvæ of beetles and Diptera, which have but two stigmata placed at the hind end of the abdomen on a simple or forked tube. There are, however, often two openings on the thorax in addition. Some water-bugs (e.g., *Nepa Ranatra*, etc.) have at the end of the abdomen two long grooved filaments which lead at their base into two air cavities. Such water-bugs can by this arrangement take up air like the Dipteran larvæ, by protruding the respiratory tube on the surface of the water.

The *tracheæ* (fig. 443), which are kept open by the spiral thickening

Fig. 443.—Tracheal branch with finer twigs (after Leydig). Z, Cellular external wall; Sp, cuticular lining (spiral fibre).

perfectly filled with air, and on that account have usually a silvery shining appearance. Their internal chitinous membrane is produced by an outer delicate and nucleated cell layer, and is thrown off with the external cuticle and renewed at each moult during larval life. The dilatations which are not unfrequently present in the course of the tracheæ, and which, in strong flying insects, as *Hymenoptera*, *Diptera*, etc., are enlarged to form air sacs of very considerable size, may with justice be compared to the air sacs of birds. They possess a delicate chitinous membrane, which exhibits no trace of the spiral fibre.

They therefore collapse with great ease, and require for their filling special respiratory movements. These are especially noticeable in the relatively clumsy *Lamellicorns* before their flight. The arrangement and distribution of the tracheal system may easily be described by starting with the origin of the principal trunks from the stigmata. Each stigma leads into one (or more) tracheal trunk, which sends out connecting branches to the neighbouring trunks and gives off a tuft of much branched tubes to the viscera. As a rule, there are formed in this way two independent lateral trunks, which communicate by transverse tubes and give off numerous secondary trunks to the internal organs. The finer branches of the secondary tubes are not

only applied externally to the viscera, but partially traverse them and serve at the same time to support them.

Tracheal gills are present in the form of leaf-like or filiform appendages on the body of the larvæ of *Phryganidæ*, *Ephemeridæ* (fig. 444), and in the rectum of the larvæ of *Æschna* and *Libellula*.

FIG. 444.—*a*, Larva of *Ephemera* with seven pairs of tracheal gills *Kt*, slightly magnified. *Tk*, An isolated tracheal gill, strongly magnified. *b*, Tracheal system of an *Agrion* larva (after L. Dufour); *Tst*, tracheal trunk; *Na*, accessory eyes.

In the last case the walls of the rectum are very muscular, and are capable of regularly pumping in and out water, thus giving rise to a kind of respiratory movement.

The so-called **fat bodies** stand in the closest relation to respiration and the nutritive processes. They are fat-like shining and usually coloured, lobed and globular bodies, which are distributed beneath the skin and between the organs, and are especially abundant during larval life. The chief importance of these organs depends on the part they play with regard to metabolism. They consist essentially of an accumulation of superfluous nutritive material, and seem to be used for nourishment and for the production of heat, and especially during the development into the perfect insect for the formation of new parts of the body and for the growth of the generative organs. The rich distribution of the tracheæ to the fat cells points to the consumption of a large amount of oxygen, and consequently to an active metabolism, which is further demonstrated by the frequent deposition of nitrogenous waste material, especially of uric acid.

The **phosphorescent organs** of the *Lampyridæ* and various *Elateridæ* show a certain resemblance to fat bodies. These organs are delicate plates, which in *Lampyris* are present on the ventral surface of several of the abdominal segments and consist partly of pale albuminous cells, and partly of granular cells, containing uric acid; richly branched tracheæ and nerves are distributed amongst these cells. The pale cells compose the lower ventral layer of the plates, and it is this layer alone which is phosphorescent. These cells, together with the terminal cells of the tracheæ, which are always very numerous, are to be regarded as the active elements, the chemical changes of which, under the influence of oxygen, and to a certain extent of the nervous system, give rise to the phenomenon of phosphorescence. The cells of the upper non-luminous layer of the plates contain a great number of refractile granules, which, according to Kölliker, consist of uric acid compounds, the final products of the metabolism which causes the phenomenon of phosphorescence.

The **nervous system** of insects presents a very high development, and a great amount of variation in arrangement; all transitions between a long ventral ganglionic chain, consisting of about twelve pairs of ganglia, and a common thoracic ganglionic mass are found (figs. 77 and 78). The brain (supra-œsophageal ganglion), which is placed in the head, attains a considerable size. It presents several groups of swellings; these are especially marked in the *Hymenoptera*, which have the highest psychical development. It gives origin to the sense nerves, and seems to be the seat of the will and of the psychical activity. The small subœsophageal ganglion supplies the mouth parts, and corresponds to several pairs of ganglia fused together.

The ventral chain, which with its lateral nerves may be compared to the spinal cord and the spinal nerves, preserves the primitive uniform segmentation in most larvæ, and is the least modified in insects with a free prothorax and long abdomen. In such insects, not only do the three large thoracic ganglia, which supply the wings and legs with nerves, remain separate, though certainly they are often strengthened by the anterior abdominal ganglia, but also a larger number of abdominal ganglia. Of the latter, the last, which is formed by the fusion of several ganglia and gives off numerous nerves to the ducts of the generative apparatus and to the rectum, is always distinguished by its considerable size. The gradually progressing concentration of the ventral cord, which may be followed out in the larval and pupal development,* is explained by the crowding together of the abdominal ganglia, as well as by the fusion of the thoracic ganglia. Of the latter, those of the meso- and meta-thorax first fuse to a large posterior thoracic mass, which then fuses with that of the prothorax to form a common thoracic mass. When the latter is finally united to the fused mass of the abdominal ganglia, the highest grade of concentration, which is found in the *Diptera* and *Hemiptera*, is reached.

The *visceral nervous system* is divided into the system of the œsophageal nerves and the true sympathetic. In the former we can distinguish unpaired and paired œsophageal nerves. The

FIG. 445.—Cerebral ganglion and œsophageal nerve ganglia of *Sphinx ligustri* (after Newport). *Gfr.*, Frontal ganglion; *g', g'*, ganglia of the paired œsophageal nerves.

The unpaired system springs from the anterior surface of the brain by two roots, which unite in front to form the so-called frontal ganglion (fig. 445 *Gfr.*) In its further course on the dorsal surface of the œsophagus it forms a number of fine plexuses in the muscular layer of that organ (fig. 445). The paired œsophageal nerves spring on either side from the posterior surface of the brain, and swell out at the sides of the œsophagus to form larger ganglia, which also supply nerves to the wall of the œsophagus. A system of pale nerves, first described by Newport

* Compare especially the numerous papers of Ed. Brandt, "Ueber die metamorphose des Nervensystems."

as *nervi respiratorii* or *transversi*, is to be regarded as a true sympathetic. These nerves are given off near one of the ganglia of the ventral chain from a median nerve which runs between the two ventral nerve cords, has a root in the ganglion, and sometimes forms a small sympathetic ganglion. After their separation they again form lateral ganglia, the nerves of which pass into the lateral nerves, but afterwards separate again from the latter, and after forming plexuses supply the tracheal trunks and muscles of the stigmata.

Of the **Sense organs**, the *eyes** attain the highest grade of perfection. The unicorneal ocelli are principally present in larval life, but two or three of them are often present on the top of the head of fully-developed insects (fig. 87). The faceted eyes are placed at the sides of the head, and are found in the fully-developed insect (fig. 85).

FIG. 443. — Tibia of the anterior leg of *Locusta viridissima* (after V. Graber). Ty, tympanic membrane with operculum.

Auditory vesicles with otoliths have not been discovered in insects. Since, however, the capacity of perceiving sound can scarcely be doubted for numerous insects, and especially for those which are capable of producing sound, we are forced to presuppose the existence of some organ for the perception of sound. In fact, in the springing *Orthoptera* apparatuses can be pointed to which probably serve as acoustic organs for the perception of sound waves. In the *Aceridæ* these are placed at the sides of the first abdominal segment close behind the metathorax (fig. 66, b), in the *Gryllodeæ* and *Locustidæ* in the tibiæ of the anterior legs, just beneath the articulation of the femora (fig. 446). In this region a tracheal trunk dilates between two lateral membranes so as to form a vesicle, on which are spread out the end cells, provided with so-called nerve rods, of a nerve springing from the first thoracic ganglion (fig. 447). Peculiar

sense organs have also been discovered in the posterior wings of beetles and in the halteres of flies.

Shining nerve rods have been found by Leydig in the nerves of

* Compare especially Leydig, "Zum feineren Bau der Arthropoden, sowie Geruchs-und Gehörorgane der Krebse und Insecten." *Müller's Archiv*, 1855 and 1860.

H. Grenacher, "Untersuchungen über das Sehorgan der Arthropoden." Göttingen, 1879.

Also V. Graber, "Die tympanalen Sinnesorgane der Orthopteren." Wien, 1875.

the antennæ, the palps, and legs, under conditions which render it possible that these nerves have the value of tactile nerves, and this is the more probable since the *sense of touch* is principally discharged by the antennæ and the palps of the oral apparatus, as well as by the tarsal joints of the legs.

Olfactory organs are very generally distributed, as might have been expected from the developed capability of tracking which many insects possess. It may be regarded as fairly certain that the surface of the antennæ is the seat of the olfactory sense. Formerly, in accordance with the views of Erichson, the numerous pits which are found, for instance, on the leaf-shaped antennæ of the *Lamellicornia*, were interpreted as olfactory pits; but it is more correct to regard with Leydig the peculiar cones and knobs of the antennæ which are connected with gangliated nerve endings as olfactory organs.

The reproduction of insects is principally sexual. The male and female generative organs are always placed in different individuals; but they correspond in their position and parts, and in their opening on the ventral surface of the hind end of the body. The testes and ovaries are provided with paired ducts ending in an unpaired portion (fig. 91). The first rudiments of the genital organs may be traced back to a very early stage of the embryonic development. Their development, however, is only completed in the

FIG. 447.—A portion of the nerve termination in the anterior leg of *Locusta viridissima* (after V. Graber). *N*, nerve; *Gz*, ganglion cells; *St*, rods in the terminal cells.

latest period of larval life, or in insects with complete metamorphosis during the pupal stage. In rare cases the full development and maturity of the sexual organs is never completed, as in the so-called sexless *Hymenoptera* (working bees, ants) and termites, which are incapable of reproduction.

The males and females are distinguished by more or less important external differences in various parts of the body; sometimes these differences lead to a marked sexual dimorphism. The males are almost always more slenderly formed, and are capable of quicker and

easier movement. They have larger eyes and antennæ, and their colours are brighter and more striking. When there is a pronounced dimorphism the females are apterous, and their form approximates to that of the larva (*Coccidæ*, *Psychidæ*, *Strepsiptera*, *Lampyris*), while the males are provided with wings.

The female generative organs are composed of paired ovaries and oviducts, the unpaired oviduct, the vagina and the external genital apparatus. The ovaries are elongated tubes, in which the eggs originate. The ova lie one behind another in a single row like a string of pearls, increasing in size from the blind end to the opening

into the oviducts (fig. 91, *a*). The arrangement of these ovarian tubes presents extraordinary variations, and there thus originates a great number of different forms of ovary, which have been described principally in the beetles by Stein. The number of the ovarian tubes also varies exceedingly, being least in some *Rhynchota*, and then in the butterflies, the latter having on each side only four very long ovarian tubes, which are many times folded (fig. 448). At their lower ends the ovarian tubes on either side open into the dilated commencement of the oviduct, which joins with that of the other side to form a median oviduct. The lower end of the latter represents the *vagina*, and often

FIG. 448.—Female sexual organs of *Vanessa urticae* (after Stein). *Or*, The ovarian tubes cut off; *Rc*, receptaculum seminis and accessory glands; *Va*, vagina; *Bc*, bursa copulatrix with duct leading to the oviduct; *Dr*, glandular appendage; *Dr'*, glandula sebacea; *R*, rectum.

receives, near the genital aperture, the ducts of special cement and sebaceous glands (*glandulae sebacea*), the secretion of which is used to surround and fasten the eggs which are about to be laid. In addition to these glands, the unpaired efferent duct of the genital apparatus is very commonly furnished with one or several usually stalked *receptacula seminis* (fig. 449), in which the semen, often introduced in the form of *spermatophores*, retains its fertilizing properties for a long time, sometimes for years, under the in-

fluence of the secretion of an accessory gland. Beneath the receptaculum seminis, a large pouch-like diverticulum, the *bursa copulatrix*, which assumes the function of the vagina, is sometimes separated from the vagina. In the butterflies (fig. 448) a narrow duct serves to convey the sperm from this bursa, which opens separately, to the receptaculum.

The male generative organs consist of paired testes and their vasa deferentia, of a common ductus ejaculatorius and of the external copulatory organ (fig. 450). The testes are long blind tubes, which are present either singly or in number on either side, and are often coiled together so as to form a seemingly compact brightly-coloured body. They may also be united to form an unpaired organ in the middle line. The testicular tubes are prolonged on either side into a usually coiled efferent duct or vas deferens, the lower end of which dilates considerably, and may even swell out to the form of a vesicle (*vesicula seminalis*). At the point where the two vasa deferentia join to form the muscular ductus ejaculatorius, one or more glandular tubes often pour their coagulable secretion into the latter; the secretion serving to form a case round the balls of spermatozoa. The transference of the spermato-

FIG. 449.—Terminal region of the female generative organs of *Musca domestica* (after Stein). *Od*, Oviduct, *Rc*, the three receptacula seminis; *Dr*, glandular appendages of the vagina; *Bl*, blind sac-like appendage.

FIG. 450.—Male generative organs of the Cockchafer; (after Gegenbaur). *T*, Testes; *Vd*, dilated portion of the seminal duct; *Dr* coiled accessory gland.

phores into the body of the female is effected by a horny tube or groove which surrounds the end of the ductus ejaculatorius. This tube, when not in use, usually lies retracted in the abdomen, and when protruded is surrounded by external organs for attachment (valves or pincers), as by a sheath. In exceptional cases (*Libellula*) the copulatory apparatus which serves to transfer the sperm is remote from the generative opening, as in the male spiders, being placed on

the ventral side of the enlarged second abdominal segment.

Almost all insects are oviparous, and only a few, as the *Tachinæ*,

some of the *Æstridæ* and of the *Pupipara*, are viviparous. As a rule, the eggs are laid shortly after fertilization, and before the commencement of the development of the embryo. In rare cases the embryo is already formed when the egg is laid. In the last case the segmentation and formation of the embryo take place in the vagina (fig. 451). The fertilization of the egg usually takes place during its passage through the oviduct, at the place where the *receptaculum seminis* opens. Since the eggs become invested with their resistant *chorion* in the ovarian tubes, from the epithelial cells of which they originate for the most part during the larval life, it is necessary that there should be special arrangements which render possible the entry of the spermatozoa and the fertilization of the ovum. For this object there exist on the upper pole of the egg (the pole turned towards the egg-tubes during the passage of the egg) one or more

FIG. 451.—Female generative organs of the viviparous *Melophagus ovinus* (*Pupipara*) (after R. Leuckart). *Ov*, Egg in the ovarian tube of one side; *Ut*, uterus; *Dr*, the glands opening into the uterus; *Va*, vagina.

pores known as *micropyles*,* which pierce the chorion and present a characteristic form and arrangement (fig. 452).

The ova originate in the narrow terminal portion of the egg-tubes, which is often prolonged into a thin thread. Here the growth of the egg-tube takes place, as well as the differentiation

of its contents into egg cells and ovarian epithelium. The ovarian tubes increase continuously in diameter towards the oviduct, in correspondence with the gradual increase of size undergone by the eggs, which are arranged one behind another in its lumen. Each egg occupies a chamber, and obtains an external resistant membrane (*chorion*), which is secreted by the epithelium which lines the chamber. The chorion shows in its external markings the peculiarities of the epithelium from which it was formed.

Besides this type, which is found in *Pulex* and in many of the *Neuroptera* and *Orthoptera*, there is a second type of ovarian tube, distinguished from the first by a more complicated structure of the ovarian chambers. The lumen of such egg-tubes encloses above the

* Compare R. Leuckart, "Ueber die Mikropyle und den feineren Bau der Schalenhaut bei den Insecten." *Müller's Archiv.*, 1855.

ovum a single (*Forficula*), or a number of yolk-forming cells (nutritive cells), so that we can distinguish in the egg-tube alternate yolk and germ compartments (fig. 453, *a* and *b*). In rare cases (*Aphides*) there is at the end of each egg-tube a common larger chamber of yolk cells, which are connected with the egg-chambers by means of "yolk-cords" (fig. 453 *c*).

Parthenogenesis and Heterogamy.—In certain insects, parthenogenesis, *i.e.*, spontaneous development of unfertilized ova, has been shown to obtain; this occurs in the *Psychidæ* (*Psyche*), *Tineidæ* (*Solenobia*), *Coccidæ* (*Lecanium*, *Aspidiotus*) and *Chermes*; also in numerous *Hymenoptera*, especially in *Bees*, *Wasps*, *Cynipidæ*, and *Tenthredinidæ* (*Nematus*). In the *Hymenoptera* which live together in the so-called animal communities, male forms only are produced from the unfertilized ova (*arrenotokia*). *Chermes* affords an example of **Heterogamy**, in that two different oviparous generations follow one another; a slender and winged summer generation, and an apterous generation which is found in autumn and spring and lives through the winter: the males are, in most cases, not yet known. The closely-allied *Aphides* (plant-lice), which were formerly supposed to present the phenomenon of an alternation of generations, behave in a similar manner. In them the summer generations are very numerous, and are succeeded by a sexually-developed autumn generation, which includes winged males as well as the oviparous and often apterous females (fig. 97, *a*, *b*). In the spring, viviparous *Aphides* are developed from the fertilized eggs. These are mostly winged (fig. 99), and in their organisation closely resemble true females. Their reproductive organs are, however, differently constructed, and are without the receptaculum seminis. Since they never copulate, they have often been regarded as asexual forms provided with germ tubes.

FIG. 452.—Micropyles (*Mk*) of insect eggs (after R. Leuckart). *a*, upper part of the egg-shell of *Anthomyia*; *b*, egg of *Drosophila cellaris*; *c*, stalked egg of *Paniscus testaceus*.

The germ apparatus, however, of the so-called Aphide asexual generation not only has a very great resemblance to the female generative apparatus of insects, but the structure and mode of origin of the germ seems to agree so closely with that of the ovum that the viviparous Aphides must be considered as a peculiarly organised generation of females, the genital apparatus of which has undergone some simplifications adapted to parthenogenesis. However that may be, it will be convenient in this case to call the ovary the *pseudovary*, and the ova which originate in it and are incapable of fertilization, the *pseudova*. From this point of view the reproduction of some

FIG. 453.—*a*, Egg tube of *Forficula*. *Nz*, Nutritive cells; *Ez*, ovum; *OE*, epithelium of the wall of the egg tube. *b*, Median part of the egg tube of a Moth. *Nz*, nutritive cells of the yolk-chamber; *Ez*, ovum in the germ-chamber; *H*, connective tissue investment, so-called serosa. *c*, Egg-tube of *Aphis platanoides* with three ovarian chambers (*Ez*—*Ez''*) and the terminal nutritive chamber with its cells *Nz*. *Ds*, yolk cord.

Diptera (*Cecidomyia*, *Miastor*, fig. 100), which can reproduce themselves while still in the larval stage, may be explained.

The **development** of the embryo takes place as a rule outside the body of the mother, and occupies a longer or shorter period of time, according to the temperature and the time of the year. The centroticithal segmentation leads to the formation of a superficial blastoderm, which surrounds the ovum, and always consists of a single layer of cells. A part of this blastoderm, on that side of the ovum which the later history shows to be ventral, becomes thickened and sharply

marked off from the rest, and forms the structure known as the *ventral plate*, which constitutes the first rudiment of the head and ventral half of the embryo.

In many cases (*Rhynchota Libellula*) the ventral plate grows out from a hill-like thickening of the blastoderm (fig. 454) into the interior of the yolk, so that an internal ventral plate arises, in the formation of which a portion, though a small one, of the external blastoderm participates. The ventral thickening, which gives rise to the ventral plate, is caused by long columnar cells, and is at first confined to a small portion of the egg; in *Hydrophilus* the posterior end (fig. 455, *a*). Inasmuch as its lateral edges become elevated

FIG. 454.—Embryonic development of *Calopteryx virgo* (after Al. Brandt). *a*, Commencing involution of the ventral plate. The blastoderm was at first one-layered and thickened at the poles. *G*, edge of ventral plate. *b*, Later stage of the involution. *c*, The embryonic membranes are developed; *Lp*, parietal (serosa); *Lv*, visceral (amnion) layer of the latter. *d*, The appendages have sprouted out on the ventral plate. *A*, Antenna; *Md*, mandible; *Mx*, first maxilla; *Mx'*, second maxilla (labium or lower lip). Then follow three pairs of legs. *e*, Eversion of the embryo which is protruded from the sheath of the visceral layer. *f*, Completion of the inversion; the hind end of the body is free; the yolk sac is on the dorsal surface.

and grow towards one another (fig. 455, *b, c*), the thickened ventral plate first assumes the form of a groove, and then, after the fusion of the lateral edges, becomes a canal, the lumen of which is soon obliterated. The roof only of this canal corresponds to the epiblast, while the cells of its floor and its sides give rise to the first rudiment of the mesoblast. At the edge of the so-called ventral plate, fresh

folds are then formed; these lead to the formation of the embryonic membranes, which are so characteristic of insect development. In

FIG. 455.—Development of the embryo of *Hydrophilus piceus* (after Kowalevski). *a*, Shield-like ventral plate with raised edges. *b*, The edges are already growing together in the middle. *c*, The groove is almost entirely closed. *d*, The tail fold of the embryonic membranes has grown over the posterior end of the closed groove and is gradually extending forward; *Am*, Amnion. *e*, The embryonic membranes have almost entirely grown over the embryo. *f*, The embryonic rudiment beneath the completely closed membranes; with seventeen primitive segments: *KL*, Procephalic lobes; *A*, antennæ. *g*, The ventral plate extends along the whole length of the ventral surface. The bi-lobed upper lip is present, also the antennæ, (*A*) the jaws, and the first rudiments of the legs; rudimentary appendages are present on the seventh segment as prominences. On the abdominal segments there are round invaginations, the first rudiments of tracheæ; there is a longitudinal groove from mouth to anus. *h*, The ventral plate covers the whole ventral surface of the ovum; the openings of the invaginations (stigmata) have become small; rudimentary extremities are still present on the first abdominal segment. The ganglia of the ventral chain have appeared. *i*, Viewed from the dorsal surface the so-called dorsal plate has closed up to a tube; *Oe* is its opening. *k*, The embryo just before hatching seen from the ventral side.

Hydrophilus these folds grow together over the ventral plate from behind forwards, and fuse with one another, so as to give rise to an

external and internal membrane, the former being called the serous membrane, and the latter the amnion (fig. 455, *d, e*).

Simultaneously with the above-mentioned appearance of the membranes (in other cases at an earlier stage of development) the ventral plate becomes divided into two symmetrical halves, the *germinal bands*, which become divided by transverse constrictions into segments (up to 17). First of all three *cephalic segments*, on which the oral appendages are subsequently developed, make their appearance behind the procephalic lobes, which bear the first rudiments of the antennæ. Behind these the rest of the *primitive segments* (*mesoblastic somites*) are successively marked off.

Inasmuch as the germinal bands become strongly contracted, their dorsally bent round, terminal portion becomes drawn more and more towards the lower part of the egg, while their lateral parts gradually grow round the yolk to form the dorsal surface of the embryo (fig. 455, *f, g, h*). With these changes the body of the embryo has assumed a closed form; it now possesses mouth and anus, the first rudiments of the internal organs and the external appendages of the segments, and is soon ready to escape from the egg and begin its independent life.

In *Hydrophilus* and the *Phryganidæ*, peculiar differentiations

appear on the dorsal surface, giving rise to a dorsal plate, which later on becomes folded, so as to form a dorsal canal (fig. 455, *i*).

The **post-embryonic development** takes place, as a rule, by means of metamorphosis, the form, organization and mode of life of the young animal, after hatching, being different from that of the sexually adult animal. It is only in the lowest forms, the partly parasitic *Aptera*, both sexes of which are without wings, that the young leave the egg as perfect animals (*Insecta ametabola*).

In those insects which pass through a metamorphosis, the manner and degree of the transformation differs greatly, so that the distinction of a complete and an incomplete metamorphosis, which was formerly employed, seems to be in a certain degree justified.

In the case of the incomplete metamorphosis (*Rhynchota*, *Orthoptera*) the development of the larva into the perfect winged insect presents a number of stages, during which the larva is capable of free locomotion and of nourishing itself. During these stages, which are marked by successive ecdyses, it gradually acquires wings and increases in size,

FIG. 456.—*Aeschna* larva with rudimentary wings and mask.

the rudiments of the generative organs are further developed, and it becomes more and more like the winged insect. In the simplest case the mode of life and the organization of the young larvæ closely resemble those of the sexually adult animal, as for instance in the *Hemiptera* and *Orthoptera genuina*, but in other cases the adult and larva may differ considerably, although not so much so as in insects with complete metamorphosis; for instance, the larvæ of the *Ephemeroidea* and the *Libellulidae* live in another medium and increase in size under different conditions of nourishment (fig. 456).

The metamorphosis is only said to be *complete* in those forms in which the larva passes through a quiescent stage, in which it is known as a *pupa* and does not take nourishment. With this stage

FIG. 457.—Metamorphosis of *Sitaris humeralis* (after Fabre). *a*, First larval form. *b*, Second larval form. *c*, Pseudo-pupa. *d*, Third larval form. *e*, Pupa.

the larval life ends and the life of the winged insect (*Imago*) begins. The larvæ of insects with complete metamorphosis differ from the sexual animal to such an extent in mode of life and nourishment, in the form of the body and in the whole organization, that though the parts of the body peculiar to the winged insect are prepared and established in larval life, yet a longer or shorter period of quiescence, in a certain sense a second embryonic period, seems necessary, during which the essential alterations of the internal organs, as well as the consolidation of the newly-established external parts, are effected (*hypermetamorphosis*, *Meloidæ*, fig. 457).

In the form of their body and the homonomous segmentation, the larvæ recall *Annelids*, with which they also often have in

common the uniform segmentation of the ganglionic chain. Nevertheless, it is probable that only a proportionately few of the larval forms have preserved the primitive form, and have a phylogenetic significance (*Orthoptera*). In most cases the insect larvæ owe their special peculiarities to secondary adaptations. In exceptional cases, the metamorphosis may be distinguished by quite special larval forms, as for instance in the *Pteromalina* (*Platygaster*, *Teleas*), the eggs of which are laid in other insect larvæ (fig. 458).

The lowest, usually parasitic larvæ are quite vermiform, and are without limbs or a separate head, the latter being represented by the anterior rings of the body (*maggots* of *Diptera* and of numerous

FIG. 453.—Larval forms of three species of *Platygaster* (after Ganin). *a*, *b*, *c*, Cyclops-like larval stages with claw-like jaws, cephalothoracic shield and abdomen. *d*, Second larval stage. *e*, Third larval stage.

Hymenoptera, fig. 66, *a*). In other cases there is indeed a separate cephalic region, but the following thoracic and abdominal segments are entirely without appendages. The larvæ of the *Neuroptera*, of many beetles, of the *Tenthredinidæ* and butterflies (caterpillars), have, on the contrary, jointed appendages on their three free thoracic segments, and frequently also a greater or less number of rudimentary appendages, the so-called prolegs, on their abdomen. There are two rudimentary antennæ on the heads of these larvæ, and a varying number of simple eyes. The mouth parts are, as a rule, adapted for biting, even when the adult animal has a suctorial tube, but, with the exception of the mandibles, they are usually rudimentary. The

mode of nourishment of the larvæ varies very greatly ; but their diet consists mainly of vegetable substances, which stand in great abundance at the disposal of the quickly-growing body. The larva usually undergoes four or five, rarely a greater number of moults, and in the course of its growth gradually assumes the form of the winged insect, not in all cases by the direct transformation of parts already present, but sometimes only after essential processes of new formation.

In this respect, however, there are considerable differences, the extremes of which are represented in the *Diptera* by the genera *Corethra* and *Musca*. In the case of *Corethra*, the larval segments and the appendages of the head are transformed directly into the corresponding parts of the perfect insect, while after the last larval ecdysis the limbs and wings are formed from the *imaginal discs*. The imaginal discs are derived from the hypodermis of the larva.

FIG. 458.f—Imago of *Platygaster*
(after Ganin).

The muscles of the abdomen and the other systems of organs pass unaltered, or with but little alteration, into those of the adult animal. The thoracic muscles, on the contrary, originate as fresh formations from rows of cells already established in the egg. With these slight changes, the active life of the pupa and the small development of the fat body are in necessary

correlation. In *Musca*, on the contrary, the pupa of which is quiescent and enclosed in a firm barrel-shaped membrane and contains a large fat body, the body of the adult animal, with the exception of the abdomen, arises by extensive transformations of the larva. The head and thorax are developed from imaginal discs, which, already established in the egg, become developed in the larva on the investing membrane of the nerves or tracheæ. It is not until the pupal stage that these discs grow together, and give rise to the head and thorax. Every thoracic segment is composed of two pairs of discs (a dorsal and a ventral), the appendages of which represent the later wings and legs. All the systems of organs of the larvæ are said to undergo a disruption during the protracted pupal stage as a result of the (recently, however, contested) process of so-called histolysis, and are replaced by new formations by aid of the fat body and the granular spheres arising from the latter.

When the larva has attained a certain size and degree of development, *i.e.*, when it is fully grown and provided with the food

material required for its future changes, in the form of the enormously developed fat body, it is ready to enter on the pupal stage. The larvæ of many insects prepare above or below the ground, by means of their spinning glands, a protective web, in which, after casting their skin, they enter the pupal stage (*Chrysalis*). The external parts of the body of the winged insect either lie against the common horny skin of the pupa, so that they are recognizable as such (*Lepidoptera*, *pupa obtecta*), or they already stand out freely from the body (*Coleoptera*, *pupa libera*). This distinction is, however, an unimportant one, since in the first case the limbs are free just after the ecdysis, and are only cemented afterwards by the hardening cuticular layer. If the pupa remains enclosed by the last larval skin (*Muscidæ*) it is termed *pupa coarctata*.

In all cases the body of the winged insect lies with its external parts sharply marked in the pupa, and the special object of the pupal life is to complete the changes of the internal organisation and the maturity of the sexual organs. When this is accomplished the winged insect bursts the pupal skin, forces its way out by means of antennæ, wings and legs, and expands those parts which have been folded together, under the influence of violent inspirations, by which the tracheæ become filled with air. The chitinous covering becomes harder and harder, the urinary secretion which has accumulated during the pupal sleep is ejected from the rectum, and the insect is capable of performing all the functions of the sexually adult animal.

The mode of life of insects is so varied that it is hardly possible to give a general account of it. The diet is both animal and vegetable, and is taken in the most varied forms, either solid or fluid, and fresh or decaying. Plants are especially subject to the attacks of insects and their larvæ, and there exists, perhaps, no *Phanerogam* which does not afford nourishment to one or more species of insects. On the other hand, insects seem useful or even necessary to the well-being of the vegetable world, for in many cases—*e.g.*, many flies, bees, and butterflies—they bring about fertilization by carrying the pollen to the stigmata of flowers.

The complex, often marvellous, and apparently intelligent actions performed by insects correspond to the perfection with which the vegetative organs discharge their functions. Such actions are largely carried out instinctively by the mechanism of the organisation, but they certainly in part depend upon psychical processes, since they presuppose memory and judgment, in connection with

the highly-developed perceptive powers of the sense organs. The animal enters the world with instinct, but, in order to perform acts depending on memory and judgment, it must first acquire the necessary psychical conditions by sense perceptions and experience (*bees*). In the inherited organisation are latent all those capabilities which have been acquired in the gradual processes of phylogenetic modifications and at the expense of psychical forces, and have, at last, as the result of frequent use, become automatic and a pure mechanical property of the organism.

The instinctive and psychical manifestations tend directly to the preservation of the individual by providing ways and means for the acquisition of food and for protection, but there is a special instinct tending to the preservation of the species and the care of the young. The most simple example of the latter is to be found in the judicious deposition of the eggs in protected localities, and on plants suitable for the nourishment of the just-hatched animal. The actions of the mother become more complicated in those cases in which the larvæ develop in specially prepared places, and have, as soon as hatched, to meet with the requisite amount of suitable nutritive material (*Sphex sabulosa*). But most wonderful are the instincts of some of the *Orthoptera* and *Hymenoptera*, which concern themselves about the fate of their young after they are hatched and carry nourishment to them during their growth. In such cases a great number of individuals become associated together for the common welfare in the so-called animal communities, in which there is a marked division of labour among the different members; males, females and sexually aborted forms or neuters (termites, ants, wasps, bees).

Some insects are capable of producing sounds,* which we must in part regard as the expression of an internal disposition. We cannot, however, thus regard the buzzing sounds produced during flight by *Hymenoptera* and *Diptera* (vibration of wings and of the foliaceous appendages within the tracheæ), or the sounds like those of a rattle which are produced in numerous beetles by the friction of certain body segments against one another (pronotum and mesonotum of the *Lamellicornia*) or with the inner sides of the wing-covers, although it is possible that such sounds are of some use for defence against hostile attacks. Peculiar vocal organs, which produce sounds for the purpose of attracting the females, are found in the male *Cicada* on the abdomen, and in the males of the *Gryllidæ* and

* H. Landois, "Die Ton-und Stimmapparate der Insecten." Leipzig, 1867.

Locustidæ, at the base of the anterior wings. Both sexes of the *Acerididæ* also produce similar though feebler chirping sounds, by rubbing the femora of the posterior legs against the edge of the wing-covers.

Insects are almost universally distributed, from the equator to the extreme limits of vegetation; certainly with a considerable diminution in the number of species, and in their size and beauty of colour. Some forms are truly cosmopolitan, e.g., *Vanessa cardui*. Fossil insects are found in increasing numbers of species, from the carboniferous formation to the tertiary period. The best preserved are those enclosed in amber and the impressions in the lithographic slate.

Order 1.—THYSANURA*
(including COLLEMBOLA).

Wingless insects, with hairy or scaly body covering; with rudimentary masticating mouth parts and setiform anal filaments, which may serve as a springing apparatus, at the end of the ten-segmented abdomen. Development without metamorphosis.

The *Thysanura* seem to have preserved most completely the primitive character of the oldest insect forms. The elongated *Campodidæ* particularly recall certain Myriapods, especially since they may have rudimentary feet on the abdomen (fig. 459, a, b). On this account the *Campodidæ* have been regarded as ancestral

FIG. 459.—a, *Campodea staphylinus* (after J. Lubbock). b, Anterior half of the body of *C. Fragilis* (after Palmén). Tr, Trachea; S, stigmata; P, legs; P', rudimentary abdominal feet; A, antennæ.

* John Lubbock, "Monograph of the Collembola and Thysanura." London, 1873.

forms of the insects. The head bears tolerably long setiform antennæ, and, as a rule, aggregated ocelli, in place of the faceted eyes. The mouth-parts consist of mandibles and maxillæ, which can be retracted into a sort of atrium. In this case an apparatus for attachment with gland is often present on the ventral side of the first abdominal segment. Tracheæ are completely absent in many *Collembola* (*Podura*), while in *Campodea* they present very simple relations. There are only three pairs of stigmata, and the trunks which spring from them do not anastomose. On

the penultimate abdominal segment there are often setiform filaments, which when forcibly bent ventralwards serve as a springing apparatus (springing fork fig. 460, a).

Fam. *Campodidæ* (fig. 459). The body is elongated, and the abdomen has ten segments and ends with two filaments. *Japyx gigas* Br., Cyprus. *J. solifugus* Hal., *Campodea staphylinus* Westw.

Fam. *Poduridæ*, spring-tails (fig. 460, a). The body is stout, globular, or elongated. The abdomen is usually reduced to a few segments, and has a ventral organ for attachment, and ends with a long, ventrally-bent fork, used in springing. *Smynturus signatus* Latr., *Podura aquatica* Deg.

Fam. : *Lepismidæ* (fig. 460, b). Body arched, elongated, and thickly covered with metallic shining scales. The abdomen has ten segments, and terminates with a long median seta and two weaker lateral setae. *Lepisma saccharina* L., *Machilis polypoda* L.

FIG. 460.—a, *Podura villosa*.
b, *Lepisma saccharina* (règne animal).

Order 2.—ORTHOPTERA.*

Insects with an incomplete metamorphosis, with two usually unequal pairs of wings.

Jaws adapted for biting.

The name of this order, which was borrowed from the wings, is by no means suitable for all the forms included, and a very great variety prevails, both in the external appearance and in the internal

* A. Serville, "Histoire naturelle des Insectes Orthoptères." Paris, 1839.
T. De Charpentier, "Orthoptera descripta et depicta." Leipzig, 1841.
L. H. Fischer, "Orthoptera Europæa." Leipzig, 1853.

organisation. The head usually bears long, multiarticulate antennæ, faceted eyes of considerable size, and also simple eyes. The oral apparatus is adapted for masticating and biting. On the under-lip (*labium*) the four lobes, and sometimes also their supports (*stipites*), remain separate from one another. The prothorax, the size of which is very variable, is always freely moveable, and separated from the mesothorax by an articulation. The form and structure of the wings is extraordinarily variable. The anterior wings frequently have the form of coriaceous wing covers, or, at any rate, are stronger and thicker than the larger posterior wings, which can be folded together. In other cases, both pairs of wings are similarly formed and have a net-like appearance, like those of the Neuroptera. The legs also vary in their form, the tarsus consisting rarely of two, usually of three, four or five joints.

The abdomen usually preserves the full number of segments, and ends with caudal appendages having the form of pincers, stylets, filaments or setæ; ten segments usually take part in its construction, the genital opening being on the ninth, and the anus on the tenth. On the abdomen of the female there is sometimes an ovipositor (*Saltatoria*). This springs from the penultimate and antepenultimate segment, and consists on either side of an upper and a lower valve, and an inner spinous rod lying on the upper valve and passing along a groove on the upper edge of the lower valve.

Many *Orthoptera* have a dilatation of the œsophagus which may be called a crop, and a gizzard; this is followed by the chylic ventricle, which often has some cæcal appendages at its anterior end. The salivary glands are often extraordinarily large, and are provided with a vesicular reservoir. The number of the Malpighian vessels is, with a few exceptions, very considerable. The ventral ganglionic cord presents three larger thoracic ganglia, and five, six, or seven smaller abdominal ganglia. Some *Orthoptera* possess tympanic auditory organs. The generative organs consist, as a rule, of numerous egg tubes and testicular sacs. Large glands open into their efferent ducts. A bursa copulatrix is absent.

All *Orthoptera* undergo an incomplete metamorphosis. The two sexes are distinguished, not only by the differences of the external copulatory organs and by the size of the abdomen, but sometimes by the size of the wings (*Periplaneta*), or by the absence of the wings in the female (*Heterogamia*, *Pneumora*); and in the jumping *Orthoptera* (*Saltatoria*) by the development of a voice organ on the body of

the male. The chirping sounds produced by this organ probably serve to call the female to the place, and to excite her to copulation. The female also, in rare cases, has the voice apparatus perfectly developed (*Ephippigera* among the *Locustidæ*). The eggs are laid under very various conditions—sometimes in the earth, sometimes on external objects in air in damp places, or in water. The embryonic development has been most accurately traced out in the *Libellulidæ*, in which an internal ventral plate is formed. The larvæ of the winged forms leave the egg without any trace of wings, and either agree with the sexual animal in mode of life and form of body, excepting in the number of joints on the antennæ and of the corneal facets, or differ from it considerably in these relations (*Ephemèridæ*, *Libellulidæ*) in that they live in quite another medium. Most of them, in the fully developed state, feed on fruits and leaves, and a few on animal substances.

FIG. 431.—*a*, *Forficula auricularia*. *b*, *Blatta orientalis* ♂ (règne animal).

Sub-order 1.—Orthoptera genuina.

Front wings small and hard, sometimes coriaceous for the protection of the hind wings and the back. The hind wings are membranous and broad, and can be folded together longitudinally. The maxillæ with

horny internal lobe toothed at the point and covered by the helmet-shaped membranous outer lobe (*galea*), with five-jointed palp. The appendages of the last abdominal segment are developed; the inferior stylets are sometimes wanting. The females often have an ovipositor. The larvæ always feed on solid substances and always live on land.

Tribe 1. Cursoria. With running legs.

Fam: *Forficulidæ*, Earwigs (*Dermatoptera*). Elongated body, with four unequal wings, of which the anterior are short horny wing-covers, which lie horizontally on the body and cover the thin membranous hind wings, which can be folded by means of joints (fig. 461, *a*). The abdomen has nine segments and ends with a pincer, the arms of which are strongly curved in the male. They feed on vegetable matters, especially on fruit, and conceal themselves by day in their haunts, from which they emerge at dusk. *Forficula auricularia* L., *Labidura gigantea* Fabr.

Fam. Blattidæ. The body flat, elongated oval, with a broad shield-like prothorax, long multiarticulate antennæ and powerful locomotory legs, with spiny tibiæ and five-jointed tarsi. The head is covered by the large prothoracic shield and is as a rule without ocelli. External lobe twice as large as the internal. The front wings are large wing-covers which overlap one another, but these, together with the hind wings, may be absent in the female (*Heterogamia*) or in both sexes. They live on solid animal matter and avoid the light in the day, living in dark hiding-places. Many species are distributed over all the world, and in great numbers cause much damage in bakeries and storehouses. The tropical forms are especially large. The females lay their eggs in cases a short time before the hatching of the young. These capsules in *Periplaneta orientalis* enclose about forty eggs, arranged in two rows. In this animal the metamorphosis is said to last four years. *Periplaneta orientalis* L., common cockroach, said to have been introduced into Europe from the East (fig. 461, b). *P. americana* Fabr., *Blatta laponica* L., *B. germanica* Fabr.

Tribe 2. Gressoria. With ambulatory legs.

Fam. Mantidæ (Fangheuschrecken). Anterior predatory legs, the jagged tibiæ of which can be folded against the toothed femora. They prey on other insects, and inhabit warm and hot countries; only the smaller species extend

FIG. 462.—*Gryllotalpa vulgaris* (règne animal).

to South Europe. The females lay their eggs in clumps on plants, and surround them with a tough secretion, which hardens so as to form a capsule. This secretion is produced by the filiform appendages of the oviduct. *Mantis religiosa* L., praying insect, in South Europe.

Fam. Phasmidæ (Gespenstheuschrecken). The body elongated, as a rule linea, with long ambulatory legs. The tarsi have five joints, and bear a large lobe for attachment between the terminal claws. Wing-covers and wings are often rudimentary or altogether wanting. The anal processes are not jointed. They live in the tropics and feed on leaves. The wingless forms resemble dried twigs, the winged dried leaves. *Bacteria calamus* Fabr., Surinam. *Phasma fasciatum* Gray, Brasil. *Phyllium siccifolium* L., East Indies.

Tribe 3. Saltatoria. With jumping legs.

Fam. Acridiidæ (Grasshoppers). With short filiform antennæ. The anterior wings are stiff and only a little broader than the anterior division of the hind wings, which during quiescence are folded up like a fan and completely covered by the front wings. The auditory organs lie on either side on the metathorax. The female has no projecting ovipositor, but has an upper and lower genital valve, each composed of two horny stylets. The males can produce a chirping sound by rubbing the toothed internal edge of the posterior femora against the projecting nervures of the wing-covers. In the female, also, this stridulating apparatus is present, though in a rudimentary form, and not more developed than in the male larvæ. The females of many species are able

to produce weak chirping sounds. They live principally in fields, meadows and mountains, the larvæ being present in spring and summer, and the sexual animals in late summer and in autumn. They fly with a rattling sound, and as a rule, only for short distances. They feed on plants. *Tettix subulata* L., *T. bipunctata* Charp., *Ædipoda migratoria* L., South and East Europe. Enormous swarms migrate together, and distribute themselves in corn-fields, causing much damage. *Acridium tataricum* L., South Europe.

Fam. **Locustidæ** (Laubheuschrecken). The body is elongated and usually coloured grass green or brown. The antennæ are very slender, and the wing covers usually lie vertically on the body. The auditory organs are in the tibia of the front legs. The females have a projecting sabre-shaped ovipositor, which consists of a right and left double valve on the eighth and ninth segments; between the valves there is, on either side, a style which arises on the ninth segment. The eggs are deposited in the earth in late summer or in autumn, and there pass the winter. The larvæ are hatched in the spring, and after

many months develop into the winged sexual animal late in the summer. The *Locustidæ* live in forests and bushes, or in fields on the tops of grass stalks and shrubs. *Locusta viridissima* L., *L. cantans* Charp., Switzerland. *Ephippigera perforata* Ross., Italy and South Germany.

Fam. **Gryllidæ** (Grabheuschrecken). Of thick cylindrical body form, with thick free head. Antennæ usually long and setiform; wing covers (anterior wings) short, placed horizontally, and the hind wings, when rolled up, project far beyond them. The anterior legs are sometimes digging feet.

FIG. 463.—*Gryllus campestris* ♂ (règne animal).

The male gives rise to shrill chirping sounds by rubbing his two wing-covers, which present the same structure, against each other, and these sounds probably attract the female. During copulation the male attaches to the female genital opening a spermatophore, which, as in the *Crustacea*, is carried about till it is empty. The females have a straight cylindrical ovipositor, which is spindle-shaped at the end; more rarely they are without an ovipositor. The *Gryllidæ* mostly live beneath the earth in holes and passages, and feed on roots and animal matters. The larvæ are hatched in summer and pass the winter in the earth. *Gryllotalpa vulgaris* Latr., mole cricket (fig. 462). In gardens and fields; very harmful. They lay two hundred to three hundred eggs, which they place, enclosed in a mass of plastered earth, at the end of their subterranean passages. *Gryllus campestris* L., field-cricket (fig. 463). *G. domesticus* L., house-cricket. *G. sylvestris*. Fabr.

Sub-order 2.—Orthoptera Pseudo-Neuroptera.

The wings thin and membranous, both pairs being similarly

constructed. They usually cannot be folded together, and possess a network of nervures more or less close.

Tribe 1. **Physopoda**. The body small, narrow and flat, with tolerably similar wings, covered with delicate hairs. The mandibles are setiform, and the mouth parts are suctorial.

Fam. *Thripsidæ*, *Thrips physapus* L., found in the flowers of chickory.

Tribe 2. **Corrodentia**. Wings with few nervures, and sometimes quite without transverse nervures. The head has strong mandibles with toothed internal edges. The first maxillæ with hooked masticatory portion, the point of which is furnished with two teeth, and with membranous external lobe. The *Corrodentia* feed on dried vegetable and animal substances.

Fam. **Psocidæ**, booklice. *Troctes pulsatorius* L., found in collections of insects and between papers. *Psocus domesticus* Burm., *Ps. strigosus* Curt.

Fam. **Termitidæ**,* white ants. The antennæ have from eighteen to twenty joints, with two ocelli in front of the eyes and strong mandibles. The delicate wings, which are of equal size, lie in rest parallel to the body.

The Termites (fig. 464) live together in communities, composed of individuals of different kinds. The winged forms are the sexual individuals; the apterous

FIG. 464.—a, Male of *Termes lucifugus* (règne animal).

forms are partly the larvæ and pupæ of the sexual forms, and partly fully developed (in species of *Calotermes* and *Termes lucifugus*) sexually aborted males and females (neuters). The latter are divided again into soldiers, which look after the protection of the community and are provided with large quadrangular head and very strong mandibles, and workers with small rounded heads and less projecting mandibles. These individuals undertake the other work of the community. In species of *Eutermes*, every trace of sexual organs may be wanting in the neuters. Some species live in South Europe, but the greater number are found in the hot parts of Africa and America, where they are notorious for their ravages and their nests. The Termites make their dwellings either in the trunks of trees, often only beneath the bark, or on the surface of the earth in the form of hills, in which they excavate passages and cavities. The nests of species of *Calotermes* are the most incomplete; they only gnaw passages in wood, which mainly run in the

* H. Hagen, "Monographie der Termiten." *Lin. Entomol.*, Tom. X. and XIV.

Ch. Lespès, "Recherches sur l'organisation et les mœurs du Termite lucifuge." *Ann. des Sc. Nat.* IV. sér., Tom. V., 1856.

Fr. Müller, "Beiträge zur Kenntniss der Termiten." *Jen. nat. Zeitschr.* Tom. VII., 1873.

direction of the axis of the tree. There is no special place for the queen. The walls of the passages are usually coated with a thin layer of excrement. In species of *Eutermes*, in which the soldiers have pointed heads, the passages are so close to one another that the wood partition between them disappears, and the wall of excrement alone separates them. When the nests project outside

FIG. 464.—*a*, Pregnant female (queen) of *Termes lucifugus*. *b*, Pupa. *c*, Pupa of the second form. *d*, Soldier. *e*, Worker. *f*, Larva. (After Ch. Lespès).

the tree, they form the so-called spherical tree-nests. There are also nests which are attached to trees from outside, and are built of earth or clay. Other species of *Eutermes* make their nests in holes in the earth beneath the roots of Palms. Some, as *Anoplotermes pacificus*, build hills of earth. In this species, soldiers are absent: the males and females leave the community shortly after

they have cast their pupal skin, probably copulate after they return from their flight to the nest, and then lose their wings, retaining only the basal stump.

The males remain behind in the community, as according to the works of Smeathman, Lespès, Bates, etc., a king is said to remain always in the company of the queen. After copulation the queen, which remains in the community, swells up to an enormous size on account of the enlargement of her ovary, and begins to lay the eggs frequently in special places in the nest. They are at once carried away by the workers. *Termes lucifugus* Ross., South Europe. *T. fatale* L., in tropical Africa, builds hills from 10 to 12 feet high. *Calotermes flavicollis* Fabr., South Europe.

Tribe 3: Amphibiotica. The larvæ live in water and possess tracheal gills.

Fam. Perlidæ. Body elongated and flat, with laterally placed eyes, three ocelli and setiform antennæ. The wings are unequal, and the posterior region of the broad hind wings can be folded downwards. The abdomen has ten segments and two long segmented filaments. The wings are often reduced in the males. The female carries the eggs for a time in a depression of the ninth abdominal segment, and finally deposits them in water. The larvæ live beneath stones. They usually have tracheal gills on the thorax, and feed principally on the larvæ of *Epheméridæ*. *Nemura nebulosa* L., *Perla bicaudata* L., *P. (Pteronarcys) reticulata* Burm., with tufted gills. Found in Siberia.

Fam. Ephemeridæ. May flies. Body slender, and soft-skinned, with hemispherical eyes, three ocelli and short setiform antennæ. The front wings are large, the posterior small and rounded, sometimes fused with the anterior or altogether absent. The mouth parts are rudimentary. The males have very long front legs. The abdomen has ten segments and terminates with three long anal filaments, of which the median one may be absent. The penultimate abdominal segment of the male has two jointed copulatory forceps. The May flies live only a short time in the winged stage, taking no nourishment and devoting themselves entirely to the business of reproduction. We often find swarms of them in the air on warm summer evenings and the next morning see their dead bodies lying in quantities on the ground. The larvæ live at the bottom of clear water and feed on other insects. They have a large head with powerful mandibles and toothed maxillæ. On the abdomen they bear six to seven pairs of swinging plates, which function as tracheal gills, and at the end of the abdomen they have three long feather-like caudal setæ. The larvæ moult frequently (in *Chloëon* more than twenty times) and, according to Swammerdam, require three years for the passage into the winged insect. After the ecdysis of the pupal skin, which is provided with the rudiments of wings, the

FIG. 465.—*Ephemera vulgata* (règne animal); Af, Anal filaments.

winged insect, which is now in the subimago stage, undergoes another ecdysis and becomes an imago. *Ephemera vulgata* L. (fig. 465). *Palingenia longicauda* Oliv.

Fam. *Libellulidæ*. Dragon flies. Large slenderly-built insects with freely moveable, transversely cylindrical head, short six- to seven-jointed thin and pointed antennæ, and four large net-like latticed wings. The mouth parts are powerfully developed, and are covered by the large upper lip. The maxillæ have fused horny lobe, and single-jointed sickle-shaped palp. The labium has a simple or divided internal lobe and separate outer lobes fused with the bi-jointed palp. The abdomen has ten joints, and on the last segment two unjointed anal styles opposed to one another, so as to form a sort of forceps. They live near water, and feed on other insects. The two sexes are usually of different colours, and their flight is rapid and prolonged. During copulation the male clasps the prothorax of the female with his abdominal forceps, while she bends her abdomen towards the base of his abdomen. Here is placed the copulatory organ, which is remote from the genital opening, and is filled with sperm prior to copulation. The larvæ live in water and are predaceous. The lower lip is modified to form a special predatory apparatus (the mask) (fig. 456). Many of them breathe by means of tracheal gills, which are placed at the end of the abdomen or in the rectum. *Calopteryx virgo* L., *Agrion puella* L., *Æschna grandis* L., *Libellula vulgata*, *flavescens* L.

FIG. 466.—*Panorpa communis* (règne animal).

Order 3.—Neuroptera.*

Insects with biting (sometimes also suctorial) mouth parts, with free prothorax and membranous wings, the nervures of which form a net-work. The metamorphosis is complete.

Most *Neuroptera* have an outward resemblance to the *Libellulidæ* and *Ephemeridæ*, while others resemble the *Lepidoptera* in their scaly wings. The two pairs of wings are usually similar and membranous, and their size is almost equal. They are traversed by a close network of nervures which, however, differs essentially from the nervation of the *Neuroptera*-like *Orthoptera*. The front wings never have the form of wing-covers, but the hind-wings can sometimes be folded together and sometimes not. They may be covered with scales and hairs (*Phryganidæ*). The mouth parts present a greater approximation to the Beetles, in that the labium only rarely shows any trace of a median slit, the two pairs of lobes being fused to a single plate. In one group (*Phryganidæ*) we find suctorial mouth parts. The mandibles in this case are aborted, and the labium and maxillæ fuse to form a tube. As a rule the antennæ are many-

* E. Pictet, "Histoire naturelle des Neuroptères." Genf 1834.

† E. Brauer und Fr. Löw, "Neuroptera Austriaca." Wien, 1857

Brauer, "Beiträge zur Kenntniss der Verwandlung der Neuropteren. *Verhand. der zool.-bot. Gesellschaft zu Wien*, Tom IV. und V.

jointed, filiform or setiform, the eyes of medium size, and the tarsuses five-jointed. The prothorax is always freely moveable, and the abdomen is composed of eight or nine segments. The nervous system is similar to that of the Orthoptera, and consists of clearly distinct thoracic and abdominal ganglia. There is always a muscular gizzard on the digestive canal (*Myrmeleontidæ*, *Panorpidæ*). A sucking stomach is found only in the *Hemerobidæ*. Six to eight long Malpighian tubes arise from the hindgut. The metamorphosis is always complete. The larvæ prey on other animals, and are provided with biting or sucking forceps (formed from the mandibles and maxillæ). They pass into a quiescent pupal stage, in which the parts of the winged insect can already be made out. The pupa is often surrounded with a cocoon, but possesses the power of locomotion to a certain degree, since before the animal passes out of the pupal stage it ceases to be quiescent and seeks out a place suitable for development. Fossil remains are found in tertiary formations and in amber.

Sub-order 1. **Planipennia.** Front and hind wings similar, never capable of being folded. The mouth parts are powerful and adapted for mastication.

Fam. **Sialidæ.** With large head bent obliquely forwards, and projecting hemispherical faceted eyes. The wings, when at rest, overlap one another like the slates on a roof. The larvæ have biting mouth-parts, with four-jointed maxillary palps and three-jointed labial palps. *Sialis lutaria* L., *Corydalis cornuta* L., *Raphidia ophiopsis* Schum. camel-neck flies.

Fam. **Panorpidæ** (Schnabelfliegen). The head is small and placed vertically; the multiarticulate antennæ are placed in the frontal region beneath the ocelli. The oral region is prolonged in the form of a beak. The wings are long and narrow, and similar to each other. The larvæ are like caterpillars. They have thirteen segments and a heart-shaped head, and biting mouth-parts. They live in damp earth, where they dig horseshoe-shaped passages, and are transformed into pupæ in oval cavities. *Panorpa communis* L. (fig. 466). *Bittacus pularius* Fabr.

FIG. 467.—*a*, Larva of *Mantispa styriaca* after hatching. *b*, The same before the pupal stage (after F. Brauer). *c*, *Mantispa pagana* (règne animal).

Fam. **Hemerobidæ** (Florfliegen). Head vertical; antennæ filiform. The two pairs of wings are transparent like glass and are nearly equal in size. The larvæ suck insects and spiders. *Mantispa pagana* Fabr. Anterior legs predatory; prothorax much elongated (fig. 467, *a*, *b*, *c*). The larvæ, after eight months' fasting, bore their way by means of their sucking forceps into the ovisacs of spiders, and suck out the eggs and the young. After the first moult, the legs are reduced to short stumps, and the body becomes like a Hymenopteran maggot. When about to enter the pupal stage, they spin a cocoon in the ovisac, and strip off the larval skin in the middle of June. The pupa breaks through the cocoon and moves freely about till it casts its skin and is transformed into the winged insect. *Chrysopa perla* L. The eggs have long stalks. The larvæ have sickle-shaped suctorial forceps, feed on Aphides and spin globular cocoons. *Hemerobius lutescens* Fabr. The larvæ feed on Aphides. *Osmylus maculatus* Fabr., *Nemoptera* (*Nematoptera* Burm.) *coa* L., Asia Minor and Turkey.

Fam. **Myrmeleontidæ** (Ant-lions). With large vertically-placed head; antennæ knobbed at the ends; prothorax short and narrow; mesothorax very large. Wings of equal size. The larvæ with toothed sucking pincers composed of mandibles and maxillæ, and short broad abdomen, live in light

FIG. 468.—*a*, *Myrmeleon formicarius* (règne animal). *b*, Its larva.

sandy soil, in which they hollow out funnels. Before entering the pupal stage they spin a globular envelope for themselves (fig. 468). *Myrmeleon formicarius* L., *M. formicalynx* Fabr., *Palpares libelluloides* L., South Europe. *Ascalaphus italicus* Fabr.

Sub-order 2. **Trichoptera**.^{*}—Wings covered with hairs or scales; the hind wings can as a rule be folded. The mouth parts with aborted mandibles; the maxillæ and the labium fuse to form a kind of suctorial proboscis. In many cases (*Oestropsidæ* Brauer) the maxillæ and labium as well as the mandibles become aborted during the pupal stage.

Fam. **Phryganidæ** (spring-flies). The small vertically-placed head with long setiform antennæ and hemispherical projecting eyes. The wings are covered with scales, and have but few transverse veins. They lie on the back in a tectiform manner. The larvæ live in water in tubular cases, which, in

^{*} J. Pietet, "Recherches pour servir à l'histoire et l'anatomie des Phryganides," Genève, 1834.

H. Hagen, "Synopsis of the British Phryganidæ," *Entomol. Annual* for 1859, 1860, 1861.

Hydropsyche and *Rhyacophila*, are fastened to stones. In the walls of these cases there are sand grains, bits of plants and empty snail shells. The larvæ have biting mouth parts and filiform tracheal gills on the body segments. They project their horny head and thoracic segments, with their three pairs of legs, from these tubes and crawl about. The pupa leaves the case, which serves also as a pupal skin, and develops into the winged insect out of the water. The perfect insect resembles the *Lepidoptera* in many respects, and lives near water on leaves, and the stems of trees. The female lays her eggs in clumps enclosed in a gelatinous case on stones and leaves near water. *Phryganea striata* L. (fig. 469). *Mystacides quadrifasciatus* Fabr., *Hydropsyche variabilis* Pict.

Order 4.—Strepsiptera.*

Insects with rudimentary anterior wings rolled up at the points and large hind wings which can be folded longitudinally. The mouth parts are rudimentary. In the female there are neither wings nor legs. The larvæ are parasitic in the body of Hymenoptera.

The mouth parts are reduced in the adult sexual animal, and

FIG. 469.—a, *Phryganea striata*. b, The larva freed from its case (règne animal).

consist of two pointed mandibles which overlap one another, and small maxillæ, which are fused with the lower lip and are provided with two-jointed palps. The prothorax and mesothorax are two very short rings, but the metathorax is unusually elongated, and covers the base of the abdomen, which consists of nine segments. The males possess small rolled-up wing covers, and very large hind wings, which can be folded longitudinally like a fan. The females have no eyes, and remain through life without wings or legs like maggots; they never leave their pupal skin nor their parasitic

* W. Kirby, "Strepsiptera, a new order of Insects," *Transact. Linn. Soc.*, Tom X.

v. Siebold, "Ueber Xenos sphecidarum und dessen Schmarotzer," *Beiträge zur Naturgeschichte der wirbellosen Thiere*, 1839.

ruv. Siebold, "Ueber Strepsiptera," *Archiv für Naturgesch.*, Tom IX., 1843.

Ctis, "British Entomology," London, 1849.

habitat in the abdomen of wasps and humble bees (*Bombyliidæ*) from which they only protrude the anterior part of their body. In copulation the males are said to open by means of their copulatory organ the dorsal tube of the female, which is at first closed. The ovaries have no oviduct, and continue as it seems at an earlier stage of development, since they—probably like those of the viviparous *Cecidomyia* larvæ—produce eggs. The eggs fall freely into the body cavity, are fertilized and develop (perhaps sometimes parthenogenetically) into larvæ, which pass out through the above-mentioned dorsal canal and become attached to larvæ of bees and wasps (fig. 470). In this larval state they are able to move about and possess, like the young larvæ of *Cantheridæ*, three well-developed pairs of legs, and two caudal setæ on the abdomen. They bore their way into the

body of their new host. About eight days later they undergo an ecdysis, and change to an apodal cylindrical maggot, which becomes a pupa within the Hymenopteran pupa, and as such bores its way out with its head from the abdomen of the latter. The males leave the pupal skin and seek the females. They seem to live only a short time.

FIG. 470.—*Stylops Childreni* (after Kirby). *a*, Larva. *b*, Female. *c*, Male.

Fam. *Stylopidae*. *Xenos Rossii* Kirb. (*X. vesparum* Ross.) parasitic in *Polistes gallica*. *Stylops melittæ* Kirb.

Order 5.—Rhynchota* = Hemiptera.

Insects with jointed rostrum, piercing (exceptionally biting) mouth parts. With usually free prothorax and incomplete metamorphosis.

The mouth parts are almost without exception arranged for taking up fluid nourishment, and are usually represented by a rostrum, in which the mandibles and maxillæ, as four rigid styles, are moved backwards and forwards. The rostrum, which is formed

* Burmeister, "Handbuch der Entomologie." II. Bd., Berlin 1835.

J. Hahn, "Die wanzenartigen Insecten." Nürnberg, 1831-1849. Continued by H. Schäffer.

F. X. Fieber, "Die europäischen Hemipteren nach der analytischen Methode." Wien, 1860.

by the labium, is a three- or four-jointed almost closed tube, which is narrowed towards the point, and is covered at the larger open base by the elongated three-cornered upper lip. The antennæ are either short and three-jointed with a setiform terminal joint, or are many-jointed and often elongated. The eyes are small and usually faceted, but they are sometimes ocelli with a simple cornea. Frequently two ocelli are found between the faceted eyes. The prothorax is usually large and freely moveable, but all the thoracic segments may be fused together. Wings are sometimes quite absent; usually four, rarely two, are present. In the first case the front wings are horny at the base and membranous at the tip (*Hemiptera*), or the front and hind wings are similarly formed and are membranous (*Homoptera*), though the anterior are often stiffer and coriaceous. The legs are, as a rule, adapted for walking, but sometimes they serve for clinging or swimming. In other cases the front legs are used to capture prey, or the posterior for springing. The alimentary canal is distinguished by the numerous salivary glands, and by the complicated chylic ventricle, which is often divided into three regions; behind the chylic ventricle usually four Malpighian tubes open into the hindgut. The ventral cord is concentrated into three, usually into two thoracic ganglia. With exception of the *Cicada*, the female genital organs have only four to eight egg-tubes, a simple receptaculum seminis and no bursa copulatrix. The testes are composed of two or more tubes, the ducts of which are usually dilated at the lower end. Many (*bugs*) emit an offensive smell, which proceeds from the secretion of a gland placed in the mesothorax or metathorax, in the latter case opening between the hind limbs. Others (*Homoptera*) secrete by means of numerous cutaneous glands a white waxy film which covers the surface of their body. They all live on vegetable or animal juices, to which they obtain access by means of the piercing styles of their rostrum. Many of them, by their appearance in great numbers on young plants, are harmful, and sometimes cause gall-like outgrowths; others are parasitic on animals. The young, when hatched, possess the form and habits of the sexually mature animal. They have, however, no wings, which make their appearance as small stumps after one of the first moults. The true *Cicada* need several years to effect their metamorphosis. The male *Coccidæ* change inside a cocoon to quiescent pupæ, and undergo accordingly a complete metamorphosis.

Sub-order 1. **Aptera=Parasitica.** Wingless *Rhynchota*, with short fleshy rostrum and broad cutting styles. Sometimes they have

rudimentary biting mouth parts, an indistinctly segmented thorax, and an abdomen which usually consists of nine segments.

Fam. **Pediculidæ**. Lice. With fleshy proboscis-sheath armed with recurved hooks, protrusible suctorial tube, and two protrusible knife-like stylets. The antennæ have five joints. The feet, which are adapted for clinging, have hooked terminal joints. The eyes are small and not faceted. The animals live on the skin of Mammalia, and suck their blood, and lay their pear-shaped eggs in the roots of the hair. The young, when hatched, do not undergo a metamorphosis, and the louse which infects the human head, is fully developed and capable of reproduction in eighteen days. *Pediculus capitis* Deg. Head-louse of man. *P. vestimenti* Burm. (larger and of pale colour). *Phthirius pubis* L. (fig. 471).

Fam. **Mallophaga (Anoplura)** (Pelzfresser). Lice-like in form, with three- to five-jointed antennæ, and biting mouth parts, no fleshy proboscis, but a sort of suctorial tube. They live on the skin of Mammalia and Birds, and feed on young hairs and feathers, but also on blood. *Trichodectes canis* Deg. *Philopterus versicolor* Burm., *Liotheum anseris* Sulz. *Menopon* Nitsch, *M. pallidum* Nitsch, on fowls.

FIG. 471.—*Phthirius pubis* (after Landois) St, Stigma; Tr, Trachea.

Sub-order 2. **Phytophthires**. * *Rhynchota* with two pairs of membranous wings. The female is usually apterous. The surface of the skin is very often covered with a dense waxy deposit, the product of cutaneous glands which

are placed in groups beneath warty prominences of the segments.

Fam. **Coccidæ** (Schildläuse). The large females have a shield-shaped body, and are wingless. The males are much smaller, and have large front wings, and sometimes also rudimentary hind wings. The fully-developed males have no proboscis or piercing weapons, and do not take in nourishment, while the unwieldy, often unsymmetrical females, which may even have lost the segmentation, insert their long rostrum into the parenchyma of plants and remain motionless. The eggs are deposited beneath the shield-shaped body

* C. Bonnet, "Traité d'Insectologie," Tom. I., Paris 1745.

J. F. Kyber, "Erfahrungen und Bemerkungen über die Blattläuse." *Germar's Magaz. der Entomol.* Tom. I., 1815.

J. H. Kaltenbach, "Monographie der Familie der Pflanzenläuse." Aachen, 1843.

R. Leuckart, "Die Fortpflanzung der Rindenläuse." *Archiv für Naturgesch.*, 1859.

and develop, protected by the drying-up body of the mother. They are generally fertilized (*Coccus*), but sometimes develop parthenogenetically (*Lecanium*, *Aspidiotus*). Unlike the female (and forming a single exception to what otherwise obtains in the order), the males undergo a complete metamorphosis; the apterous larvæ surround themselves with a cocoon, and are transformed into quiescent pupæ. Many *Coccidæ* cause great damage in conservatories. Others are useful in industry, in that they produce a colouring matter (cochineal), while others are useful in causing, by their puncture, an outflow of vegetable juices which when dried, are used by man (*lac*, *manna*). *Aspidiotus nerii*. Bouché, found on the Oleander, *Lecanium hesperidum* L., *L. persicæ* Bouché. *Kermes ilicis* L., on *Quercus coccifera*, also *K*, ? (*Coccus*) *lacca* Kerr., on *Ficus religiosa* in the East Indies. *Coccus cacti* L., (fig. 472) lives on *Opuntia coccinellifera*, Mexico, gives cochineal. *C. adonidum* L., *C. (?) manniparus* Ehbgs., on *Tamarix* (manna).

Fam. **Aphidæ**,* plant-lice. As a rule, there are four transparent wings, with a scanty venation. The wings may, however, be absent in the female, and rarely in the male. The *Aphidæ* live on vegetable juices, and are found on roots, leaves and buds of quite definite plants. They frequently live in the spaces of gall-like swellings or deformities of leaves, which are produced by the punctures of the plant-lice. Many of them possess, on the dorsal surface of the antepenultimate segment, two "honey tubes," from which is secreted a sweet fluid—the honeydew—which is eagerly sought for by ants. In addition to the usually apterous females, which, as a rule, only appear in autumn with the winged males and lay fertilized eggs after copulation, there are also viviparous, usually winged generations, which appear principally in the spring and in summer, and which produce their living brood without the assistance of males. Bonnet observed nine generations of viviparous aphides succeed one another. They are distinguished from the true oviparous females, not only by their form and colour, and, in many cases, by the possession of wings, but also by essential peculiarities in the generative apparatus and the eggs (*pseudova*, germs). The receptaculum seminis is absent, and the eggs undergo their embryonic development in the very long egg-tubes. Viviparous and oviparous aphides usually succeed one another in regular alternation, since the females lay fertilized eggs in the autumn, which survive the winter and in the spring give birth to viviparous aphides, the descendants of which are also viviparous, and produce viviparous forms through a number of generations. It is only in the autumn that the males and the oviparous females are born which copulate. Viviparous individuals of many forms seem to pass the winter in ant-hills. Sexual forms (at time of birth already mature, wingless and without proboscis) are sometimes found in the spring; they are in all probability produced by such viviparous forms which have persisted through the winter. This has been shown to be the case for

FIG. 472.—*Coccus cacti*. *a*, Female. *b*, Male (after Burmeister).

* Derbès, "Notes sur les Aphides du pistachier térébinthe." *Ann. des Sc. Nat.* 1872.

Pemphigus terebinthi by Derbès. Here the sexual animals are succeeded by apterous asexual animals, which produce the galls, and the descendants of which are the winged asexual generations which are dispersed and pass through the winter. The reproduction of *Chermes* and *Phylloxera* is different, in that in place of the viviparous generations there is a special oviparous sexual form, which also produces eggs capable of developing parthenogenetically. The apterous females of the fir-tree lice pass the winter at the base of the young buds, increase in size in spring in the same place, undergo several moults, and lay a number of eggs. The young, when hatched, pierce the swollen pointed leaves of the young shoots and produce galls. They develop later into winged females. In *Phylloxera quercus*, besides the two generations, there is another generation, which appears in autumn and consists of very small movable males and females (without suctorial proboscis or alimentary canal). These animals arise from two kinds of eggs which are laid on the roots. The female, after copulation, lays only a single egg. It is the same with the famous vine-lice (*Ph. vastatrix*), the larvæ of which pass the winter on the roots of the vine

(fig. 473). The principal enemies of the Aphides are the larvæ of the *Ichneumonidæ* (*Aphidius*), *Syrphidæ*, *Coccinellæ* and *Hemero-bidæ*.

a. Leaf-lice, s.st. *Schizoneura lanigera* Hartg., on apple trees. *Lachnus pini* L., *L. juglandis* L., *L. fagi* L., *Aphis brassicæ* L., *A. rosæ* L.

b. Bark-lice. *Chermes abietis* L., *Ch. laricis* Hartg., *Phylloxera quercus* v. Heyd., on oak leaves. *Ph. vastatrix*, vine-lice, with winged and apterous generations.

Fam. *Psyllidæ* (*Psyllodes*), leaf-fleas. Antennæ long, with ten joints. In the fully-developed stage always winged. The hind

FIG. 473.—*Phylloxera vastatrix*. a, Wingless root-louse seen from the back, b, from the ventral surface. c. Winged form.

legs serve for springing. Their puncture often occasions deformities of flowers and leaves. *Psylla alni* L., *Livia juncorum* Latr.

Sub-order 3. Homoptera-Cicadaria. Both pairs of wings are, as a rule, membranous. Sometimes the front pair is coriaceous, not transparent and coloured. They lie, when at rest, obliquely on the body. The head is relatively large, and often prolonged into processes. The rostrum always arises low down, and apparently between the front legs; it has three joints. In many species the hind legs are springing legs, with which the animal jumps before flight. The females have an ovipositor, and often lay the eggs beneath the bark and in the twigs of plants. The larvæ of larger species may live several years (fig. 474).

Fam. **Cicadellidæ** (Kleinzirpen). *Jassus biguttatus* Fabr., *Ledra aurita* L., *Tettigonia vittata* L. *Aphrophora*. The prothorax is trapezoidal (seven-cornered). The larvæ eject a bubbly foam out of the anus (cuckoo-spittle), and envelop themselves in it. The wing covers are coriaceous. Posterior tibiæ have three strong spines. *A. spumaria* L.

Fam. **Membracidæ** (Buckelzirpen). *Centrotus cornutus* L., *Membracis lateralis* Fabr.

Fam. **Fulgoridæ** (Leuchtzirpen). In many species the abdomen is thickly covered with long strings and flakes of wax, which in one species (*Flata limbata*) is so richly secreted that it is collected and sold as Chinese wax.

Fulgora laternaria L., the lantern carrier of Surinam, is erroneously said by Merian to emit light from its lantern-shaped frontal process. *F. candelaria* L., Chinese lantern-carrier. *Lystra lanata* L., and other American species. *Flata limbata* Fabr., China.

Fam. **Cicadidæ** = **Stridulantia** (Singeicaden). The thick abdomen of the male is provided with a voice organ, which produces loud, shrill, chirping sounds (fig. 474). They are very shy, and remain concealed between leaves in the day time. They

feed on the juices of young shoots, and their puncture causes a flow of sweet plant juices, which harden and become manna (*Cicada orni* L., Sicily). The females have a saw-like ovipositor placed between two jointed valves. The larvæ, when hatched, crawl on the earth, into which they burrow with their shovel-like front legs, and suck the juice of roots.

FIG. 474.—*Cicada orni* (after Packard). *a*, Larva. *b*, Pupa. *c*, Male, *Ty*, Stridulating apparatus.

Cicada orni L., South Europe. *C. septemdecim* Fabr., Brazil. *C. hamatodes* L., South Germany.

Sub-order 4. Hemiptera (Bugs). The wings of the front pair are half horny and half membranous (*hemelytra*), and lie horizontally on the body. Many species are apterous, as are the females of some species of which the males have wings. The first thoracic segment is large, and freely moveable. The proboscis arises from the frontal region, and when at rest usually lies folded beneath the thorax. Some species of the *Reduviidæ* produce a shrill sound, as *Pirates stridulus*, by the movement of the neck on the prothorax.

Tribe 1. Hydrocores = **Hydrocorisæ** (Water-bugs). The antennæ are shorter than the head, having only three or four joints, and are

more or less hidden from view. The rostrum is short. They feed on animal juices.

Fam. **Notonectidæ** (Rückenschwimmer). *Corixa striata* L., *Notonecta glauca* L., water-bug.

Fam. **Nepidæ**, water-scorpions (fig. 475). *Naucoris cimicoides* L., *Nepa cinerea* L., water-scorpion. *Ranatra linearis* L.

Tribe 2. Geocores (Land-bugs). Antennæ directed forwards, and of medium length, having four or five joints. The rostrum is usually long.

Fam. **Hydrometridæ** (*Ploteres*) (Wasserläufer). *Hydrometra lacustris* L., *Limnobates stagnorum* L., *Velia rivulorum* Latr.

Fam. **Reduvidæ** (*Reduvini*) (Schreitwanzen). *Reduvius personatus* L., *Pirates stridulus* Fabr., South Europe.

Fam. **Acanthiadæ** (*Membranacei*), skin-bugs. *Acanthia lectularia* L., bed-bug. *Aradus depressus* Fabr. (*corticalis* L.).

Fam. **Capsidæ** (Blindwanzen), *Capsus trifasciatus* L., *Miris erraticus* L.

Fam. **Lygæidæ** (*Lygæodes*) (Langwanzen). *Lygæus equestris* L., *Pyrrhocoris apterus* L. (Feuerwanze).

Fam. **Coreidæ** (*Coreodes*) (Randwanzen). *Coreus marginatus* L., *Alydus calcaratus* L.

Fam. **Pentatomidæ** (Schildwanzen). *Pentatoma junipera* L., *P. rufipes* L., *P. oleracea*.

FIG. 475.—*Nepa cinerea*
(règne animal).

Order 6.—Diptera * (Antliata).

Insects with piercing and sucking mouth parts, with membranous front wings. The hind wings reduced to small knobs (halteres). The metamorphosis is complete.

The designation of this order, which is derived from the apparent number of the wings, does not correspond accurately to the actual state of matters. Two pairs of wings are present, the front pair always as large glassy and transparent plates, the hind pair in a rudimentary condition as stalked knobs (*halteres*). On the inner margin of the front wings two lobes are marked off by indentations; an outer lobe (*alula*), and an inner one (*squama*) which may cover

* J. W. Meigen, "Systematische Beschreibung der bekannten europäischen, zweiflügeligen Insecten," 7 Theile. Aachen, 1818-1838.

Wiedemann, "Aussereuropäische zweiflügelige Insecten," 2 Theile. Hamm. 1828-1830.

N. Wagner, "Ueber die viviparen Gallmückenlarven," *Zeitschr. für. wiss. Zool.*, Tom. XV., 1865.

A. Weissmann, "Die Entwicklung der Dipteren," Leipsig. 1864.

A. Weissmann, "Die Metamorphose der *Corethra plumicornis*," 1866.

the hind wings. The latter are composed of a spherical head at the end of a thin stalk. Leydig described at the base of the halteres a ganglion with nervous rods, which he concluded was an auditory apparatus. The head is freely moveable, and usually spherical in form. It is articulated to a short and narrow neck, and is distinguished by the large faceted eyes, which in the male sex may meet in the median line of the face and frontal region. There are as a rule three ocelli. The antennæ are constructed on two different types; they may either be very short and composed of three joints, frequently bearing a tactile hair at the extremity (*arista*), or they may be filiform and of considerable length and composed of a great number of joints. But since in the first case the terminal joint is again divided into a number of smaller joints, and the tactile hair may be also jointed, it is impossible to draw a sharp distinction between the two types. The mouth parts form the kind of suctorial tube known as a proboscis (*haustellum*), in which the jaws (mandibles and maxillæ) and an unpaired rod (*epipharynx*) attached to the upper lip may appear as horny, setiform or knife-shaped piercing organs. When the maxillæ only are present as paired rods, the unpaired piercing stylet seems to correspond to the fused mandibles. The proboscis, which is principally formed by the labium, ends with a swollen spongy tongue, and is without labial palps, while the maxillæ are provided with palps, which, in cases of fusion with the labium, are situated on the proboscis. The abdomen is frequently stalked, and consists of five to nine segments. The legs have five-jointed tarsuses, which end with claws and usually with sole-like lobes for attachment.

The nervous system presents very different degrees of concentration according to the length of the body. While in flies of very stout build, the ganglia of the abdomen and thorax fuse together to form a common thoracic ganglion; in the Diptera with longer bodies, not only are the three thoracic ganglia distinct, but several, even five or six, separate abdominal ganglia are present. With regard to the alimentary canal, the presence of a stalked suctorial stomach as an appendage of the œsophagus and the number—four—of the Malpighian tubes may be mentioned. The two tracheal trunks are dilated to two great vesicular sacs at the base of the abdomen. This is correlated with the power of active flight possessed by these insects.

The male genital organs consist of two oval testes with short vasa deferentia, to which are added firm copulatory appendages. The

ovaries are not connected with any special bursa copulatrix, but have three receptacula seminis in connection with the vagina (fig. 449), and often end with a retractile ovipositor.

There is rarely a striking difference between the two sexes. The males have as a rule larger eyes, which in some cases meet each other in the middle line; their abdomen also is frequently differently shaped to that of the female, and in exceptional cases the colouring is different (*Bibio*). The mouth-parts, too, may differ; for example, the male gad-flies (*Tabanidae*) are without the knife-shaped mandibles, which form the principal part of the female armature. The males of the *Culicidae* also are without the piercing weapons, and have multiarticulate hairy antennæ, while the antennæ of the female are filiform, and are composed of fewer joints.

The metamorphosis is complete, and the larvæ, which are usually apodal, have either a clearly separate head with antennæ and ocelli (most *Nemocera*), or a short, usually retracted, cephalic region, without antennæ or eyes (at most with an X-shaped pigment spot), with quite rudimentary mouth parts, sometimes with two oral hooks, serving for attachment.

In the first case the larvæ have masticating mouth-parts and feed on other animals; in the latter case they are known as maggots and suck up fluids or semi-liquid substances. After several moults the larvæ either change

FIG. 476.—*Melophagus ovinus*. *b*, *Hippobosca equina* (after Packard).

within the hardened larval skin to pupæ (*P. coarctata*), or casting the larval skin are transformed into moving pupæ (*P. oblecta*), which often swim freely in water, and may be provided with tracheal gills. The differences which the development of the winged insect from the larval organism presents in the two groups have been already mentioned (p. 550).

Many Diptera when flying give rise to buzzing sounds. This is caused by the vibrations of various parts of the body; partly of the wings and partly of the segments of the abdomen, with participation of the voice apparatus on the four stigmata of the thorax. Here, beneath the margins of the stigmata, the tracheal trunk forms a vesicle with two delicately folded leaflets, which

are set in vibration beneath two external valves by the expiration of air.

Sub-order 1. **Pupipara*** (fig. 476). Lice flies. The body is stout; the three thoracic segments are fused together, the abdomen is broad and often flattened. The antennæ are short, and often consist of but two joints. The suctorial proboscis is formed by the upper lip (labrum) and the maxillæ. The legs are provided with toothed clasping claws, and the wings may be rudimentary or absent. The development of the embryo and of the larva takes place in the uterus-like vagina. The maggot which issues from the egg (without pharyngeal framework or buccal hooks) swallows the secretion of large glandular appendages of the uterus (fig. 451); it undergoes several moults, and is completely developed when it is born, which occurs just before it enters the pupal stage. They are parasitic, like lice, on the skin of warm-blooded animals, rarely of insects.

Braula cæca, Nitzsch., Bee louse.
Nycteribia Latreillei Curt., without eyes and is parasitic on species of *Vespertilio*. *Melophagus ovinus* L., Sheeptick. *Anapera pallida* Meig., parasitic on Swallows. *Hippobosca equina* L., horse-louse.

Sub-order 2. **Brachycera** (Flies). Body of very various

shape, frequently thick and stout, with an abdomen com-

posed of from five to eight segments. Antennæ short, and usually composed of three joints with large, usually secondarily ringed terminal joint, to which is attached a simple or ringed bristle. Wings are almost always present. The larvæ live in decaying matter in earth and water, partly also as parasites; they are, in great part, maggots with hooked jaws, and pass into the pupal stage within the moulted cask-shaped larval skin (fig. 477). Many of them have the form of a pupa obtecta.

Tribe 1. **Muscaria**. With frontal vesicle; proboscis usually with fleshy terminal lobe; maxillæ as a rule aborted; larvæ without jaw

FIG. 477.—*Gastrophilus equi* (after F. Brauer).
 a, Larva. b, Male.

* L. Dufour. "Études anatomiques et physiologiques sur les Insectes Diptères de la famille des Pupipares." *Ann. des Sc. Nat.*, II. ser., Tom. III., 1843.

R. Leuckart, "Die Fortpflanzung und Entwicklung der Pupiparen." *Abhand. der naturf. Gesellschaft zu Halle*, Tom. IV.

capsule and as a rule with two or four oral hooks. The pupæ are always barrel-shaped.

Fam. **Phoridae**. *Phora incrassata* Meig. Live as larvæ in Bee hives.

Fam. **Acalyptera**. *Trypeta Cardui* L., *Tr. signata* Meig., in cherries. *Chlorops lineata* Fabr. (Weizenfliege), Larvæ in blades of grass. *Scatophaga stercoraria* L., dung-flies, on dung heaps. *Piophilæ casei* L., cheese-flies.

Fam. **Muscidae**. *Musca domestica* L., house-fly. *M. Cæsar* L. (Goldfliege). *M. vomitoria* L., the abdomen is of a shining blue colour. *M. cadaverina* L., (Aasfliege). *Sarcophaga carnaria* L. (Fleischfliege), viviparous. *Tachina puparum* Fabr., *T. (Chrysosoma) viridis* Fall., *T. grossa* L., *T. larvarum* L. The larvæ are parasitic, principally in caterpillars.

Fam. **Conopidae**. *Conops flavipes* L., the larvæ live in the abdomen of *Hymenoptera*. *C. rufipes* Fabr. (in *Ædipoda*).

Fam. **Stomoxyidae**. *Stomoxy calcitrans* L. (Stechfliege), resembles the house-fly.

Fam. **Æstridæ*** (Biesfliegen). The proboscis is aborted. The females have an ovipositor and lay their eggs or their living larvæ (in which case the ovipositor is absent) on certain places on Mammalia, e.g., in the nostrils of Stags, or on the breast of the Horse. The larvæ with dentated body rings, and frequently with oral hooks, live in the frontal sinuses, beneath the skin, and even in the stomach of certain Mammalia. Under the skin they produce boils. *Hypoderma bovis* L. *H. Actæon* Br., on the Stag. *H. tarandi* L. *Dermatobia hominis* Goudot, on Ruminants, *Felidæ* (Jaguar) and Men in South America. *Estrus auribarbis* Wied. The larvæ are brought by the flies into the nasal cavities of the Stag. *Gastrus (Gastrophilus) equi* Fabr. (fig. 477). The egg is deposited on the breast of the Horse, and licked off by the latter. The larva, when hatched, attaches itself to the walls of the stomach by its oral hooks, undergoes several moults, and is passed with the excrements before the pupal stage.

Fam. **Syrphidæ** (Schwebfliegen). *Syrphus pirastri* L., *Eristalis tenax* L., *E. æneus* Fabr. Larvæ with respiratory tube, in sewers and stagnant water.

Fam. **Platypezidæ** (Pilzfliegen). *Pl. boletina* Fall.

Tribe 2. Tanystomata. The proboscis is usually long and has styliform predatory jaws. Larvæ with jaw sheath and hooked jaws.

Fam. **Dolichopodidæ**. *Dolichopus pennatus* Meig. *D. nobilitatus* L.

Fam. **Empidæ** (Tanzfliegen). *Empis tessellata* Fabr.

Fam. **Asilidæ** (Raubfliegen). *Asilus germanicus* L., *A. crabroniformis* L., *Laphria gibbosa* Fabr. *L. flava* Fabr.

Fam. **Bombyliidæ** (Hummelfliegen). *Anthrax morio* Fabr. (*sinuatus* Fall.). The larvæ live in the nests of *Megachile muraria* and *Osmia tricornis*. *Bombylius major* L., *B. medius* L.

Fam. **Henopiidæ**. *Henops gibbosus* L. (Mundhornfliege). *Lasia flavitarsis* Wied.

Fam. **Therevidæ** (*Xylotomæ*), (Stiletfliegen). *Thereva annulata* Fabr. *Th. plebeja* L., *Scenopinus fenestralis* L.

Fam. **Tabanidæ** (Gadflies). Proboscis short, horizontally projecting, and provided with six or four (male) stylets and two-jointed palp. In the male

* F. Brauer, "Monographie der Æstriden." Wien, 1863.

the knife-shaped mandibles are wanting. Their puncture is severe, and they suck blood. *Chrysops cæcutiens* L., *Tabanus bovinus* L. (Rinderbremse). *Hæmatopota pluvialis* L. (Regenbremse).

Fam. **Leptidæ** (Schnepfenfliegen). *Leptis scolopacea* L., *L. vermileo* L., South Europe. The larva digs holes in the sand, and there, like the Ant-lion, captures insects.

Fam. **Xylophagidæ** (Holzfliegen). *Xylophagus maculatus* Fabr. The larvæ live in beech wood. *Beris clavipes* L.

Fam. **Stratiomyidæ** (Waffenfliegen). *Stratiomys chamæleon* L., *St. Odonatomyia hydroleon* L., *Sargus cuprarius* L.

Sub-order 3. **Nemocera** (Tipulariæ). Longhorns (fig. 478). *Diptera* of elongated form, with many-jointed, usually filiform, antennæ, which in the males are sometimes tufted. They have long

slender legs, and large, naked or hairy wings.

The palps are usually of considerable length, and with four or five joints. The proboscis

is short and fleshy, and often armed with

piercing setæ. The halteres are free. The

larvæ have usually a perfectly differentiated

head (*Eucephala*), more rarely a retractile jaw

capsule (*Tipulidæ*, *Cecidomyia*); they live in

water, in earth, and in vegetable matter

(galls and fungi), and some of them have a respiratory tube.

After moulting the larval skin the eucephalous larvæ become quiescent or freely moveable pupæ; the latter are provided with tracheal

gills on the neck and tail. The insect when hatched swims, till the

wings are hard, on the burst pupal skin as on a boat. The females

of many species suck blood (gnats), and become a veritable pest in

certain districts where they appear in swarms.

Fam. **Bibionidæ** (*Musciformes*). Body fly-like; antennæ six- to eleven-jointed. The abdomen has seven segments. *Bibio marci* L., *B. hortulanus* L. The males are black, the females brick red with a black head. *Simulia reptans* L., *S. columbascensis* Fabr. (Kolumbaczer Mücke). Suck blood. In Hungary they attack the herds of cattle in swarms.

FIG. 478.—*Cecidomyia tritici* (after Wagner). *a*, Female with protruded ovipositor. *b*, Larva. *c*, Pupa.

Fam. **Fungicolæ** (Pilzmücken). The larvæ, which are without rudimentary feet on the second segment, live in fungi. *Sciara Tomæ* L. The larvæ before entering the pupal stage come together in great numbers, and wander about in long sinuous chains. *Mycetophila fusca* Meig., (Pilzmücke), *Sciophila maculata* Fabr. (Schattenmücke).

Fam. **Noctuiiformes** (owl-like gnats). *Psychoda phalanxoides* L., *Ptychoptera contaminata* L. (Faltenmücke).

Fam. **Culiciformes**. The larvæ live in water, in rotten wood, or in earth. *Chironomus plumosus* L., *Corethra plumicornis*, Fabr. The larvæ have four tracheal vesicles and a circle of setæ on the anal segment; live in water.

Fam. **Culicidæ** (gnats). The larvæ live in water and have respiratory tube and appendages at the posterior end of the body. *Culex pipiens* L. (Singmücke). The palp of the male is tufted and longer than the proboscis. The females sting.

Fam. **Gallicolæ** (gall-flies). The larvæ live in galls. *Cecidomyia destructor*

FIG. 479.—a, *Pulex avium* ♂ (after Taschenberg). A Antenna; Mt. Maxillary palp. b, Larva of *Pulex irritans*.

Say, Hessian fly. Notorious in the United States as a destroyer of crops since the year 1778. Imported (?) into the country in straw by the Hessian troops. *C. tritici* Kirb., in wheat. *C. secalina* Loew. *C. salicis* Schrk. etc. The viviparous larvæ belong to the genus *Miastor*.

Fam. **Limnobiidæ** (Schnaken). The larvæ are found in earth or rotten wood. *Tipula oleracea* L., (Kohlschnaken). *Ctenophora atrata* L. (Kamm-mücke).

Sub-order 4. **Aphaniptera** (Fleas). *Diptera*, with laterally compressed body and distinctly separated thoracic rings. Wings are absent, but there are two lateral plate-like appendages on the meso- and meta-thorax. The antennæ are very short and arise in a depression behind the simple ocelli. The mandibles have the form of toothed saw-like stylets, the maxillæ are broad plates with four-jointed palps. The under lip (labium) is three-jointed and forms

the proboscis sheath. The larvæ have a distinct head and jaws (fig. 479).

Fam. Pulicidæ. *Pulex irritans* L., flea of man. The dorsal surface of the male is concave and serves for the reception of the larger female. The large apodal larvæ have a distinctly separated head, and live in sawdust and between boards, where the elongated oval eggs are deposited. *Sarcopsylla penetrans* L., sand-flea (Chigoe), lives free in South America in the sand (fig. 480). The female however bores into the skin of the human foot and of various Mammalia, and there deposits the eggs. The escaping larvæ give rise to ulcers.

Order 7.—Lepidoptera* (Butterflies and Moths).

Insects with suctorial mouth parts, which form a spirally rolled proboscis, with four similar wings which are completely covered with scales, with fused prothorax and complete metamorphosis.

The head is moveably articulated and thickly covered with hairs. It bears semi-circular faceted eyes and sometimes two ocelli. The antennæ are always straight and many-jointed, but vary much in form, being often seti-

FIG. 480.—*a*, Gravid female of *Sarcopsylla penetrans*. *b*, Foot of a field mouse with *Rhynchoprion* attached (after H. Karsten).

form or filiform, or even club-shaped, and not rarely denticulate or pectinate. The mouth parts are modified for sucking up fluid nourishment, especially the nectar of flowers, but are occasionally very short and hardly capable of being used. The upper lip and mandibles are reduced to rudiments, but the maxillæ are elongated and closely jointed, and their inner sides are grooved, so that when applied together they form a tube—the spirally rolled proboscis (fig. 481). The proboscis is furnished with small spines used for tearing the nectaries of flowers; while the nectar ascends through it into the mouth, being sucked up by pumping movements of the

* E. J. C. Esper, "Die europäischen Schmetterlinge in Abbildungen nach der Natur, mit Beschreibungen." 7 Bde. Erlangen, 1777—1805.

F. Ochsenheimer und F. Treitschke, "Die Schmetterlinge von Europa." 10 Bde. Leipzig, 1807-1835.

W. Herrich-Schäffer, "Systematische Beschreibung der Schmetterlinge von Europa." 5 Bde. Regensburg, 1843-1855.

W. Herrich-Schäffer, "Lepidopterorum exoticorum species novæ aut minus cognitæ. Regensburg, 1850-1865.

œsophagus. The maxillary palps are as a rule rudimentary (except in the *Tineidæ*). When at rest the proboscis lies rolled up beneath the mouth, and on either side of it are placed the large three-jointed labial palps, which are often tufted with hairs and are situated on the rudimentary triangular lower lip.

The three thoracic rings are intimately fused with one another, and like almost all external parts of the body are thickly covered with hairs. The wings are in most cases very large, but in rare cases are quite rudimentary (female *Geometridæ*); the anterior are the largest, and are distinguished by their partial or complete covering of scale-like hairs which overlap one another in a tectiform manner, and cause the extremely various colouring, tracing, and iridescence of the wings. These scales consist of small, usually finely ribbed and

toothed plates, which are attached by styli-form roots in pores of the integument of the wings, and are comparable to flattened out hairs. They arise during the pupal period. The arrangement of the nervures is of systematic value. The essential arrangement is a large median cell near the root of the wing, from which six to eight radial nervures pass to the

FIG. 481.—Mouth-parts of butterflies, (after Savigny); *a*, of *Zygæna*; *b*, of *Noctua*. *A*, Antennæ; *Oc* eyes; *Md*, mandibles; *Mxt* maxillary palps; *Mx*, maxilla; *Lt*, labial palps; *Lr*, labrum.

external lateral edges, while above and below the middle cell single independent nervures run parallel to the upper or lower fringed margin. The two pairs of wings are frequently connected with one another by retinacula, the upper edge of the hind wings being covered by spines or setæ, which catch in a band of the anterior wings. The legs are delicate and weak, their tibiæ are armed with spurs of considerable size. The tarsuses are in general five-jointed. The abdomen has six or seven segments and is thickly covered with hairs, and ends not unfrequently with a strongly projecting tuft of hairs.

Nervous system.—The brain is bi-lobed, and is provided with large

optic lobes, and special swellings for the origin of the antennal nerves. The ventral ganglionic chain is reduced, leaving the subœsophageal ganglion out of consideration, to two thoracic ganglia (of which the larger second ganglion shows traces of constrictions and arises from the fusion of four ganglia) and four or five ganglia in the abdomen. In the larval condition, on the other hand, there are eleven pairs of ventral ganglia.

The alimentary canal possesses a long œsophagus, which is connected with a stalked suctorial stomach, and usually six much coiled Malpighian tubes, of which the three on either side open by a common duct (figs. 47 and 48).

Generative organs.—The ovaries consist on either side of four very long many-chambered egg-tubes, which contain a great quantity of eggs, and have, in consequence, a moniliform appearance. The duct apparatus always possesses a long-stalked receptaculum seminis with glandular appendages, and a large bursa copulatrix which opens independently beneath the genital opening. The two long testicular canals are packed together so as to form an unpaired, usually brightly coloured body, from which pass off the two vasa deferentia, which are much convoluted and receive the contents of two accessory glandular tubes before uniting to form a ductus ejaculatorius. The two sexes are often so different in size, colour, and the structure of the wings, that there is a sexual dimorphism. The males are often more brightly and beautifully coloured (a means of exciting the females). The dimorphism, or even polymorphism (seasonal dimorphism), found in the female sex of many butterflies, is worthy of remark. **Parthenogenesis** occurs exceptionally in silkworms (*Bombyx mori*), in many *Psychidæ*, and some moths (*Solenobia*), the larva-like females of which have no wings (fig. 482).

Development.—The larvæ when hatched (caterpillars) possess masticating mouth parts and feed principally on plants, leaves and wood. On the head, which is large and covered with hard skin, there are a pair of three-jointed antennæ and six ocelli, each of which is divided into three parts. In all cases there are abdominal feet behind the three pairs of conical five-jointed thoracic legs. There may be only two pairs of such legs, as in the caterpillars of the

FIG. 482.—a, Female of *Psyche helix*. b, Male. c, Case of the male; d, of the female caterpillar.

Geometridæ, or five pairs, which then belong to the third to the sixth and the last abdominal segments. The caterpillars establish themselves before passing into the pupal stage in some protected place, or they spin cocoons and become transformed into *pupæ obtectæ**, from which the winged insects issue either in a few weeks or in the following year. The winged insects, as a rule, live only for a short time, and die after copulating and laying their eggs. Some of them, however, pass the winter in sheltered localities (*Rhopalocera*). Some very widely distributed species of caterpillars cause great damage to forests and cultivated plants, a damage which is, however, limited by the persecution which they suffer from certain *Ichneumonidæ* and *Tachinaria*. Fossil remains of butterflies have been found in tertiary formations and in amber. Linnæus' classification of the *Lepidoptera* into diurnal, twilight, and nocturnal butterflies has been superseded by the establishment of several groups and a number of families.

Tribe 1. *Microlepidoptera*. Very small and delicately formed *Lepidoptera*, usually with long setiform antennæ. The caterpillars have as a rule sixteen legs, of which the abdominal feet are provided with a circle of hooks round the sole. Many of them bore passages in the parenchyma of leaves, others live in leaves folded together, and others in buds. Some few are found in water, e.g., *Nymphula* and other *Pyralidæ*. The greater number remain hidden during the day.

Fam. *Pterophoridæ* (Federgeistchen). Plume-moths. *Pterophorus pentadactylus* L., *Pt. pterodactylus* L., *Alucita hexadactyla* L.

Fam. *Tineidæ* *Yponomeuta evonymella* L., spindle-tree moth. The caterpillars live together in cocoons; several species live on fruit trees. *Solenobia pincti*=*lichenella* L., *S. triquetrella* Fisch., R., the female is apterous. The caterpillars (sac-bearers) live in short sacs. Some of them reproduce parthenogenetically. *Tinea granella* L., (Kornmotte). Lays its eggs in grain. The caterpillars (known as grain worms) eat the grain. *T. pellionella* L., (Pelzmotte) *T. tapezella* L. (Tapetenmotte). Clothes-moth.

Fam. *Tortricidæ* (Wickler). *Tortrix viridana* L., in the oak. *Grapholitha funebrana* Tr., in plums. *Gr. (Carpocapsa) pomonella* L., in apples.

Fam. *Pyralidæ* (Zünsler). *Crambus pascuellus* L., *Botys urticae* L., *Galleria mellionella* L., in bee-hives. *Pyralis pinguicula* L. (Fettschabe). Tabby-moth. *Scopula frumentalis* L. (Saatemotte).

Tribe 2. *Geometrina*. Loopers. For the most part of slender build and with large wings, which in repose are tectiform. The antennæ are setiform and the basal joint is thickened. The caterpillars have ten to twelve feet; they move in a looping manner. When at rest

* Compare M. Herold, "Entwicklungsgeschichte der Schmetterlinge." Cassel und Marburg, 1815.

they cling with the posterior feet. Many species are hurtful to fruit trees.

Fam. **Phytometridæ**. *Larentia populata* L., *Cheimatobia brumata* L., winter moths. The females, which have rudimentary wings, lay their eggs on the trunks of fruit trees in late autumn.

Fam. **Dendrometridæ**. *Acidalia ochreata* Scop., *Geometra papilionaria* L., *Abraxa* (*Zerene*) *grossulariata* L., Harlequin, Magpie Moth.

Tribe 3. **Noctuina** (Eulen). Nocturnal *Lepidoptera* with broad body which is narrower behind, and dull coloured wings. The antennæ are long and setiform, in the male sometimes pectinate. The wings when at rest are tectiform. The legs are long and have strong spurs on the tibiæ. The caterpillars, which are sometimes naked, sometimes covered with hairs, have usually sixteen, more rarely, in consequence of the reduction or absence of the anterior legs, fourteen or twelve legs. The greater number pass the pupal stage in the earth.

Fam. **Ophiuridæ** (Ordensbänder). *Catocala paranympa* L. (gelbes Ordensband). *C. fraxini* L. (blaues Ordensband). *C. nupta* L., *C. sponsa* L., *C. promissa* Esp. (rothe Ordensbänder).

Fam. **Plusiadæ** (Goldeulen). *Plusia gamma* L., *Pl. chrysitis* L.

Fam. **Agrotidæ**. *Agrotis segetum* tr. *A. tritici* L., *Triphæna pronuba* L.

Fam. **Orthosiadæ**. *Orthosia jota* L.

Fam. **Cuculliadæ**. *Cucullia verbasci* L., *C. absynthii* L.

Fam. **Acronyctidæ**. *Acronycta psi* L., *A. rumicis* L., *Diloba cæruleocephala* L. The caterpillar is harmful to fruit trees.

Tribe 4. **Bombycina** (Spinner). Nocturnal *Lepidoptera* of clumsy build, with body thickly covered with hairs so as often to have a woolly appearance. The antennæ are setiform, and in the male pectinate. The wings are tolerably broad and tectiform when at rest. The larger and clumsier females fly but little; but the males, which are often brightly coloured, move with greater rapidity. In some cases the wings are reduced (*Orgyia*) or are absent (*Psyche*) in the female sex. The eggs, which are often laid in groups and are covered with a woolly mass, give origin to caterpillars with sixteen legs and a thick covering of hairs; the caterpillars spin complete cocoons in which they become pupæ above ground. The caterpillars of some species live together in common cocoons; some (*Psychidæ*) prepare a sac in which they conceal their bodies. Parthenogenesis occurs.

Fam. **Euprepiadæ** (Bärenspinner). The caterpillars with very long hairs, are known as woolly bears. *Euprepia cæja* L., *E. plantaginis*, etc.

Fam. **Liparidæ**. *Liparis monacha* L., the caterpillar is very harmful to leafy trees and Coniferæ. *L. dispar* L., *Orgyia antiqua* L. The female is apterous. *O. (Dasychira) pudibunda* L.

Fam. **Notodontidæ**. *Notodonta ziczac* L., *N. dromedarius* L. *Onethocampa processionea* L., the caterpillars live on oaks. *Harpyia vinula* L. (Gabelschwanz). The caterpillar has pharyngeal gland and two protrusible anal filaments.

Fam. **Bombycidæ**. *Gastropacha quercifolia* L. (Kupferglucke). *G. potatoria* L. *G. rubi* L., *G. pini* L., *Clisiocampa neustria* L.; *Bombyx mori* L. Silk-spinner originally from South Asia, but now bred in South Europe and China on account of the silk obtained from its cocoons. The caterpillar (silkworm) lives on the leaves of the mulberry. (The disease of silkworms, the muscardine, is produced by *Botrytis Bassiana*).

Fam. **Saturnidæ**. *Saturnia pyri* Borkh. *S. carpini*, *spini* Borkh., *Attacus cynthia*, *Yamamai*, *ceropia* cultivated for silk. *Agria tau* L.

Fam. **Psychidæ**. The caterpillars carry about sacks in which they are transformed into pupæ. *Psyche atra* L., *Ps. helix* L. The sacs are spirally coiled and have a second lateral opening, and are different in the two sexes. *Fumea nitidella* Hb.

Fam. **Zygænidæ**. *Zygæna filipendulæ* L.

Fam. **Cossidæ**. The caterpillars live mostly in the medulla of plants. *Cossus ligniperda* Fabr., *cesuli* L., *Hepialus humuli* L. The caterpillar lives in hop roots.

Tribe 5. Sphingina (Schwärmer). *Lepidoptera* with elongated body, pointed at the end, and usually a very long rolled proboscis. The anterior wings are long and narrow. The hind wings are short. The antennæ are short, and, as a rule, taper at the points. The wings lie when at rest horizontally on the body and always have a retinaculum. The caterpillars are flat, and provided with an anal horn and sixteen legs. They pass their pupal stage in the earth. The adult insects fly about in the twilight, some species also in the day (*Macroglossa*).

Fam. **Sesiadæ**. *Sesia apiformis* L., *S. bembeciformis* Hb.

Fam. **Sphingidæ**. Hawk-moths. *Macroglossa stellatarum* L. (Taubenschwanz), Humming-bird Hawk-moths. *Sphinx elpenor* L., *S. porcellus* L. (Weinschwärmer), *S. Nerii* (Oleanderschwärmer), *S. convolvuli* L., *Acherontia atropos* L., death-head. The caterpillar lives on potatoes. *Smerinthus populi* L. (Pappelschwärmer), *S. tiliæ* L. (Lindenschwärmer), *S. ocellatus* L. (Nacht-pfauenauge), Eyed Hawk-moth.

Tribe 6. Rhopalocera. Butterflies. *Lepidoptera* of slender build, usually with brightly coloured wings. The antennæ are club-shaped, or knobbed at the end. The legs are slender. The tibiæ of the front legs are short, and sometimes reduced. The *Rhopalocera* fly by day, and when at rest hold the wings upright, often applied together. The caterpillars have sixteen feet, and are either naked or thickly covered with hairs and spines. They develop, for the most part without cocoons and attached to extraneous objects by fibres, into the pupa, which is often of a shining metallic colour.

Fam. *Hesperiidæ*. *Hesperia comma* L., *H. sylvanus* Schn.

Fam. *Lycænidæ* (*Polyommaticidæ*), (Bläulinge). *Polyommatus Arion* L., *P. Damon* Fabr. *P. virgaureæ* L., *Thecla rubi* L., green hairstreak. *T. quercus* L., purple hair streak. *T. betulæ* L.

Fam. *Satyridæ*. *Satyrus Briseis* L., *S. Hermione* L., *Erebia* Bsdv. (*Hipparchia* Fabr.), *E. Janira* L., etc.

Fam. *Nymphalidæ*. The caterpillars have spiny outgrowths, rarely covered with fine hairs. The pupa is attached by its posterior extremity. *Apatura iris* L. (purple emperor). *Limenitis populi* L. (Eisvogel). *Vanessa prorsa* L. (*V. levana* is the spring generation). *V. cardui* L., painted lady. *V. atalanta* L., Admiral. *V. antiopa* L. (Camberwell beauty). *V. io* L., peacock. *V. urticæ* L. (Kleiner Fuchs), small tortoiseshell. *Argynnis paphia* L., silver-washed Fritillary, *A. aglaia* L. (dark green Fritillary), *Melitæa cinxia* L.

Fam. *Pieridæ* (Weisslinge). *Pieris cratægi* L. Blackveined white. *P. brassicæ* L., large white (Kohlweissling). *P. napi* L., green-veined white. *P. rapæ* L., small white. *Colias hyale* L., *C. rhamni* L. (Citronenvogel).

Fam. *Equitidæ*. *Papilio Podalirius* L., *P. Machaon* L. (Swallowtail). *Doritis Apollo* L. The females have a pouch-like appendage at the posterior end of the body.

FIG. 483.—*Hydrophilus piceus* (règne animal). a, Beetle. b, Larva. c, Pupa.

Order 8.—Coleoptera.*

Insects with masticating mouth-parts and horny front wings (tegmina). Prothorax freely moveable. The metamorphosis is complete.

The chief characters of this large, but tolerably well-defined, group of insects depend upon the structure of the wings. In the state of rest the anterior wings, as wing-covers (elytra), cover the posterior membranous wings which are transversely and longitudinally folded, and lie horizontally on the abdomen (fig. 483). The hind wings alone are used in flight, while the front wings are modified to perform a protective function, and usually correspond in size and form to the soft-skinned dorsal surface of the abdominal region, of

* W. E. Erichson, "Zur systematischen Kenntniss der Insectenlarven," *Archiv für Naturgesch.*, Tom. VII., VIII., and XIII.

Th. Lacordaire, "Genera des Coléoptères," Paris, 1854-1866.

L. Redtenbacher, "Fauna Austriaca, die Käfer," 3 Aufl. Wien., 1873.

Gemminger und Harold, "Catalogus Coleopterorum, etc.," München, 1868.

Kowalevski Lc., "Entwicklungsgeschichte des Hydrophilus, etc."

which, however, they leave in some cases the last segment (*pygidium*), or in other cases (*Staphylinæ*) several segments, exposed. As a rule, when the insects are at rest, the straight internal edges of both wing-covers are shut closely together, while the outer edges are bent round the sides of the abdomen. Sometimes the inner edges of the wings are fused together, so that the power of flight is abolished. In rare cases the wings are altogether absent. The head is seldom free, but as a rule is sunk into the freely moveable prothorax, and bears very variously shaped, usually eleven-jointed, antennæ. In the male the latter are of considerable size and have

FIG. 484.—*a*, *Cicindela campestris*.
b, *c*, Its larva with the two dorsal
hooks on the fifth abdominal
segment (règne animal).

a considerable extent of surface. Ocelli are with few exceptions absent, but the faceted eyes are only absent in certain blind species, which live in caves. The mouth parts are adapted for masticating and biting, and sometimes show transitional forms to those of the *Hymenoptera*. The maxillary palps are usually four-jointed and the labial palps three-jointed. In the predatory beetles, the external lobe of the maxilla has a palp-like form and articulation. The labium, which is simplified by the reduction of its parts, is in rare cases elongated to form a divided tongue. The large prothorax (cervical shield) is moveably articulated with the mesothorax, which is usually weakly developed; and on it, as well as on the other thoracic segments, the pleura extend on to the sternal surface. The

legs vary very much in shape, but usually end with a five-, rarely with a four-jointed tarsus. The tarsus is rarely composed of a smaller number (from one to three) of joints. The abdomen is attached to the metathorax by its broad base, and always possesses a greater number of dorsal than of ventral plates, of which some may fuse with one another. The smaller terminal segments are usually retracted and concealed by the preceding.

The nervous system of the *Coleoptera* varies in the greater or less concentration of the ventral ganglionic cord. The subœsophageal ganglion is followed by two or three thoracic ganglia, with the posterior of which one or two abdominal ganglia may be fused. In

the abdomen there are usually a series of separate ganglia (2 to 7). The latter may, however, fuse together to form a long mass or be drawn into the thoracic ganglia.

The long coiled **alimentary canal** dilates in the carnivorous beetles to form a gizzard, which is followed by a shaggy chylic ventricle. The number of Malpighian tubes is, as in *Lepidoptera*, confined to four or six.

The **males** and **females** are easily distinguished by the form and size of the antennæ, the structure of the tarsal joints, and by special relations of size, form and colour. In the female the numerous egg-tubes unite in very various arrangements, and a bursa copulatrix is often present. The males possess a large horny penis, which, when at rest, is retracted into the abdomen and is protruded by means of a powerful muscular apparatus.

Almost all the larvæ have mouth parts adapted for biting, rarely suctorial pincers. They feed under the most different conditions, as a rule concealed and removed from the light, and usually in the same way as the perfect insect. They are either grub-like and apodal, but with a distinctly developed head (*Curculionidæ*), or they possess, in addition to the three pairs of legs on the thorax, also stumps on the last abdominal segments.

Many larvæ, as those of the *Cicindela*, have a peculiar apparatus for capturing their prey (fig. 484). In place of the faceted eyes, which have not yet appeared, ocelli are present in varying number and position. Some beetle larvæ, like the larvæ of the *Diptera* and *Hymenoptera*, live as parasites and feed inside bees nests on the eggs and honey (*Meloë*, *Sitaris*) (fig. 485). The pupæ of beetles, which are either suspended and attached to objects or lie on the earth or in holes, have their limbs freely projecting.

Fossil *Coleoptera* are found in coal formations and are specially numerous in amber.

Tribe 1. Cryptotetramera = Pseudotrimera. The tarsuses are composed of four joints, of which one joint is rudimentary. Latreille considered them to be three-jointed.

Fam. *Coccinellidæ* (Lady Birds). *Coccinella septempunctata* L. The larvæ feed on Aphides. *Chilocorus bipustulatus* L.

FIG. 485.—*a*, *Meloe violaceus*. *b*, *Sitaris humeralis* (règne animal).

Fam. **Endomychidæ** (Pilzkäfer). *Endomychus coccineus* L. *Lycoperdina succinata* L.

Tribe 2. Cryptopentamera = Pseudotetramera. One joint of the five-jointed tarsus is reduced and concealed.

Fam. **Chrysomelidæ** (Blattkäfer). The adult insects are mostly of a bright colour and feed on leaves. Their larvæ have a cylindrical thick-set body, which is very generally covered with warts and spiny prominences; they always have well-developed legs; they likewise feed on leaves, into the parenchyma of which some of them (*Hispæ*) burrow, and present the peculiarity of using their excrements to prepare cases which they carry about with them (*Clythra*, *Cryptocephalus*). Before entering the pupal stage they attach themselves to leaves by the hind end of their body. *Haltica oleracea* Fabr. Harmful to cabbage leaves. *Lina populi* L. *Chrysomela varians* Fabr.

Fam. **Cerambycidæ** (*Longicornia*) (Bockkäfer). Some species (*Lamia*) produce a peculiar sound by rubbing the head against the prothorax. The elongated grub-like larvæ have a horny head with powerful mandibles, short antennæ, and usually no legs or ocelli. They live in wood, in which they bore passages and sometimes cause great damage. *Lamia textor* L., *Cerambyx heros* Scop., *C. cerdo* Fabr., *Prionus coriarius* Fabr.

Fam. **Bostrychidæ** (Borkenkäfer). *Coleoptera* of small size and cylindrical body shape. The larvæ are of stout cylindrical shape and without legs, the place of which is taken by ridges covered with hairs like those of the *Curculionidæ*. The adult insects and larvæ bore passages in wood, on which they feed. They live in companies, and belong to the most dreaded destroyers of forests of conifers. The way in which they eat into the bark is very peculiar, being characteristic of the individual species and indicative of their mode of life. The two sexes meet in the superficial passages, which the female, after copulation, continues and lengthens in order to lay her eggs in pits, which she hollows out for that purpose at the end of them. The larvæ when hatched eat out lateral passages, which, as the larvæ increase in size and get further from the main passage, become larger and give rise to the characteristic markings on the inside of the bark. *Bostrychus chalcographus* L., *B. typographus* L., under the bark of pine-trees. *B. stenographus* Duft.

Fam. **Curculionidæ** (Rüsselkäfer). Weevils. Head prolonged into a proboscis in front. Larvæ cylindrical, without or with very rudimentary legs and ocelli; they are almost entirely phytophagous; and indeed they live under the most various conditions, some inside buds and fruit, others under bark, or on leaves, or in wood. *Culandra granaria* L., in grain known as black grain-worms. *Balaninus nucum* L., Nut-weevil. *Hyllobius abietis* Fabr., *Apion frumentarium* L.

Tribe 3. Heteromera. The tarsuses of the two anterior pairs of legs are five-jointed, of the posterior pair four-jointed.

Fam. **Oedemeridæ**. *Oedemera virescens* L.

Fam. **Meloidæ** (*Cantharidæ*). They furnish a substance used in the preparation of vesicants. The larvæ live partly parasitically on insects, partly free under the bark of trees, and some of them pass through a complicated metamorphosis called by Fabre hypermetamorphosis; they possess at first three pairs of legs; in later stages they lose these, and the body acquires a cylindrical

form (fig. 457). *Meloe* L. The beetles live in grass, and when touched they give out an acrid pungent fluid between the joints of the legs. The larvæ creep on the stalks of plants, penetrate into the flowers of *Asclepiadæ*, *Primulacæ*, etc., and attach themselves fast to the body of bees (*Pediculus melittæ* Kirby), in order to be carried to the bees' nest, in which they nourish themselves chiefly on honey. *M. proscarabæus* L., *M. violaceus* Marsh. *Lytta vesicatoria* L., Spanish fly. *Sitaris humeralis* Fabr., South Europe (fig. 485).

Fam. *Rhipiphoridæ*. The larvæ live in wasp nests (*Metocæus*), or in the abdomen of cockroaches (*Rhipidius*). *Rhipiphorus bimaculatus* Fabr.

Fam. *Cistelidæ*. *Cistela fulvipes* Fabr., *C. murina* L.

Fam. *Tenebrionidæ*. *Tenebrio molitor* L., Larva known as meal-worm. *Blaps mortisaga* L.

Tribe 4. Pentamera. Tarsus usually five-jointed.

Fam. *Xylophaga*. Tarsus sometimes only four-jointed. The larvæ sometimes feed on dead animal matters, sometimes bore cylindrical horizontal passages in wood, and are therefore destructive to furniture and wooden material as well as to living trees. *Lymeria navale* L., on docks in oak. *Anobium pertinax* L., death watch, produces a ticking noise in wood. *Ptinus fur* L., *Pt. rufipes* Fabr.

Fam. *Cleridæ*. The variegated larvæ live under bark and for the most part on other insects. *Clerus formicarius* L., *Trichodes apiarius* L. The larva is parasitic in bee-hives.

Fam. *Malacodermata*. *Malachius æneus* Fabr. *Cantharis* (*Telephorus*) *violacea* Payk., *C. fusca* L. *Lampyrus* Geoffr., Glow-worm. Female apterous, or only with two small scales. Light organs in the abdomen *L. noctiluca* L., *L. splendidula* L. Female with two small scales instead of wing-covers.

Fam. *Elateridæ* (Springkäfer). The elongated body is distinguished by the very free articulation between the prothorax and mesothorax; and by the possession of a spine upon the prothorax which fits into a pit on the mesothorax. These two arrangements enable the beetle to jump up when lying on its back. The larvæ live under the bark of trees on the wood, sometimes in the roots of grain and turnips, and may be very destructive. *Agriotes lineatus* L., *Lacon murinus* L., *Elater sanguineus* L., *Pyrophorus noctilucus* L., in Cuba, prothorax dilated to the form of a vesicle and phosphorescent.

Fam. *Buprestidæ* (Prachtkäfer). Body elongated, pointed behind, often brightly coloured, with a metallic lustre. The elongated vermiform larvæ are without ocelli and, as a rule, legs; and possess a very broadened prothorax. They live like the larvæ of the *Cerambycidæ*, to which they present a general resemblance, in wood, and bore flat ellipsoidal passages. *Trachys minuta* L., *Agilus biguttatus* Fabr., *Buprestis rustica* Fabr., *B. flavomaculata* Fabr.

Fam. *Lamellicornia* (Blatthornkäfer). The antennæ are seven- to eleven-jointed; the basal joint is large, and the terminal joints (three to seven) are widened to a fan shape. In many the anterior legs are adapted for digging. The soft-skinned larvæ possess a horny head, moderately long legs, and a curved abdomen, which is dilated behind to the form of a sac; they feed sometimes on leaves and roots, sometimes on putrefying vegetable and animal substances, and enter into the pupal stage after two or three years sojourn in a cocoon beneath the earth. *Lucanus cervus* L., stag beetle. Larvæ in rotten wood of old oaks. The beetle feeds on the sap which comes from the oak. *L. parallelipipedus* L.,

Copris lunaris L., *Aphodius subterraneus* Fabr., *Geotrupes vernalis* L., *G. stercorarius* L., *Rhizotrogus solstitialis* L., *Melolontha vulgaris* Fabr., Cockchafer. The larvæ at first live together and feed on fresh vegetable substances, later (in the second and third years) on roots, which they destroy, doing great damage. Towards the end of the fourth summer the beetle is usually developed from the pupa, which lies in a smooth round hole, but it remains in the earth till the next spring. *M. hippocastani* Fabr., *Cetonia aurata* L., *Ateuchus sacer* L., *Oryctes nasicornis* L.

Fam. **Dermestidæ** (Speckkäfer). *Attagenus pelli* L. (Pelzkäfer). *Dermestes lardarius* L., (Speckkäfer).

Fam. **Histeridæ** (Stutzkäfer). *Hister maculatus* L., *Ontophilus striatus* Fabr.

Fam. **Silphidæ** (Aaskäfer). Beetles and larvæ live on and lay their eggs in decomposing animal and vegetable matters; some of them even attack living insects and larvæ. When attacked many defend themselves by the ejection of a stinking anal excretion. *Silpha thoracica* Fabr., *S. obscura* Fabr. *Necrophorus vespillo* Fabr., *N. germanicus* Fabr. (Todtengräber).

Fam. **Pselaphidæ**. Live in the dark under stones and in colonies of ants. *Pselaphus Heisei* Herbst, *Claviger testaceus* Pr.

Fam. **Staphylinidæ** (Kurzdeckflügler). *Myrmedonia canaliculata* Fabr. Live among ants. *Staphylinus maxillosus* L., *Omalium rivulare* Payk.

Fam. **Hydrophilidæ** (Palpicornia). Swimming beetles with short club-shaped antennæ and long maxillary palps, which often project beyond the antennæ. Feed on plants. *Hydrophilus piceus* L., *Hydrobius fuscipes* L.

Fam. **Dytiscidæ**. Swimming-beetles, with filiform, ten- or eleven-jointed antennæ and broad swimming legs beset with setæ; the hind legs project back and are especially adapted for swimming by the possession of a close covering of swimming-hairs. *Colymbetes fuscus* L., *Dytiscus marginalis*, Sturm.

Fam. **Carabidæ**.* Running beetles, with eleven-jointed filiform antennæ, powerful pincer-shaped mandibles, and running legs. The elongated larvæ possess four-jointed antennæ, four to five ocelli on each side, sickle-shaped projecting pincers, and fairly long five-jointed legs. *Harpalus æneus* Fabr., *Brachinus crepitans* K. (Bombardierkäfer). *Carabus auratus* L., *Procrustes coriaceus* L.

Fam. **Cicindelidæ**. Tiger-beetles. Mandibles with three teeth. The larvæ form subterranean passages, possess a broad head, very large sickle-shaped curved jaws, and bear on the dorsal surface of the eighth segment of the body two horny hooks for attachment in the passage, at the opening of which they lie in wait for prey. *Cicindela campestris* L. (fig. 484).

Order 9.—HYMENOPTERA.†

Insects with biting and licking mouth parts, fused prothorax, four membranous wings with only few nervures. Metamorphosis complete.

The body has as a rule an elongated form, and possesses a freely

* Dejean, "Species général des Coléoptères, etc." Tom I.-V., Paris, 1825-1831.

† L. Jurine, "Nouvelle méthode de classer les Hyménoptères et les Diptères." Tom. I., Hyménoptères. Genève, 1807.

C. Gravenhorst, "Ichneumologia Europæa," Vratislaviæ, 1829. J. Th. C. Ratzeburg, "Die Ichneumoniden der Forstinsecten." 3 Bde. Berlin, 1844-1852.

G. Dahlbom, "Hymenoptera Europæa, præcipue borealia." Lund, 1845.

v. Siebold, "Beiträge zur Parthenogenesis der Arthropoden." Leipzig, 1871.

moveable head with large faceted eyes which in the male are almost in contact, and three ocelli (fig. 486).

In the antennæ a large basal joint (shaft) and eleven to twelve shorter joints can usually be distinguished, or they are not crooked, in which case they consist of a greater number of joints.

The mouth parts are biting and licking; the upper lip and mandibles are constructed as in beetles and Orthoptera; the maxillæ and labium, on the other hand, are elongated and adapted for licking, and when at rest are frequently bent round. In bees the tongue can be considerably elongated and assume the form of a proboscis; in this case the lobes of the jaws also become considerably extended, and form a kind of sheath around the tongue. The maxillary palps are usually six-jointed; the labial palps on the other hand only four-jointed, but the number of joints may be reduced.

As in the *Lepidoptera* and *Diptera*, the prothorax is firmly connected with the following thoracic segments, inasmuch as the

FIG. 486.—*Apis mellifica*. *a*, Queen. *b*, Worker. *c*, Drone.

pronotum at least (excepting in the leaf- and wood-wasps) is fused with the mesonotum, while the rudimentary prosternum remains freely moveable. On the mesothorax two small moveable scales (*tegulæ*) are found over the base of the forewing, and behind the scutellum the anterior part of the metanotum is developed into the posterior shield (*postscutellum*). Both pairs of wings are membranous, transparent, and traversed by but few nervures; the anterior are considerably larger than the posterior. From the outer edge of the latter small hooks arise, which are attached to the inferior edge of the anterior pair, thus bringing about the connection between the two pairs of wings. Sometimes the wings are absent in one of the two sexes, or in the workers amongst many social *Hymenoptera*. The legs possess five-jointed, usually broadened tarsuses with long first tarsal joint. The abdomen is rarely attached to the thorax by its whole breadth (sessile); as a rule the first or the two first segments of the abdomen are narrowed to a thin stalk, bringing about the connection with the

thorax (stalked). In the female sex the abdomen ends with an ovipositor (*terebra*), which as a rule is retracted, or with a poison spine (*aculeus*). The latter develops from six warts, of which four belong to the ventral side of the penultimate, two to that of the antepenultimate segment. The sting (fig. 487) consists of the grooved piece (sting-groove), two piercing stylets and two sting-sheaths (with oblong plates) and is retracted when at rest. The grooved piece, the furrow of which is directed downwards, arises from the inner pair of warts of the penultimate segment, while the

piercing stylets on the edge of the grooved piece correspond to the pair of warts of the antepenultimate segment. Finally the segments also take part in the formation of this apparatus, inasmuch as they furnish powerful supporting plates for the sting (quadratic plate and angular piece).

The nervous system consists of a large complicated brain, an infra-oesophageal ganglion, two thoracic ganglia (the ganglia of the mesothorax and metathorax are fused with the anterior abdominal ganglion), and five to six ganglia in the abdomen.

FIG. 487.—Stinging apparatus of the honey bee from the dorsal side (after Kraepelin). *GD*, poison gland; *Gb*, poison reservoir; *D*, gland; *Str*, grooved piece with the two stylets; *Ba*, swollen base of the grooved piece; *B*, curved root of the same; *W*, angular piece; *Sh*, sheath of spine; *O*, oblong plate; *Q*, quadratic plate; *Stb*, *Stb'*, the two piercing spines on the ventral side of the grooved piece.

The alimentary canal frequently attains to a considerable length, especially in those Hymenoptera which with a longer life cumber themselves with the care and nourishment of the young. Large salivary glands are present. The narrow oesophagus usually dilates to a suction stomach, more rarely to a spherical gizzard (ants). A considerable number of short Malpighian tubules open into the intestine (hindgut).

In connection with the great power of flight, the longitudinal tracheal trunks give rise to vesicular dilatations, of which two at the base of the abdomen are conspicuous by their size.

The female sexual organs usually possess very numerous (up to one hundred) many-chambered egg tubes, and a large receptaculum seminis with accessory glands. A special bursa copulatrix is absent (fig. 488). When a sting is developed, filiform or branched poison glands with a common reservoir and a duct opening into the sheath of the sting, are present. In the male sex the ducts of the two testes are connected with two accessory glands, while the common ductus ejaculatorius ends with a large protrusible penis.

With the exception of the leaf-wasps (*Tenthredinidæ*), and wood-wasps (*Uroceridæ*), the larvæ are apodal and live either parasitically in the body of insects (the *Pteromalinæ* pass through various larval stages, undergoing a kind of hypermetamorphosis) or in plants, or in brood spaces (cells) formed of animal and vegetable substances.

The former, like the caterpillars of the butterflies, possess, besides the six thoracic

FIG. 488.—The viscera in the abdomen of the queen bee (after R. Leuckart). *D*, alimentary canal; *R*, rectum with rectal glands and anus; *Gk*, chain of ganglia; *Ov*, ovary; *Rc*, receptaculum seminis; *Gb*, reservoir of poison gland; *St*, sting.

legs, six to eight pairs of abdominal legs, and live free on leaves; the latter are grub-like, find the nutritive material in their cells, and are in part fed during their growth. Almost all—*e.g.*, the larvæ of bees and wasps—possess a small retractile head with short mandibles and pointed pieces (maxillæ and labium). The anus is not developed, for the stomach is blind and does not communicate with the hindgut, which receives the Malpighian tubules. Most of the larvæ, when they enter the pupal stage, spin an irregular investment or a firmer cocoon of silk-like fibres. The larvæ of bees and wasps then soon undergo a moult (when they get rid of their excrementitious matters), and enter upon a stage which precedes that of the pupa and is called by v. Siebold the *pseudopupa* (fig. 489).

Sub-order 1.—Terebrantia.

Female with ovipositor as tube or borer (*terebra*), which projects freely at the end of the abdomen, and is sometimes retractile.

Tribe 1. Phytophaga. Abdomen sessile. Trochanter composed of two rings. Larvæ phytophagous, resemble caterpillars.

Fam. Tenthredinidæ (Leaf-wasps). Saw-flies. Abdomen sessile with short borer. The larvæ have rarely three, usually nine to eleven pairs of legs, and resemble caterpillars. The females lay their eggs in the epidermis of leaves, the puncture causes the flow of sap, which the egg imbibes and thereby increases in size. The young larvæ feed on leaves, often in early stages live in societies, and become pupæ in a cocoon. They are distinguished from the caterpillars by the greater number of legs, and by the two ocelli on the horny head. *Lyda betulæ* L., *Tenthredo* (*Athalia*) *spinarum* Fabr., larvæ sometimes on roses. *Nematus ventricosus* Klg., larvæ on gooseberries. *Cimbex femorata* L.

Fam. Uroceridæ (Wood-wasps). Abdomen with first tergum split, and usually long, freely projecting ovipositor (egg-borer). The females bore holes in wood and deposit their eggs therein. The larvæ bore further into the wood and live a long time. *Sirex gigas* L.

FIG. 489.—a, Larva of the bumble bee about to become a pupa. b, Pseudo-pupa (Semi-pupa). c, pupa (after Packard).

Tribe 2. Gallicola. Abdomen stalked. Larvæ apodal and aprocous,

usually living in vegetable cells.

Fam. Cynipidæ (Gall-wasps). Thorax humped. Abdomen usually short, laterally compressed. The ovipositor (egg-borer) arises on the ventral side, and is as a rule retracted. The females bore into plant tissues and cause, by the irritation of an acrid fluid, an abnormal flow of vegetable fluids, thus giving rise to the outgrowths known as *galls*, on which either one or several apodal larvæ feed. Certain galls, especially those of the oaks of Asia Minor (*Aleppo*), contain tannic acid, and are on this account used in industry. In many species the females only are at present known; the eggs in such cases develop parthenogenetically. Many larvæ are parasitic in *Diptera* and *Aphides*. *Cynips quercus folii* L., *Rhodites rosæ* L., produces the bedeguar of roses. *Figites scutellaris* Latr., parasitic on the grubs of *Sarcophaga*.

Tribe 3. Entomophaga. Abdomen stalked. Female with freely projecting ovipositor (spine). Larvæ apodal and without anus, usually parasitic in the larvæ of other insects.

Fam. Pteromalidæ. The larvæ are parasitic in all possible insect larvæ, frequently in parasites, and pass through a complicated metamorphosis, extremely remarkable for the succession of very different stages. *Pteromalus puparum* L., *Teles clavicornis* Latr., *Platygaster* Latr., (fig. 458).

Fam. **Braconidæ**. They principally persecute caterpillars, as well as beetle larvæ living in dead wood. *Microgaster glommeratus* L., in caterpillars, *Bracon impostor* Scop., *Br. palpebrator* Ratzbg.

Fam. **Ichneumonidæ**. *Ichneumon incubitor* L. *I. (Trogus) lutorius* Ratzbg., *Pimpla (Ephialtes) manifestator* L., *Ophion luteus* L.

Fam. **Evaniadæ**. *Ecania appendigaster* L., *Foenus jaculator* L.

Sub-order 2.—Aculeata.

With retractile perforated sting and poison gland in the female sex. Abdomen always stalked; the antennæ of male usual thirteen-jointed, of the female twelve-jointed. The larvæ are apodal and without anus.

Fam. **Formicidæ*** (Ants) (fig. 490). They live together in communities, which contain, besides the winged males and females, a great excess of small apterous workers with stronger prothorax. The latter are sometimes of two kinds, known as soldiers and true workers, distinguished by the size of the head and jaws. The workers are aborted females and resemble the true females in possessing a poison gland, the acid secretion (formic acid) of which they either pour out with the help of the sting or, in the absence of the latter, eject into the wound made by the mandibles.

The dwellings of the ants consist of passages and cavities, which are placed in rotten wood, in the earth, or in hill-like heaps which they throw up. Winter provisions are not carried into these spaces, since the ant-workers, which with the queens alone survive the winter, fall into a kind of winter sleep.

In the spring queens are found in addition to the workers. From the eggs of the queens larvæ proceed, which are carefully reared and protected by the workers. The larvæ in egg-shaped cocoons become pupæ (ants' eggs) and develop, some of them to workers and some to winged sexual animals, which appear with us sooner or later in the course of the summer, and copulate in the flight. After copulation the males die, the females lose their wings and are carried back by

FIG. 490.—*Formica (Camponotus) herculeana*. *a*, Female. *b*, Male. *c*, Worker. *d*, Larva of *Formica rufa*. *e*, pupa with case, so-called ant egg. *f, g*, Pupa liberated from the case.

* P. Huber, "Recherches sur les mœurs des Fourmis indigènes." Geneva, 1810.

Latreille, "Histoire naturelle des Fourmis." Paris, 1802.

A. Forel, "Les Fourmis de la Suisse." Zurich, 1874.

the workers into their dwellings, to deposit their eggs, or found with some of the workers new societies.

In the tropics the ants undertake migrations in great numbers, and may become a regular plague when they enter houses and destroy all eatables. Many forms (*Oecodoma* species) are especially destructive to young trees and plants, which they strip of foliage. Some species, however, render service in attacking Termites and in destroying other pernicious insects, such as the cockroaches, even in the dwellings of man. Many species, especially of the genus *Ecton*, are predatory ants and destroy other ant colonies. Certain species are said to make war with foreign ant states and to carry off their young, which they bring up for service in their own colony (Amazon colonies. *F. rufa*, *rufescens*). The relatively high psychical activity of these insects is undeniable; many instances of it have been disclosed by the thorough observations of P. Huber. They keep Aphides as we do milch cows; they carry provisions into their dwellings; they go out to battle in regular columns, and offer up their lives bravely for the community. In contrast to the war-like features of the slave-states are the friendly relations of the ants to other insects, which, as *Myrmecophila*, live in the ant dwellings (larvæ of *Cetonia*, *Myrmecophila*, etc.). *Formica herculeana* L., *F. rufa* L., *Myrmica acervorum* Fabr., with sting.

Fam. **Chrysididæ** (Gold wasps). The females lay their eggs in the nests of other Hymenoptera, especially of the digging wasps (*Fossoria*), with which they have on this occasion to carry on war. *Chrysis ignita* L.

Fam. **Heterogyna** (*Mutillidæ*, *Scoliadæ*). Males and females very different in form, size and structure of antennæ. The females, with shortened wings or apterous, live solitarily and lay their eggs on other insects or in bees' nests, and do not trouble themselves with the nourishment and care of their young. *Mutilla europæa* L., *Scolia* (*Scoliadæ*) *hortorum* Fabr. The larva lives parasitically on that of the nasicorn beetle.

Fam. **Fossoria*** (Digging wasps). Solitary Hymenoptera, with unbent antennæ and elongated legs; the tibiæ are armed with long spines. The females, which live on honey and pollen, dig passages and tubes usually in sand and in earth and in dry wood, and deposit at the end of them their cells, each of which contains an egg and animal nutritive matter for the future larva. Some (*Bembex*) carry fresh food daily to their growing larvæ, contained in open cells; others place in the closed cell as many insects as the larva requires for its development. In the last cases the introduced insects are not completely killed, but merely crippled by a sting in the ventral nerve cord. The individual species usually capture quite definite insects (*caterpillars*, *Curculionidæ*, *Buprestidæ*, *Acridiæ*, etc.), which they overpower and paralyse in a very remarkable manner. For example, *Cerceris bupresticida* attacks *Buprestis*, while *C. Dufourii* chooses *Cleonus ophthalmicus*. The digging wasp seizes the head of the beetle with its mandibles and inserts its sting into the thoracic ganglia between the articulation of the prothorax. *Sphex flavipennis*, which constructs three cells at the end of a horizontal passage, two or three inches long, attacks *Grylla*, and *Sphex albisecta* species of *Ædipoda*. *Ammophila holosericea* supplies each of its brood cells with four or five caterpillars; *A. sabulosa* and *argentata* only with one very large caterpillar, which is paralysed

* Fabre, "Observations sur les mœurs des *Cerceris*;" also "Études sur l'instinct et les métamorphoses des Sphéigiens," *Ann. des Sc. Nat.*, ser. 4, Tom IV. and VI.

by a sting in a median apodal body segment. *Pompilus viaticus* L., *Ammophila sabulosa* L., *Crabro cribarius* L.

Fam. *Vespidæ* * (Wasps). Body slender, smooth. Anterior wings are narrow and can be folded together longitudinally. They are sometimes solitary, sometimes they live in societies; in the last case the workers also are winged. The females of the solitary wasps build their brood-cells in sand or on the stalks of plants with sand and clay, and fill them rarely with honey, usually with insects, especially caterpillars and spiders; they thus approach the *Fossoria* in their mode of life. The social wasps approximate to bees in the organization of their society. They construct their nests of gnawed wood, which they manufacture into lamellæ resembling paper, and fasten together into regularly hexagonal cells. The combs, which are composed of a simple layer of cells attached to one another, are either suspended freely on the branches of trees, or in holes in the earth and in hollow trees, or surrounded by a common leafy investment, on the under surface of which the holes for exit are placed. In the latter case the internal structure frequently consists of several horizontally-suspended combs which are placed one above the other, like the floors of a house, and are connected by buttresses. The openings of the hexagonal vertically placed cells look downwards. The foundation of each wasp nest is laid in the spring by a single female, which was fertilized in the preceding autumn and has survived the winter. She begets, in the course of the spring and summer, workers, which help to increase the size of the nest and to rear the offspring, and of which the larger forms produced in the summer not rarely lay eggs, which develop parthenogenetically into males. The larvæ are fed with insects which have been well chewed, and are transformed in a delicate case into pupæ in the closed cells. The perfect insects feed as a rule on sweet substances and honey juices, which they are said occasionally to gather in (*Polistes*). Males and females first appear in late summer and copulate in the flight high up in the air. The males soon die and the whole colony is generally dissolved in the autumn; the fertilized females, on the other hand, survive the winter under stones and moss in order to found new societies in the following year. *Odynerus parietum* L., *Polistes gallica* L. Nests are without investment of leaves and consist of a stalked comb. The fertilized females, which have survived the winter, produce according to v. Siebold at first only female offspring, whose eggs remain unfertilized and develop parthenogenetically into males. *Vespa crabro* L., hornets. *V. vulgaris* L.

Fam. *Apidæ*† (Bees). Tibia and tarsus, especially of the hind legs, broadened; the first tarsal joint, especially of the hinder legs, covered with hairs like a brush. Anterior wings cannot be folded together. Body hairy. The hairs on the hind legs or on the belly serve as a collecting apparatus for the pollen. The labium and maxillæ often reach a very considerable length. The latter are applied as a sheath to the tongue, and bear only rudimentary palps. The bees are solitary and social, and place their nests in walls, under earth and in hollow trees, and feed their larvæ with honey and pollen. Some do not build nests, but lay their eggs in the filled cells of other bees (parasitic bees). *Andrena cineraria* L., *Dasypoda hirtipes* Fabr., *Nomada ruficornis* Kirb.,

* H. de Saussure, "Études sur la famille des Vespides." 3 vols. Paris, 1852 to 1857.

† F. Huber, "Nouvelles observations sur les Abeilles." 2 vols. Paris, 1814.

Megachile (*Chalicodoma*) *muraria* Fabr., *Osmia* *bicornis* L., *Anthophora* *pilipes* Fabr., *Xylocopa* *violacea* Fabr. Wood-bees construct perpendicular passages in wood, and divide them by transverse walls into cells.

Bombus Latr. Bumble bee. Body heavy; hairy like fur. The nests are usually placed in holes under the earth, and include only a small number, about fifty to two hundred, rarely as many as five hundred workers, in addition to the fertilized female. They do not construct combs, but pile up irregular masses of pollen, in which the eggs are deposited, and which serve as food for the hatching grubs. The latter eat out cellular cavities in the pollen masses and form oval cocoons, which are free but irregularly placed by the side of one another. The nest is founded by a single female which has survived the winter. She at first alone has the burden of rearing the brood; subsequently, however, this is shared by the hatched workers of different size, which themselves lay unfertilized eggs. *B. lapidarius* Fabr., *muscorum* Ill., *terrestris*, Ill., *hypnorum* Ill.

Apis L., honey-bee. The workers with lateral separated eyes, with one-jointed maxillary palps. The external surface of the hinder tibiæ is pressed into the form of a pit, and is surrounded by simple marginal setæ (basket, fig. 491, *K*); the inner surface of the tarsus is beset with regular rows of setæ (brush, fig. 491 *B*, *b*). The female (queen) with shorter tongue, longer abdomen, without brush. The male (drone), with large eyes in contact, broad abdomen, and short mouth parts, without basket and brush. *A. mellifica* L., honey bee, distributed over Europe and Asia as far as Africa.

FIG. 491.—*a*, Hind leg of a worker of *Apis mellifica*. *K*, basket on the tibia; *B*, enlarged tarsal joint with brush on the under side. *b*, brush, more strongly magnified.

The workers build perpendicular combs in hollow trees, or in other protected places; under the influence of human cultivation, in suitably arranged baskets or hives. The wax used in the construction of the comb is produced in the organism as a result of metabolism (honey being the source), and is exuded in the form of small tablets between the segments of the abdomen. The combs consist of two layers of horizontal hexagonal cells, the bases of which are formed of three rhomboidal plates. The smaller cells serve for the reception of provisions (honey and pollen) and for the brood of workers, the larger for the reception of honey and the drone brood. Outside, at the edge of the comb, there are at definite times a small number of large irregular queen cells, in which the female larvæ are brought up. When the cells are filled with honey, or the larvæ contained in them have reached the stage of pupæ, they are closed up. A small opening at the bottom of the hive serves for entry and exit; all other clefts and fissures are closed with wax, and no light enters the interior of the nest. In no other Hymenopteran society is the division of labour so strictly carried out as in that of the bees. There is only one fertilized queen, and she alone lays the eggs (she may lay more than three thousand eggs in one day). The working bees divide amongst themselves the business of collecting honey, preparing wax, and feeding the brood, and the completion of the nest. The drones, which exist only at the swarming time, and then only in proportionately small numbers (two hundred to three hundred in a society of twenty

thousand to thirty thousand workers) have the privilege of enjoying themselves and of doing no kind of work in the hive ; they arise from unfertilised eggs and are killed in the autumn (slaughter of drones). The queen and the workers live through the winter consuming the stored-up provisions, and kept warm by the heat produced by the dense population of the hive. In the first days of spring the queen deposits eggs, first in the workers' cells and later in the drone cells. Some royal cells are then constructed, and at intervals she deposits a fertilised egg in each of them. The larvæ in the royal cells receive a richer nourishment and royal food, and become sexually mature females (queens), capable of copulating. Before the oldest of the young queens is hatched—sixteen days from the deposition of the egg is required for this, while the workers develop in twenty days, the drones in twenty-four—the queen-mother leaves the hive with a part of the inhabitants (first swarm). The young queen either kills all the other royal larvæ and remains in the old hive, or if she is prevented from doing this by the workers, and the population is still large enough, she also leaves the old hive with a part of the workers before the appearance of a second queen (second swarm). Soon after her metamorphosis the young queen makes her marriage flight, and returns after impregnation to the hive. The queen is only impregnated once in the course of her life, which lasts four or five years ; she is henceforward able to produce male and female offspring. If the wings of the queen are paralysed and she is unable to copulate, she lays eggs which only give rise to drones ; the same is the case with the fertilised queen in her old age, when the contents of the receptaculum seminis is exhausted. Workers also may lay eggs which develop into drones ; the larvæ destined to develop into workers may, if the food supply at any early stage be abundant, become queens. As parasites in bee-nests may be mentioned the death's head moth, the wax moth, the larva of the bee-wolf, (*Trichodes apiarius*), and the bee-louse (*Braula cæca*).

The genera *Melipona* Ill., *Trigona* Jur., comprise small American species of bees ; they appear, however, to be less closely related to the genus *Apis* than has been hitherto believed. With regard to the economy of the society, one of the most striking deviations they present, is that the brood-cells are filled with honey before the deposition of the eggs and afterwards closed, so that the just-hatched grub is provided beforehand with all the food material (Fr. Müller). The workers also prepare large reservoirs for the storage of the honey. Among the former there are forms as in *Dombus*, that do not build nests, but lay their eggs in the nests of other species.

INDEX.

- Aasfliege, 576.
 Aaskäfer, 590.
 Abdominalia, 446.
 Abiogenesis, 96.
 Abraxas, 583.
 Abyla, 250.
 Acalepha, 250.
 Acalyptera, 576.
 Acanthia, 572.
 Acanthobothrium, 327.
 Acanthocephala, 359, 343.
 Acanthometra, 191.
 Acarina, 489.
 Acephalocysts, 336.
 Achæta, 392.
 Acherontia, 584.
 Achtheres, 436.
 Acidalia, 583.
 Acineta, 205.
 Acmostomum, 312.
 Acœla, 313.
 Acraspeda, 233.
 Acridium, 527, 558.
 Acrocladia, 295, 296.
 Acronycta, 583.
 Acrophalli, 347.
 Actinaria, 232.
 Actinia, 230, 232.
 Actinometra, 286, 289.
 Actinophrys, 188.
 Actinosphærium, 188.
 Actinotrocha, 389.
 Actinozoa, 223.
 Aculeata, 595.
 Aculeus, 592.
 Adambulacral plates, 291.
 Adapis, 173.
 Adaptation, 145.
 Adaptions of embryos and larvæ, 157.
 Adelo-codonic gonophore, 236.
 Adenoid connective tissue, 38.
 Admiral, 585.
 Æga, 222, 460.
 Ægineta, 242.
 Æginopsis, 236.
 Æquorea, 238, 242.
 Æschna, 562.
 Æschna rectal, Respiration of, 72.
 Agalmidæ, 249.
 Agalmopsis, 247, 248, 249.
 Agassiz, L, 139.
 Agelena, 504.
 Aglia, 584.
 Agrilus, 589.
 Agrion, 562.
 Agriotes, 589.
 Agrotis, 583.
 Alary muscles, 533.
 Alaurina composita, 313.
 Albertus Magnus, 133.
 Albunea, 478.
 Alcinoë, 266.
 Alciopa, 380.
 Alciopea, 379.
 Alcippe, 446.
 Alcyonaria, 228, 231.
 Alcyonium, 231.
 Aldrovandus, 133.
 Alima, 472.
 Alpheidæ, 476.
 Alternation of generations, 123.
 Alucita, 582.
 Alula, 572.
 Alydus, 572.
 Ambulacral brains, 277.
 Ambulacral branchiæ, 277.
 Ambulacral feet, 273.
 Ambulacral Gills, 275.
 Ambulacral groove, 291.
 Ambulacral ossicles, 271, 290.
 Ambulacral plates, 271.
 Ambulacral surface, 269.
 Ambulacral vascular system, 272.
 Ametabola, 547.
 Ammophila, 596.
 Ammothea, 496.
 Amœba, 186.
 Amœbidium, 209.
 Ampharete, 382.
 Amphibia, Vascular system of, 65.
 Amphibiotica, 561.
 Amphidiscs, 218.
 Amphihelia, 232.
 Amphileptus, 195, 204.
 Amphinomidæ, 374.
 Amphioxus, Vascular system of, 63.
 Amphipeltis, 451.
 Amphipoda, 451.
 Amphipods, Parasites of, 362.
 Amphiporus, 342, 340.
 Amphistomum, 317.
 Amphitrocha, 378.
 Amphiuira, 278, 279, 285, 294.
 Anal, vesicles of Chaetifera, 388.
 Analogy, 52.
 Anapera, 575.
 Anatifa, 445.
 Anceus, 459.
 Anchitherium, 172.
 Anchorella, 436.
 Ancylostomum, 352.
 Andoctonus, 510.
 Andrena, 597.
 Anelasma, 445.
 Anguilla, 351.
 Anguillula, 357.
 Anilocra, 460.
 Animals and plants, 15.
 Anisopoda, 459.
 Annelida, 362.
 Anobium, 589.
 Anochanus, 279.
 Anopla, 342, 339, 341.
 Anoplotermes, 560.

- Anoplura, 568.
 Antedon, 289.
 Antennæ, 84.
 Antennal Gland of
   Thoracostraca, 461.
 Antennularia, 242.
 Anthophora, 598.
 Anthozoa, 223, 229, 230.
 Anthrax, 576.
 Antimere, 25.
 Antipatharia, 232.
 Antipathes, 232.
 Anthiata, 572.
 Ant-lion, 564.
 Ants, 595.
 Apatheon, 177.
 Apatura, 585.
 Aphalaspidae, 177.
 Aphaniptera, 578.
 Aphides, Reproduction
   of, 106, 128.
 Aphis, 569, 570.
 Aphodius, 590.
 Aphrodite, 379.
 Aphrophora, 571.
 Apical plate of Annelids,
   363.
 Apical pole of Echinoder-
   mata, 268.
 Apiocrinus, 289.
 Apiocystites, 289.
 Apion, 588.
 Apis, 598.
 Apoda, 299, 446.
 Apolemia, 246, 249.
 Aporosa, 232.
 Apseudes, 456.
 Apsilus, 401.
 Aptera, 567.
 Apus, 419.
 Arachnida, 484.
 Aradus, 572.
 Araneida, 498.
 Arcella, 186.
 Archæoniscus, 451.
 Archæopteryx, 175.
 Archegosaurus, 177.
 Archenteron, 116, 117.
 Archiannelida, 365, 376.
 Archigetes, 339.
 Arenicola, 381.
 Arethusa, 249.
 Argas, 495.
 Argulus, 438.
 Argynnis, 585.
 Argyroneta, 499, 504.
 Arista, 573.
 Aristotle, classification
   of, 132.
 Aristotle's lantern, 276.
 Armadillo, 457, 460.
 Arrhenotokia, 543.
 Artemia, 419.
 Arterial, 73.
 Artery, 62.
 Arthropoda, 405.
 Arthrostraca, 449.
 Articulata, 289.
 Ascalaphus, 564.
 Ascaltis, 222.
 Ascandra, 222.
 Ascaris, 347, 346, 351.
 Ascetta, 222.
 Ascella, 222.
 Ascomorpha, 404.
 Ascon, 222.
 Ascoris, 222.
 Asculmis, 222.
 Ascyssa, 222.
 Asellus, 460.
 Asilus, 576.
 Aspidochirota, 298, 299.
 Aspidiotus, 543, 569.
 Asplanchna, 404.
 Astacus, 477.
 Astasia, 169.
 Asteracanthion, 285,
   293.
 Asteriada, 293, 279.
 Asterias, 293.
 Asteridea, 279, 292.
 Asteroidea, 279, 290.
 Asterope, 427.
 Astræa, 229, 232.
 Astræidæ, 232.
 Astroides, 233.
 Astronyx, 294.
 Astropecten, 275, 292,
   293.
 Astrophyton, 294.
 Atax, 495.
 Ateuchus, 590.
 Athalia, 594.
 Athorybia, 248, 249.
 Atolls, 230.
 Atrocha, 377.
 Attacus, 584.
 Attagenus, 590.
 Atypus, 504.
 Auditory organs, 85.
 Aulasternum, 400.
 Aurelia, 261.
 Aurelio Severino, 133.
 Auricularia, 281, 282,
   283, 298.
 Autolytus, 372, 379.
 Aves, vascular system
   of, 67.
 Bacillus, 206.
 Bacteria, 206, 557.
 Baer, C. E. von, 137.
 Balaninus, 588.
 Balanoglossus, 299, 302.
 Balantidium, 205.
 Balanus, 446.
 Bark lice, 127, 570.
 Barrier reefs, 230.
 Bathybius, 186.
 Bathyrinus, 289.
 Bdella, 495.
 Bear-caterpillars, 583.
 Bed-bug, 572.
 Bedeguar of roses, 594.
 Bee-louse, 575, 599.
 Bees, 597.
 Beetle-mites, 495.
 Bee-wolf, 599.
 Bell Animalcule, 198.
 Bembex, 596.
 Beris, 577.
 Beroe, 264, 266.
 Bibio, 574, 577.
 Biesfliegen, 576.
 Biogenesis, 96.
 Bipalium, 315.
 Bipinnaria, 281, 283, 292,
   293.
 Bird spider, 504.
 Birgus, 478.
 Bittacus, 563.
 Bivium, 269.
 Bladder-Worm, 332.
 Blaps, 589.
 Blastoidea, 289.
 Blastopore, 114.
 Blastosphere, 113.
 Blastostyle, 236.
 Blastotrochus, 227, 232.
 Blatta, 557.
 Blatthornkäfer, 589.
 Blattkäfer, 588.
 Bläulinge, 585.
 Blendwanzen, 572.
 Blood-corpuscles, 32.
 Bockkäfer, 588.
 Body cavity, 50.
 Body cavity, primary,
   50, 116.
 Bombardierkäfer, 590.
 Bombus, 598.
 Bombycina, 583.
 Bombylius, 576.
 Bombyx, 581, 584.
 Bone, development of,
   40, 42.
 Bonellia, 392.
 Bonnet, 133.
 Book-lice, 559.
 Bopyrus, 460.
 Borkenkäfer, 588.
 Borlasia, 340, 342, 343.
 Bos taurus, origin of, 143.

- Bostrychus, 588.
 Bothriocephalidæ, 336.
 Bothriocephalus, 330, 331, 337, 334, 327.
 Botrytis, 584.
 Botys, 582.
 Brachinus, 590.
 Brachiolaria, 281, 292, 293.
 Brachionus, 404.
 Brachycera, 575.
 Brachyura, 478.
 Bracon, 595.
 Brain, 80, 82.
 Branchellion, 400.
 Branchiæ, 69.
 Branchiæ of Chaetopods, 367.
 Branchiobdella, 400.
 Branchiopoda, 418.
 Branchiostegite, 463.
 Branchipus, 419.
 Branchiura, 436.
 Braula, 575, 599.
 Brisinga, 293.
 Brissus, 297.
 Brittle stars, 293.
 Brontotheridæ, 173.
 Brown tubes of Gephyræa, 388.
 Buckelzirpen, 571.
 Budding, 96.
 Buffon, 139.
 Bugs, 571, 567.
 Bunodes, 225.
 Buprestis, 589.
 Bursæ of Ophiuridea, 294.
 Bursaria, 205.
 Butterflies, 579.
 Calandrar, 588.
 Calanidæ, 435.
 Calappa, 478.
 Calcareous sacs of Lumbricus, 383.
 Calcareous sponges, 222.
 Calcispongiæ, 222.
 Callidina, 404.
 Caligus, 436.
 Callianassa, 477.
 Calopteryx, 562.
 Calotermes, 559, 561.
 Calycophoridæ, 249.
 Calycozoa, 254, 257.
 Calymene, 484.
 Calyptopis, 474.
 Camberwell beauty, 585.
 Camel-neck flies, 563.
 Campanularia, 242.
 Campanulariæ, 241.
 Campodea, 554.
 Cancer, 478.
 Cantharidæ, 588.
 Cantharis, 589.
 Canthocamptus, 435.
 Capillary, 63.
 Capitella, 377.
 Capitellidæ, 375.
 Capitibranchiata, 381.
 Caprella, 454.
 Capsus, 572.
 Carabus, 590.
 Carchesium, 205.
 Carcinus, 478.
 Cardo, 523.
 Carididæ, 477.
 Carina of Cirripedia, 439.
 Carmarina, 242.
 Carotid arteries, 66.
 Carp-lice, 438.
 Cartilage, 39.
 Cartilage calcified, 40.
 Caryocrinus, 289.
 Caryophyllæus, 326, 328, 334, 338.
 Caryophyllia, 232.
 Catenula, 312, 313.
 Caterpillar, 549, 581.
 Catocala, 583.
 Catometopa, 478.
 Cecidomyia, 578.
 Cecidomyia, reproduction of, 106, 128, 544.
 Cecrops, 436.
 Cell, 12, 29.
 Cellular tissue, 37.
 Central plate, 271.
 Centrolecithal, 112.
 Centrotus, 571.
 Cephalic branchiæ of chaetopoda, 369.
 Cephalopoda, eye of, 90.
 Cephalothorax of Arthropoda, 407.
 Cephalotrichidæ, 343.
 Cephalothrix, 343.
 Cephalotrocha, 378.
 Cephea, 261.
 Cerambyx, 588.
 Ceraospongia, 221.
 Cerapus, 453, 455.
 Ceratium, 196.
 Cercaria, 129, 320.
 Cercaria macrocerca, 321.
 Cercheris, 596.
 Cercomonas, 194.
 Cerebratulus, 343.
 Cerianthus, 225, 232.
 Cestidæ, 263.
 Cestoda, 325.
 Cestum, 264, 265, 266.
 Cetochilus, 435.
 Cetonia, 590, 586.
 Chaetifera, 389.
 Chaetogaster, 386.
 Chaetognatha, 357.
 Chaetonotus, 404.
 Chaetopoda, 367.
 Chaetopterus, 382.
 Chaetosomidæ, 357.
 Chalicodoma, 598.
 Chalineæ, 220.
 Charybdea, 259.
 Charybdeidæ, 252, 251,
 Cheese-flies, 576.
 Cheese-mites, 492.
 Cheimatobia, 583.
 Cheiracanthus, 345.
 Cheliceræ, 484.
 Chelifer, 511.
 Chelura, 453, 455.
 Chermes, 543, 570.
 Chermes, reproduction of, 127.
 Chernetidæ, 511.
 Chiaja, 266.
 Chigoe, 579.
 Chilocorus, 587.
 Chilodon, 205.
 Chilognatha, 520.
 Chilopoda, 518.
 Chirodota, 299.
 Chironomus, 578.
 Chitin, 79.
 Chlamydomonas, 194.
 Chloëon, 561.
 Chlorophyll, 20, 21.
 Chlorops, 576.
 Chondracanthus, 423.
 Chorion, 98, 542.
 Choroid of eye, 88.
 Chromulina, 195.
 Chondrosia, 221.
 Chrysaora, 261.
 Chrysididæ, 596.
 Chrysis, 596.
 Chrysomela, 588.
 Chrysomitra, 246, 250.
 Chrysopa, 564.
 Chrysops, 577.
 Chrysosoma, 576.
 Chthonius, 511.
 Chyle, 57, 67.
 Chylific ventricles, 530.
 Chyme, 57.
 Cicada, 567, 571.
 Cicadellidæ, 571.
 Cicadidæ, 571.
 Cidaridea, 273, 274, 295, 296.
 Cidaris, 293.

- Ciliary body, 90.
 Ciliata, 196.
 Cilioflagellata, 196.
 Cimbex, 594.
 Cincindela, 590.
 Cineras, 445.
 Cirri of Chætopods, 367.
 Cirri of Vermes, 307.
 Cirripedia, 438.
 Cirrus, sac of Trematodes, 318.
 Cirrus, sheath of Cestoda, 329.
 Cirrus of Trematodes, 318.
 Cistela, 589.
 Citigradæ, 504.
 Citronvogel, 585.
 Cladocera, 419.
 Claspers of Tanäidæ, 459
 Clathrulina, 188.
 Clava, 241.
 Clavidæ, 241.
 Claviger, 590.
 Clavulæ, 272.
 Clavulæ of Echinoidea, 296.
 Claw, 34.
 Clepsidrina, 208.
 Clepsine, 400.
 Clerus, 589.
 Climate, influence of, 148.
 Climate in relation to fauna, 160.
 Clisiocampa, 584.
 Clitellus of Lumbricus, 323, 385.
 Clothes moth, 582.
 Clubiona, 504.
 Clypeaster, 297.
 Clypeastridæ, 295, 296.
 Clypeastridea, 268, 273, 296.
 Clythia, 242.
 Clythra, 588.
 Cnethocampa, 584.
 Cnidaria, 222.
 Cnidoblast, 212, 223.
 Cnidocil, 223.
 Coccidæ, 567, 568.
 Coccidia, 209.
 Coccinella, 587.
 Coccus, 569.
 Coccygeal glands, 77.
 Cochineal, 569.
 Cockchafer, 590.
 Cockroach, 557.
 Codosiga, 196.
 Cœlenterata, 209.
 Cœlom, 50.
 Coenenchym, 227.
 Cænobita, 478.
 Cænurus, 331, 333
 Cold-blooded, 74.
 Coleoptera, 585.
 Colias, 585.
 Collembola, 553.
 Collosphæra, 191.
 Collozoum, 191.
 Colpodella, 194.
 Colpoda, 205.
 Columella of Actinozoa, 228.
 Colymbetes, 590.
 Comatula, 276, 286, 288, 289.
 Complemental males of Cirripedia, 442.
 Compsognathus, 177.
 Conchoderma, 445.
 Conjugation, 202.
 Connective tissues, 37.
 Conochilus, 404.
 Conops, 576.
 Contractile Vacuole, 180.
 Convoluta, 311, 314, 313.
 Convolutidæ, 313.
 Copepoda, 428.
 Copris, 590.
 Coral, mushroom, 232.
 Coral organ, 231.
 Coral Polyps, 223.
 Coral, red, 231.
 Coral reefs, 230.
 Coral, star, 232.
 Coral, white, 232.
 Corallium, 231.
 Cordylophora, 241
 Corethra, 578.
 Coreus, 572.
 Corixa, 572.
 Cornca, 87.
 Cornularia, 231.
 Cornuspira, 187.
 Coronula, 446.
 Corophium, 454.
 Correlation, 51.
 Corrodentia, 559.
 Corycæus, 436.
 Corydalis, 563.
 Corymorpha, 240, 241.
 Cossus, 584.
 Costa, 528.
 Costa of Actinozoa, 228.
 Coxa, 526.
 Crabro, 597.
 Crab-spiders, 594.
 Crambus, 582.
 Crangon, 477.
 Craspedota, 238.
 Craspedota, 258.
 Craterolophus, 258.
 Crayfish, 477.
 Crevettina, 454.
 Cribrellum, 499.
 Crickets, 558.
 Crinoidea, 279, 286.
 Crinoids, 289.
 Criodrilus, 385.
 Crocodilia, heart of, 67.
 Crop, 57, 530.
 Crustacea, 411.
 Cryptocephalus, 588.
 Cryptoniscus, 460.
 Cryptopentamera, 588.
 Cryptophialus, 446.
 Crystalline cone, 87.
 Cteniza, 504.
 Ctenodiscus, 275, 293.
 Ctenophora, 261, 578.
 Ctenophor type, 211.
 Cubitus, 528.
 Cuckoo-spittle, 571.
 Cucullanus, 348, 353.
 Cucullia, 583.
 Cucumaria, 299.
 Culex, 578.
 Culicidæ, 574.
 Culiciformes, 578.
 Cumacea, 469.
 Cunina, 239, 242.
 Curculionidæ, 588.
 Cursoria, 556.
 Cutaneous gland, 77.
 Cuticle, 35.
 Cuvier, 135.
 Cuvieria, 297.
 Cuvier, organs of, in Holothuroidea, 298.
 Cyamus, 454.
 Cyanea, 261.
 Cyathophyllidæ, 230.
 Cyclometopa, 478.
 Cyclops, 435.
 Cydippe, 265, 266.
 Cylicomastiges, 196.
 Cylicozoa, 257.
 Cymothoa, 460.
 Cynipidæ, 594.
 Cynips, 594.
 Cyphophthalmus, 506.
 Cypridina, 427.
 Cypris, 428.
 Cypris-stage of Cirripedia, 443.
 Cyrtopia, 474.
 Cysticereus, 332, 335.
 Cystic-worm, 332.
 Cystidea, 289.
 Cystosoma, 453.
 Cystotænia, 335.
 Cythere, 427.

- Dactylocalyx, 221.
 Dactylozooids, 246.
 Daphnia, 422.
 Darwin, 145.
 Dasychira, 583.
 Dasypoda, 597.
 Death-head moth, 584.
 Death-watch, 589.
 Decapoda, 475.
 Deep sea Fauna, 163.
 De Geer, 133.
 Degradation, 158.
 Delamination, 114.
 Demodex, 492.
 Dendrochirota, 299.
 Dendrocœla, 311, 314.
 Dendrocœlum, 315.
 Dendrometridæ, 583.
 Dendrophyllia, 233.
 Dentine, 41.
 Dermal branchiæ, 277.
 Dermanyssus, 495.
 Dermatobia, 576.
 Dermatodectes, 492.
 Dermatophili, 492.
 Dermatoptera, 556.
 Dermestes, 590.
 Derostomea, 312.
 Derostomum, 313.
 Descent, evidence in favour of theory of, 151.
 Desmoscolecidæ, 357.
 Desor, Type of, 341.
 Deutoplasm, 111.
 Development, 107.
 Diaptomus, 435.
 Diastylis, 470.
 Diffugia, 186.
 Digenous reproduction, 97.
 Digging-wasps, 596.
 Digonopora, 316.
 Diloba, 583.
 Dimorphism, facts of, in favour of theory of descent 152, sexual 101, 153.
 Dinoceras, 173.
 Dinosauridæ, 175.
 Dioecious, 100.
 Diopatra, 374, 379.
 Diphyes, 246, 250.
 Diplophysa, 250.
 Diplozoon, 324.
 Dipneumones, 504.
 Diporpa, 325.
 Diptera, 572.
 Direct development, 120.
 Directive body, 109.
 Discoidal segmentation, 112.
 Discoideæ, 250.
 Discomedusa, 260, 261.
 Discophora (Coelenterate), 259, 394.
 Discophora, see Hirudinea.
 Dissepimenta of Actinozoa, 228.
 Dissepiments of Annulida, 364.
 Distomea, 318, 321.
 Distomum, 317, 322.
 Distomum cygnoides, 321.
 Distomum hæmatobium, 321.
 Dochmius, 350, 352.
 Dolichopus, 576.
 Dolomedes, 502, 504.
 Doritis, 585.
 Dorsibranchiata, 370, 379.
 Dorylaimus, 357.
 Dracunculus, 356.
 Dragon-fly, 562.
 Dromia, 478.
 Drone, 598.
 Ductus Botalli, 66.
 Dung-flies, 576.
 Duodenum, 57.
 Dynamena, 242.
 Dysdera, 499.
 Dytiscus, 590.
 Earwigs, 556.
 Ecdysis of Arthropoda, 407.
 Echinaster, 273, 293.
 Echineibothrium, 338, 326.
 Echiniscus, 497.
 Echinococcifer, 335.
 Echinococcus, 336, 331, 333.
 Echinocucumis, 297.
 Echinocyamus, 297.
 Echinoderidæ, 404.
 Echinodermata, 266.
 Echinoidea, 294.
 Echinometra, 295, 296.
 Echinorhynchus, 362.
 Echinus, 296.
 Echiuroidea, 389.
 Echiurus, 387, 392.
 Ecton, 596.
 Ectoderm, 213, 49, 116.
 Ectolecithal, 112.
 Ectolithia, 189.
 Ectoplasm, 54.
 Eisvogel, 585.
 Elastic fibres, 39.
 Elater, 589.
 Eleutheroblasteæ, 240.
 Ellipsocephalus, 484.
 Elytron, 369, 528.
 Embolic invagination, 114.
 Embryology in relation to descent theory, 157.
 Embryonic development, 119.
 Empidæ, 576.
 Enchelidium, 357.
 Enchytræus, 384.
 Encrinus, 289.
 Endoderm, 116, 49, 213.
 Endogenous cell formation, 30, 31.
 Endomychidai, 588.
 Endoplasm, 54.
 End-organs, 47.
 Endoskeleton, 79.
 Endothelium, 34.
 Enopla, 339, 342.
 Enoplus, 357.
 Enterocœle, 116.
 Enteroplea, 404.
 Enteropneusta, 299.
 Entoconcha, 299.
 Entolithia, 189.
 Entomophaga, 594.
 Entomostraca, 416.
 Entoniscus, 459, 460.
 Entozoa, 308.
 Epeira, 505.
 Ephemera, 531, 562.
 Ephemeridæ, 561.
 Ephialtes, 595.
 Ephippigera, 558.
 Ephryopsis, 261.
 Ephyra, 125, 253, 251.
 Ephyra-Medusæ, 259.
 Epiblast, 114.
 Epibole, 115.
 Epimerum, 525.
 Epipharynx, 524.
 Episternum, 525.
 Epistom of Decapoda, 476.
 Epistylis, 205.
 Epithelium, 34.
 Equitidæ, 585.
 Equus, phylogeny of, 172.
 Erebia, 585.
 Erichthus, 472.
 Eristalis, 576.
 Errantia, 378.
 Erythræus, 495.
 Eschscholtzia, 266.
 Estheria, 419.
 Eucephala, 577.
 Eucharis, 266.
 Euchlanis, 404.

- Eucope, 242.
 Eucopopoda, 435.
 Eucopidae, 234, 224, 242.
 Eucyrtidium, 190.
 Eudendrium, 241.
 Eudoxia, 250.
 Euglena, 196.
 Eulyphe, 186.
 Euisopoda, 460.
 Ennice, 379.
 Euphausia, 475.
 Euphausia, eyes of, 409.
 Euplectella, 221.
 Euprepia, 583.
 Eurhamphæa, 266.
 Euryalidæ, 273, 275, 294.
 Eurylepta, 316.
 Eurypterus, 480.
 Eusmilia, 232.
 Euspongia, 221.
 Eustrongylus, 352.
 Eutermes, 559.
 Eutyphis, 456.
 Evadne, 422.
 Evania, 595.
 Exoskeleton, 78.
 Eyes, 85.

 Fabricia, 372.
 Facetted eye, 88.
 Faltenmücke, 578.
 Fan of Arthropoda, 409.
 Fan-tracheæ, 70, 410.
 Fasciola, 316.
 Fascioles, 272, 296.
 Fat, 39.
 Fauna of deep sea, 163.
 Fauna, relation of to recent fossil forms, 170.
 Feathers, Sea, 231.
 Federgeistchen, 582.
 Femur, 526.
 Fertilisation of ovum, 109.
 Fetteschabe, 582.
 Feuerwanze, 572.
 Fibrillar tissue, 38.
 Field cricket, 558.
 Figites, 594.
 Filaria, 347, 349, 352, 356.
 „ host of, 356.
 Filariidæ, 355.
 Filigrana, 382.
 Final causes, doctrine of, 51.
 Fir-tree lice, 570.
 Fission, 96.
 Flabellum, 232.
 Flagellata, 193.
 Flata, 571.
 Flea, 579.

 Fleischfliege, 576.
 Flies, 575.
 Floscularia, 404.
 Floscularidæ, 404.
 Fœnus, 595.
 Foramen Panizzæ, 67.
 Foraminifera, 184.
 Fore-gut, 56.
 Forficula, 556.
 Formica, 596.
 Formicidæ, 595.
 Formikalia, 249.
 Fossils, Conditions of formation of, 168; Relation of, to living species, 170.
 Fossoria, 596.
 Free cell formation, 30.
 Fringing reefs, 230.
 Fritillary, 585.
 Frost-butterflies, 583.
 Fulgora, 571.
 Fumca, 584.
 Fungia, 232.
 Fungicolæ, 578.
 Fungidæ, 232.
 Fureilia, 474.

 Gabelschwanz, 584.
 Gadflies, 576.
 Galathea, 477.
 Galaxea, 232.
 Galea, 523.
 Galeodes, 512.
 Galleria, 582.
 Gall flies, 578.
 Gall-flies, Reproduction of, 128.
 Gallicola, 594.
 Gallicolæ, 578.
 Galls, 594.
 Gall-wasps, 594.
 Gamasus, 495.
 Gammarus, 455.
 Ganglion cells, 45.
 Gastræa theory, 118.
 Gastropacha, 584.
 Gastrophilus, 576.
 Gastrotricha, 404.
 Gastrotrocha, 378.
 Gastrovascular space of Coelenterata, 209.
 Gastro-vascular system, 60.
 Gastrula, 49, 114, 118.
 Gastrus, 576.
 Gebia, 477.
 Gecarcinus, 469, 479.
 Gelasimus, 479.
 Gelatinous sponges, 221.
 Gemmules, 218.

 Genera, Origin of, 149.
 Generatio equivoca, 10.
 Geocentrophora, 313.
 Geocores, 572.
 Geodesmus, 316.
 Geographical distribution, 159.
 Geological periods, Characteristics of, 177.
 Geological record, Improvement of, 168.
 Geological table, 165.
 Geometra, 583.
 Geometridæ, 580.
 Geometrina, 582.
 Geophilus, 519.
 Geopiana, 316.
 Geoplanidæ, 315.
 Geotrupes, 590.
 Gephyrea, 386.
 Germ-cell, 105.
 Germinal bands, 547.
 Germinal disc, 112.
 Germinal streak, 115.
 Germinal vesicle, 110.
 Germs of Trematodes, 319.
 Germ-stock, 96.
 Geryonia, 239, 242.
 Geryonopsidæ, 242.
 Gessner 133.
 Gibocellum, 506.
 Gigantostraca, 479.
 Gills 69, Tracheal, 70.
 Glabellum, 484.
 Gland, 36.
 Glands, cutaneous, 77.
 Glassy sponges, 221.
 Glaucoma, 205.
 Gleba, 250.
 Globigerina, 187.
 Glomeris, 516, 521.
 Glomerulus, 77.
 Glossa, 524.
 Glow-worm, 589.
 Glycera, 377, 379.
 Glyciphagus, 493.
 Glyptodon, 170.
 Gnat, 578.
 Gnathobdellidæ, 400.
 Gnathostoma, 345.
 Gnathostomata, 435.
 Goethe, 137.
 Goldfliege, 576.
 Gold-wasps, 596.
 Gonium, 195.
 Gonophore, 237.
 Gonophores of Siphonophora, 246.
 Gonospora, 208.
 Gonyleptus, 506.

- Gordiidae, 356.
 Gordius, 346, 345, 348, 357.
 Gorgonia, 231.
 Gorgonidas, 224.
 Grain-worms, 582.
 Grantia, 217, 222.
 Grapholitha, 582.
 Grapsus, 479.
 Grasshoppers, 557.
 Gregarinidae, 207.
 Gressoria, 557.
 Gromia, 187.
 Gryllotalpa, 527, 558.
 Gryllus, 558.
 Gymnocopa, 380.
 Gymnophthalmata, 238.
 Gynæcophorus, 322.
 Gyrator, 314.
 Gyrodactylus, 325.
 Gyropeltis, 438.

 Hæmatopota, 577.
 Hæmatozoa, 356.
 Hæmentaria, 400.
 Hæmoglobin, 33.
 Hæmopsis, 400.
 Hairstreak butterflies, 585.
 Halichondria, 221.
 Halicryptus, 394.
 Halisarca, 221.
 Halistemma, 249.
 Halla, 379.
 Halocypris, 427.
 Halomitra, 232.
 Halosauridae, 175.
 Halteres, 528, 572.
 Halteria, 205.
 Haltica, 588.
 Hamm, 133.
 Harlequin, 583.
 Harpacticus, 435.
 Harpalus, 590.
 Harpyia, 584.
 Harvey, 133.
 Haustellum, 573.
 Haversian canals, 41.
 Hawk-moths, 584.
 Heart of vertebrata, Evolution of, 64.
 Heat, animal, 73.
 Heliaster, 293.
 Heliosphæra, 190.
 Heliozoa, 187.
 Hemerobidae, 564.
 Hemerobius, 564.
 Hemiaspis, 480.
 Hemiaster, 279.
 Hemielytra, 571.
 Hemiptera, 566, 571.

 Henops, 576.
 Hepato-pancreas, 59.
 Hepialus, 584.
 Herbert on fertility of Hybrids, 142.
 Heredity, 145.
 Hermaphroditism 99, incomplete, 100.
 Hermella, 382.
 Hermit Crabs, 478.
 Hesperia, 585.
 Hesperornis, 176.
 Hessian fly, 578.
 Heterodera, 357.
 Heterogamia, 555, 557.
 Heterogamy, 127, 130, 131, 543.
 Heterogamy, incomplete, 131.
 Heterogyna, 596.
 Heteromera, 588.
 Heteronereis, 373, 379.
 Heterotricha, 205.
 Heuschrecken, 557.
 Hexactinellidae, 220.
 Hexactinia, 231.
 Hexapoda, 521.
 Hibernation, 74.
 Hilaire, E. G. St., 137.
 " " on mutability of species, 144.
 Hindgut, 56.
 Hippa, 478.
 Hipparchia, 585.
 Hipparion, 172.
 Hippidae, 477.
 Hippobosca, 575.
 Hippodidae, 249.
 Hirudinea, 394.
 Hirudo, 400.
 Hispa, 588.
 Hister, 590.
 Histolysis, 550.
 History of Zoology, 131.
 Holoblastic, 111.
 Holopus, 289.
 Holothuria, 299.
 Holothurians, 279.
 Holothuroidea, 297.
 Holotricha, 204.
 Holzfliegen, 577.
 Homarus, 477.
 Homology, 52.
 Homoptera, 570.
 Homothermic, 74.
 Honey-dew, 569.
 Hoof, 34.
 Hormiphora, 266.
 Hormiscium, 206.
 Hornets, 597.
 Horny sponges, 221.

 Horse-louse, 575.
 House-fly, 576.
 Humble bee, 598.
 Hummelfliegen, 576.
 Humming-bird Hawk-moth, 584.
 Hyalonema, 222.
 Hyalospongia, 221.
 Hybrid 142, Fertility of, 142.
 Hydatid plague, 336.
 Hydatina, 404.
 Hydra, 240.
 Hydrachna, 495.
 Hydractinia, 241.
 Hydranth, 244.
 Hydrobius, 590.
 Hydrocorallia, 240.
 Hydrocores, 571.
 Hydromedusæ, 236.
 Hydrometra, 572.
 Hydrophilus, 590.
 Hydrophilus, development of, 545.
 Hydrophyllia, 246.
 Hydropsyche, 565.
 Hydrosoma, 244.
 Hydrotheca, 241, 234.
 Hydrozoa, 233.
 Hylobius, 588.
 Hymenocaris, 448.
 Hymenoptera, 590.
 Hyperia, 455.
 Hyperida, 455.
 Hyperina, 455.
 Hypermetamorphosis, 548, 588.
 Hypoblast, 114.
 Hypoderma, 576.
 Hypodermis Arthropoda, 407.
 Hypodermis of Vermes, 303.
 Hypodermis or Nematoda, 345.
 Hypopharynx, 524.
 Hypopus, 493.
 Hypotricha, 205.
 Hystrix, 379.

 Ibla, 445.
 Ichneumon, 595.
 Ichthydina, 404.
 Ichthyobdellidae, 399.
 Ichthyornithes, 175.
 Idotea, 460.
 Idyopsis, 266.
 Iliæ, 478.
 Ileum, 57.
 Imaginal disc, 550.
 Imago, 548.

Imperforata, 187.
 Inachus, 478.
 Inæquitelæ, 504.
 Individual, 24, 25.
 Infundibulum of Ctenophora, 263.
 Infusoria, 191.
 Insecta, 521.
 Instinct, 94.
 Iphimedia, 453.
 Irenæus, 435.
 Iris, 88.
 Irregular Sea-urchins, 268.
 Isidor of Seville, 133
 Isis, 231
 Isogonism, 240.
 Isopoda, 456.
 Isopods, Parasites of, 362.
 Itch-mites, 492.
 Ixodes, 493.

 Japyx, 528, 554.
 Jassus, 571.
 Jejunum, 57.
 Jera, 460.
 Julius, 521.

 Kammücke, 578.
 Kermes, 569.
 Kidneys, 75.
 Kleinzirpen, 571.
 Kochlorine, 446.
 Kohlschnaken, 578.
 Kolumbaczer, 577.
 Kornmotte, 582.
 Kupferglucke, 584.
 Kurzdeckflügler, 590.

 Labidura, 556.
 Labium, 523.
 Labrum, 523.
 Lac, 569.
 Lachnus, 570.
 Lacinia, 523.
 Lacon, 589.
 Lady-bird, 587.
 Læmodipoda, 454.
 Lagenæ, 187.
 Lamark, 144.
 Lamellicornia, 589.
 Lamia, 527, 588.
 Lampyrus, 536, 589.
 Land-bugs, 572.
 Land Crabs, 479.
 Langwanzen, 572.
 Lantern-carrier, 571.
 Laomedæa, 242.
 Laphria, 576.
 Larentia, 583.

Larva, 119.
 Larva of Lovén, 362.
 Lasia, 576.
 Lateral lines of Nematoda, 346.
 Laterigradæ, 504.
 Laurer's canal, 318.
 Leaf-flea, 570.
 Leaf-lice, 570.
 Leaf-wasps, 594.
 Lecanium, 543, 569.
 Ledermüller, 133.
 Ledra, 571.
 Leech, 394.
 Leeuwenhoek, 133.
 Lemnisci of Acanthocephala, 360.
 Lens, 87.
 Lepadidæ, 445.
 Lepas, 445.
 Lepidocentrus, 295.
 Lepidoptera, 579.
 Lepisma, 554.
 Leptidæ, 577.
 Leptodera, 350, 357.
 Leptodiscus, 198.
 Leptodora, 422.
 Leptoplana, 311, 316.
 Leptostraca, 448.
 Leptus, 495.
 Lernæa, 436.
 Lernæocera, 436.
 Lernæodiscus, 447.
 Lernæopodidæ, 436.
 Lestornis, 177.
 Lestrigonus, 455.
 Leucaltis, 222.
 Leucandra, 222.
 Leucetta, 222.
 Leuchtzirpen, 571.
 Leucifer, 471, 476.
 Leucilla, 222.
 Leucochloridium, 321.
 Leucon, 470.
 Leuconia, 222.
 Leuconidæ, 217.
 Leucoris, 222.
 Leucortis, 222.
 Leucosolenia, 217, 222.
 Leuculmis, 222.
 Leucyssa, 222.
 Levantine sponges, 221.
 Libellula, 541, 562.
 Libellula, Development of, 545.
 Libellula, Rectal respiration of, 72.
 Lice, 568.
 Lice-flies, 575.
 Ligia, 459, 460.
 Ligula, 338.

 Ligulidæ, 323.
 Limenitis, 585.
 Limexylon, 589.
 Limicolæ, 385.
 Limnobates, 572.
 Limnobiidæ, 578.
 Limnochares, 495.
 Limnodrilus, 385.
 Limnoria, 455, 460.
 Limulus, 483.
 Lina, 588.
 Linckia, 292, 293
 Lineus, 343.
 Linguatulida, 487.
 Linnæus, 134.
 Liotheum, 568.
 Liparis, 583.
 Liriope, 242.
 Lithistidæ, 220.
 Lithobius, 520.
 Lithodes, 478.
 Lithotrya, 444.
 Liver, 59.
 Liver Fluke, 317, 322.
 Livia, 570.
 Lobophora, 258, 297.
 Lobosa, 185.
 Lobster, 477.
 Locusta, 558.
 Longhorns, 577.
 Longicornia, 588.
 Loopers, 582.
 Lophogaster, 475.
 Lophoseris, 232.
 Loricata, 477.
 Loven's larva, 308, 362.
 Lucanus, 589.
 Lucernaria, 258.
 Luidia, 275, 293.
 Lumbriculus, 385.
 Lumbricus, 385.
 Lungs, 69.
 Lungs, Effect of appearance of, on vascular system, 65.
 Lycænidæ, 585.
 Lycæretus, 374.
 Lycoridæ, 379.
 Lycosa, 504.
 Lyda, 594.
 Lyell, 144.
 Lyell's doctrine of gradual changes, 166.
 Lygæus, 572.
 Lymnæus, Pulmonary cavity of, 72.
 Lymph, 67.
 Lymphatic system, 67.
 Lysianassa, 451, 455.
 Lysidice, 379.
 Lystra, 571.

- Lytta, 589.
 Machilis, 554.
 Macrobiotus, 497.
 Macroglossa, 584.
 Macrostomum, 312.
 Macrura, 477.
 Macula acustica, 85.
 Madrepora, 233.
 Madreporaria, 228, 232.
 Madrepores, 229.
 Madreporic plate, 273.
 Madreporidæ, 233.
 Mæandrina, 232.
 Mæandrinidæ, 229.
 Maggot, 549.
 Magpiemoth, 583.
 Maja, 478.
 Malachius, 589.
 Malacobdella, 342, 343.
 Malacodermata, 589.
 Malacostraca, 447.
 Mallophaga, 568.
 Malpighi, 133.
 Malpighian body, 76.
 Malpighian tubes, Arthropoda, 409.
 Malpighian tubules, 75.
 Mammalia, Vascular system of, 67.
 Man, First traces of, 178.
 Mandibles of Crustacea, 412.
 Manna, 569.
 Mantis, 527, 557.
 Mantispa, 564.
 Manubrium, 211.
 Marginal bodies, 234, 239, 254.
 Marine Fauna, 162.
 Marrow, 41.
 Marsupialida, 258.
 Marsupialis, 252.
 Mask, 562.
 Masticatory organs, 56.
 Maxilla of Crustacea, 413.
 May Flies, 561.
 Meal-worm, 589.
 Meckelia, 343.
 Medusa aurita, 261.
 Medusæ, 236.
 Medusa, Relation of to Polyp, 236.
 Medusa type, 211.
 Medusites circularis, 256.
 Medusoids, 211.
 Megachile, 598.
 Megalonyx, 170.
 Megalotrocha, 401.
 Megatherium, 170, 173.
 Melicerta, 404.
 Melipona, 590.
 Melitæa, 585.
 Melithæa, 231.
 Meloë, 589.
 Melolontha, 590.
 Melophagus, 575.
 Membracis, 571.
 Membranacei, 572.
 Membranous labyrinth, 85.
 Menopon, 568.
 Mentum, 524.
 Mermis, 345, 356.
 Mermithidæ, 356.
 Meroblastic, 111.
 Meromyaria, 345.
 Merostomata, 479.
 Mesenteric filaments, 224.
 Mesoderm, 116, 213.
 Mesostomea, 313.
 Mesostomum, 313.
 Mesothorax, 525.
 Mesotrocha, 378.
 Metabolism, 10.
 Metachæta, 378.
 Metagenesis, 123, 130, 131.
 Metamere, 27, 305.
 Metamorphosis, 126.
 Metamorphosis retrogressive, 158.
 Metanauplius, 432.
 Metathorax, 525.
 Metazoa, 54.
 Metæcus, 589.
 Miastor, 578.
 Miastor, Pædogenesis of, 544.
 Micrococcus, 206.
 Microgaster, 595.
 Microlepidoptera, 582.
 Micrommata, 504.
 Microstomea, 312.
 Microstomidæ, 309.
 Microstomum, 314.
 Microtænia, 336.
 Micrura, 343.
 Midgut, 56.
 Migration, 74.
 Miliola, 187.
 Millepora, 241.
 Milleporidæ, 233.
 Milnesium, 497.
 Mimicry, 155.
 Miris, 572.
 Mites, 489.
 Mole cricket, 558.
 Molpadia, 299.
 Monadinæ, 193.
 Monads, 194.
 Monas, 194, 206.
 Monera, 182.
 Mongrels, Sterility of, 143.
 Monocaulus, 240.
 Monocelis, 311, 313.
 Monocystidea, 208.
 Monocystis, 208.
 Monogenous reproduction, 97.
 Monogonopora, 315.
 Monophyes, 250.
 Monostomum, 317, 321.
 Monothalamia, 186.
 Morphology, 52.
 Morphology, Evidence of, for descent theory 151.
 Mososaurus, 175.
 Mucous connective tissue, 37.
 Müllerian duct, 101.
 Mundhorn-fliege, 576.
 Musca, 576.
 Muscardine, 584.
 Muscaria, 575.
 Musciformes, 577.
 Muscle-epithelium, 43.
 Muscular tissue, 43.
 Mushroom coral, 232.
 Mutilla, 596.
 Mycetophila, 578.
 Mygale, 504.
 Mygalidæ, 499, 504.
 Mylodon, 173.
 Myoblast, 43.
 Myriapoda, 514.
 Myrmecia, 504.
 Myrmecophila, 596.
 Myrmedonia, 590.
 Myrmeleon, 564.
 Myrmica, 596.
 Mysis, 474.
 Mysis, Auditory organ of, 414.
 Mystacides, 565.
 Myxospongia, 221.
 Myxospongiæ, 220.
 Myzostoma, 380.
 Nadina, 313.
 Naidesæ, 385.
 Nail, 34.
 Nais, 386.
 Natural selection, 145.
 Natural system, 150.
 Naucoris, 527, 572.
 Nauplius, 406, 415.
 Nausithoë, 260, 261.
 Nausithoë, Eye of, 255.

- Nautilus, Eye of, 90.
 Nebalia, 448.
 Necrophorus, 590.
 Nectocalyces, 246.
 Nemathelminthes, 343.
 Nematocalyces, 242.
 Nematocysts, 212.
 Nematus, 543, 594.
 Nemertes, 342, 343.
 Nemertini, 339.
 Nemocera, 577.
 Nemoptera, 564.
 Nemura, 561.
 Nepa, 527, 534, 572.
 Nephelis, 400.
 Nephridia, 308.
 Nephrops, 477.
 Nereilepas, 379.
 Nereis, 379.
 Nerve fibre, 46.
 Nerve tissue, 45..
 Nervous system, Gradations of, 80.
 Nervures, 528.
 Neuromuscular cells, 80.
 Neuropodia of Annelids, 365.
 Neuroptera, 562.
 Niphargus, 455.
 Noctiluca, 196.
 Noctuiiformes, 578.
 Noctuidina, 583.
 Nomada, 597.
 Nonionina, 184.
 Notodelphys, 435.
 Notodonta, 584.
 Notodromus, 428.
 Notommata, 401, 404.
 Notonecta, 572.
 Notopoda, 478.
 Notopodia of Annelids, 365.
 Notum, 525.
 Nuclear fluid, 29.
 Nuclearia, 194.
 Nuclear plate, 30.
 Nuclear substance, 29.
 Nucleolus, 29.
 Nucleus, 12, 13, 29.
 Nucleus, Division of, 30.
 Nummulina, 187.
 Nutritive polyp, 236.
 Nut-weevil, 588.
 Nycteribia, 575.
 Nymphaliadæ, 585.
 Nymphula, 582.
 Obelia, 242.
 Obisium, 611.
 Oceanidæ, 234.
 Ocellata, 239, 241.
 Ochracea, 195.
 Octactinia, 230, 231.
 Octobothrium, 324.
 Octorchis, 242.
 Ocular plates, 278.
 Oculina, 232.
 Oculinidæ, 229.
 Ocypoda, 478.
 Odontolæ, 176.
 Odontornithes, 175.
 Odontosyllis, 379.
 Odynerus, 597.
 Ecodoma, 596.
 Edemera, 588.
 Edipoda, 558.
 Erstedtia, 340.
 Esophagus of Anthozoa, 60.
 Estridæ, 542, 576.
 Estropsidæ, 564.
 Oken, 137.
 Olenus, 484.
 Olfactory organs, 91.
 Oligochaeta, 382.
 Olynthus, 217.
 Omalium, 590.
 Onchocotyle, 324.
 Oniscus, 460.
 Ontophilus, 590.
 Onychophora, 512.
 Oostegites of Arthropoda, 451.
 Opalina, 204.
 Operculata, 446.
 Ophiactis, 292.
 Ophiaster, 273, 293.
 Ophiiderma, 294.
 Ophioglypha, 294.
 Ophioplepis, 294.
 Ophion, 595.
 Ophiothrix, 294.
 Ophiura, 294.
 Ophiuridæ, 273, 275, 279.
 Ophiuridea, 291, 293.
 Ophiuridæ, 583.
 Opisthomum, 313.
 Oral pole of Echinodermata, 268.
 Orbitella, 505.
 Orbulina, 187.
 Orchestia, 455.
 Ordensbänder, 583.
 Organ, 25.
 Organ coral, 231.
 Oribates, 495.
 Orohippus, 172.
 Orthoptera, 554.
 Orthosia, 583.
 Oryctes, 590.
 Orygia, 583.
 Osculum, 210.
 Osmia, 598.
 Osmylus, 564.
 Osteoblasts, 42.
 Ostracoda, 423.
 Otion, 445.
 Otolith, 85, 239.
 Otolith plate of Ctenophora, 204.
 Ovary, 97.
 Ovipositors, 529.
 Ovum, 33, 97.
 Ovum, fertilization of, 109.
 Oxycephalus, 456.
 Oxyrhyncha, 478.
 Oxystomata, 478.
 Oxytricha, 205.
 Oxyuris, 344, 348, 351.
 Pædogenesis, 128.
 Pagurus, 478.
 Painted Lady, 585.
 Palæaster, 292.
 Palæmon, 220, 477.
 Palæocarabus, 469.
 Palæocrangon, 469.
 Palæontology, Evidence in favour of descent theory, 163.
 Palææ of Annelids, 368.
 Palingenia, 562.
 Palinurus, 477.
 Pali of Actinozoa, 228.
 Pallas on domestic hybrids, 143.
 Palp, 413, 523.
 Palpares, 564.
 Palpicornia, 590.
 Palps of Chaetopoda, 369.
 Pandora, 266.
 Panorpidæ, 563.
 Papilio, 585.
 Paraglossa, 524.
 Paramæccium, 205.
 Paramere, 27.
 Paraneucleus, 201.
 Parapodia, 305, 365.
 Parasita, 435.
 Parasitica, 567.
 Parthenogenesis, 105, 410, 543.
 Parthenogenesis of Phyllopoda, 418.
 Paste-worm, 357.
 Pauropus, 521.
 Peacock butterfly, 585.
 Pectinaria, 382.
 Pedal ganglion, 82.
 Pedata, 299.
 Pedicellariæ, 271.
 Pediculus, 568, 589.

- Pedipalpi, 506.
 Pedipalpus, 484.
 Pedunculata, 445.
 Pelagia, 236, 260, 261
 Pelodera, 357.
 Pelodytes, 346, 350.
 Peltocaris, 448.
 Peltogaster, 447, 460
 Pelzfresser, 568.
 Pelzkäfer, 590.
 Pelzmotte, 582.
 Pemphigus, 570.
 Penæus, 477.
 Pennella, 436.
 Pennatula, 231.
 Pennatulidæ, 231.
 Pentacrinus, 289.
 Pentacta, 274.
 Pentamera, 589.
 Pentastomidæ, 408.
 Pentastomum, 488.
 Pentatoma, 572.
 Pentatrematites, 289.
 Perforata, 181, 232.
 Perichondrium, 39
 Peridinium, 196.
 Periosteum, 41.
 Peripatus, 514.
 Periplaneta, 557.
 Perischæchinidæ, 295.
 Peritricha, 205.
 Perla, 561.
 Perlidæ, 561.
 Petalopus, 180.
 Phalangiida, 505.
 Phanerocarpæ, 255.
 Phanero-codonic gono-
 phore, 236.
 Phascolosoma, 394.
 Phasma, 557.
 Philodina, 404.
 Philopterus, 568.
 Pholcus, 505.
 Phora, 576.
 Phoronis, 389.
 Phosphorescent organs
 of insect, 536.
 Phoxichilidium, 496.
 Phreoryctes, 385.
 Phronima, 455.
 Phrosina, 455.
 Phryganea, 565.
 Phryganidæ, 564.
 Phrynus, 507.
 Phthirus, 568.
 Phyllacanthus, 296.
 Phyllium, 557.
 Phyllophorus, 278.
 Phyllopoda, 416.
 Phyllosomata, 471.
 Phylloxera, 570.
 Phylloxera, Reproduc-
 tion of, 128.
 Phylogeny, 122.
 Physalia, 244, 249.
 Physematium, 194.
 Physometridæ, 583.
 Physophora, 248, 249.
 Physophoridae, 244, 248.
 Physopoda, 559.
 Phytophaga, 594.
 Phytophthires, 568.
 Pieris, 585.
 Pigment of eye, 86, 88.
 Pilidium, 341.
 Pilzfliegen, 576.
 Pilzkäfer, 588.
 Pilzmücken, 578.
 Pimpla, 595.
 Pinnotheres, 478.
 Pinnulæ, 270, 288.
 Piophila, 576.
 Pirates, 572.
 Pisa, 478.
 Pisces, vascular system
 of, 64.
 Piscicola, 399.
 Planaria, 315.
 Plane, median, 27; sa-
 gittal, 27; transverse,
 27.
 Planipennia, 563.
 Plant-lice, 569.
 Plants and animals, 15
 Planula, 117, 124, 255.
 Plasmodium, 30.
 Platygaster, 594.
 Platygaster, larvæ of, 549.
 Platyhelminthes, 309.
 Platypezidæ, 576.
 Platyscelus, 456.
 Pleopods of Isopoda, 457.
 Pleuron, 483, 525.
 Pliny, system of, 132.
 Ploteres, 572.
 Plume-moths, 582.
 Plumularia, 237, 242.
 Plusiadæ, 583.
 Pluteus, 281, 282, 292,
 294, 296.
 Pneumatocyst, 244.
 Pneumatophore, 244.
 Pneumora, 555.
 Podocerus, 455.
 Podocoryne, 237, 241.
 Podophora, 296.
 Podophrya, 205.
 Podura, 554.
 Poikilothermic, 74.
 Poison glands, 532.
 Polar areas of Cteno-
 phora, 264.
 Polar body, 104.
 Polian vesicles, 272.
 Polistes, 566, 597.
 Pollicipes, 445.
 Polycactinia, 225.
 Polybostrichus, 372, 379.
 Polycelis, 311, 315.
 Polychæta, 374.
 Polycirrus, 378.
 Polycladus, 311.
 Polycystidea, 208.
 Polycystinidæ, 190.
 Polycyttaria, 196.
 Polydesmus, 521.
 Polydora, 382.
 Polygastrica, 192.
 Polygordius, 375.
 Polymorphina, 180.
 Polymorphism, 23, 126.
 Polymorphism, Facts of,
 in favour of Theory
 of Descent, 152.
 Polymorphism of social
 insects, 155.
 Polymyaria, 345.
 Polynoe, 379.
 Polymmatidæ, 585.
 Polyophthalmus, 372.
 Polyparia, 227.
 Polyphemus, 422.
 Polypoid, 211.
 Polypomedusæ, 233.
 Polyp type, 210.
 Polystomea, 317, 318, 322
 Polystomella, 187.
 Polystomum, 323, 324.
 Polythalamia, 186.
 Polyxenus, 521.
 Polyzonium, 515, 521.
 Pompilus, 597.
 Pontobdella, 400.
 Pontonia, 477.
 Porcellana, 460, 478.
 Porcellio, 457, 460.
 Porifera, 214.
 Porpita, 250.
 Portunus, 478.
 Postabdomen of Arthro-
 poda, 407.
 Postscutellum, 526, 591.
 Pou de poissons, 438.
 Prachtkäfer, 589.
 Præabdomen of Arthro-
 poda, 407.
 Præstomium of Chæti-
 fera, 387.
 Praniza, 459.
 Prawns, 477.
 Praying insect, 557.
 Priapulus, 394.
 Primitive streak, 115.

- Prionus, 588.
 Procrustes, 590.
 Proglottis of cestoda, 326.
 Proleg, 549.
 Pronucleus, 109.
 Prosoponiscus, 451.
 Proserochmus, 340, 341.
 Prostate, 99.
 Prostomum, 311, 312, 314.
 Protaster, 292.
 Proterosaurus, 177.
 Prothorax, 525.
 Protodrilus, 365, 375.
 Protopleas, 446.
 Protoplasm, 12.
 Prototracheata, 512.
 Protozoa, 182.
 Protula, 372, 382.
 Proventriculus, 530.
 Pselaphus, 590.
 Pseudonavicellæ, 208.
 Pseudophyllidæ, 338.
 Pseudopodia, 54, 186.
 Pseudopupa, 593.
 Pseudoscorpionidea, 510.
 Pseudospora, 194.
 Pseudotetramera, 588.
 Pseudova, 544.
 Pseudovarities of Aphides, 106.
 Psocus, 559.
 Psolus, 299.
 Psorosperms, 208.
 Psyche, 543, 584.
 Psychidæ, 581.
 Psychoda, 578.
 Psylla, 570.
 Psyllidæ, 570.
 Psyllodes, 570.
 Pteraster militaris, 284.
 Pterodactylidæ, 175.
 Pteromalus, 594.
 Pteronarcys, 561.
 Pterophorus, 582.
 Pteroptus, 495.
 Pterygotus, 480.
 Ptinus, 589.
 Ptychoptera, 578.
 Pulex, 579.
 Pupa, 548.
 Pupa coarctata, 551, 574.
 Pupa libera, 551.
 Pupa obtecta, 551, 574, 575.
 Pupa of Cirrpedia, 443.
 Pupil, 88.
 Pupipara, 542, 575.
 Purple, visual, 87.
 Pygidium, 484.
 Pygidium of Coleoptera, 586.
 Pygnogonida, 495.
 Pygocephalus, 469.
 Pyralis, 582.
 Pyrophorus, 589.
 Pyrrhocoris, 572.
 Quadrilatera, 478.
 Radial vessels, 272.
 Radiata, 266.
 Radii of Echinodermata, 267.
 Radiolaria, 189.
 Radius, 528.
 Rami communicantes, 82.
 Ranatra, 534, 572.
 Randwanzen, 572.
 Rapacia, 379.
 Raphidia, 563.
 Raubfliegen, 576.
 Ray, 134.
 Réaumur, 133.
 Receptaculum seminis, 99.
 Redi, 133.
 Redia, 129, 319.
 Reduviidæ, 572.
 Regenbremse, 577.
 Renilla, 231.
 Reptiles, Vascular system of, 66.
 Respiration, Renewal of external medium, 72.
 Respiratory organs, 67.
 Respiratory trees, 277.
 Reticular connective tissue, 38.
 Reticularia, 186.
 Retina, 87.
 Retinacula of Acanthocephala, 359.
 Retinulæ, 88.
 Rhabditis, 344, 349, 357.
 Rhabdocela, 311, 313.
 Rhabdonema, 346, 350.
 Rhabdosoma, 455.
 Rhachis, 483.
 Rhipidius, 589.
 Rhipidogorgia, 231.
 Rhipiphorus, 589.
 Rhizocephala, 446.
 Rhizocerinus, 289.
 Rhizoglyphus, 492.
 Rhizopoda, 181.
 Rhizostoma, 261.
 Rhizostomæ, 261.
 Rhizostomidæ, 252.
 Rhizotrogus, 590.
 Rhodites, 594.
 Rhopalocera, 582, 584.
 Rhopalonema, 242.
 Rhyacophila, 565.
 Rhynchocoela, 339.
 Rhynchodesmus, 315, 316.
 Rhynchota, 566.
 Rhyncobdellidæ, 399.
 Ribs, 528.
 Rinderbremse, 577.
 Root-lice, 127.
 Röscl von Rosenhof, 133.
 Rosette of Echinoidea, 296.
 Rostellum of Cestoda, 327.
 Rotalia, 187.
 Rotatoria, 400.
 Rotifer, 404.
 Rotifera, 400.
 Rotula, 297.
 Roux, Breeding experiments, 142.
 Rückenschwimmer, 572.
 Rudimentary organs, Meaning of, 156.
 Rugosa, 230.
 Rüttimeyer, on origin of ox, 143.
 Sabella, 382.
 Sabellaria, 382.
 Sac-bearers, 582.
 Saccharomyces, 206.
 Saccocirrus, 381.
 Sacconereis, 372, 379.
 Sacculina, 447.
 Sænurus, 385.
 Sagartia, 225.
 Sagitta, 357.
 Sagittal plane of Ctenophora, 262.
 Salivary gland, 58.
 Salpingoeca, 196.
 Saltatoria, 557.
 Salticus, 504.
 Saltigradæ, 504.
 Sapphirina, 436.
 Sarcode, 19, 22.
 Sarcolemma, 45.
 Sarcophaga, 576.
 Sarcopsylla, 579.
 Sarcoptidæ, 492.
 Sargus, 577.
 Sarsia prolifera, 239.
 Saturnia, 584.
 Satyrus, 585.
 Saw-flies, 594.
 Scalpellum, 445.
 Scaphognathite of Decapoda, 476.
 Scatophaga, 576.

- Scenopius, 576.
 Schaeffer, 133.
 Schattenmücke, 578.
 Schelling, 137.
 Schildläuse, 568.
 Schildwanzen, 572.
 Schistocephalus, 338.
 Schizaster, 297.
 Schizomycetes, 206.
 Schizoneura, 570.
 Schizopoda, 472.
 Schizoprora, 311, 313, 314.
 Schizostomum, 312.
 Schnabelfliegen, 563.
 Schnaken, 578.
 Schnepfenfliegen, 577.
 Schreitwanzen, 572.
 Schwarmer, 584.
 Schwebfliegen, 576.
 Sciara, 578.
 Sciophila, 578.
 Slater on Zoological Provinces, 160.
 Sclerodermites, 231.
 Sclerostomum, 350, 352.
 Sclerotic, 88.
 Scolex, 333.
 Scolia, 596.
 Scolopendra, 519.
 Scopula, 582.
 Scorpion, 510.
 Scorpionidea, 508.
 Scorpion-spiders, 506.
 Scuta of Cirripedia, 439.
 Scutellidæ, 297.
 Scutellum, 526.
 Scutigera, 518, 520.
 Scyllarus, 477.
 Scyphistoma, 125, 233, 255.
 Scyphomedusæ, 231, 236, 250.
 Sea feathers, 231.
 Sea long-worm, 343.
 Sea-urchins, 294; Regular, 296.
 Sebaceous glands, 77.
 Secretory organs, 74.
 Sedentaria, 380.
 Sedimentary formations:—
     Conditions of formation of, 166, 169.
     Determination of age of, 164.
     Table of, 165.
 Segment, 27.
 Segmental organs, 75, 308.
 Segmentation cavity, 116.
 Segmentation of ovum, 110.
 Selection, Artificial, 145.
 Selection, Sexual, 152.
 Semæostomeæ, 260.
 Semen, 97.
 Semitæ of Echinoidea, 296.
 Sense organs, 83.
 Septa of Actinozoa, 228.
 Sergestes, 477.
 Sericteria, 532.
 Serolis, 460.
 Serpula, 382.
 Sertularia, 242.
 Sesia, 584.
 Sex, 104.
 Sexual reproduction, 97.
 Sexual selection, 152.
 Sheeptick, 575.
 Shell glands, 75.
 Shell glands, Crustacea, 410.
 Sialis, 563.
 Sida, 422.
 Silkworm, 584.
 Silpha, 590.
 Simonea, 492.
 Simple eye, 89.
 Simulia, 577.
 Singcicaden, 571.
 Singmücke, 578.
 Siphonophora, 236, 243.
 Siphonostomata, 435.
 Sipunculoidea, 392.
 Sipunculus, 394.
 Sirex, 594.
 Siriella, 474.
 Sitaris, 589.
 Skeleton, 78.
 Smellers of Tanäidæ, 459.
 Smerinthus, 584.
 Smynthurus, 554.
 Solaster, 293.
 Solenobia, 543, 581, 582.
 Solifugæ, 511.
 Solpuga, 512.
 Spanish fly, 589.
 Spatangidæ, 296, 279, 295.
 Spatangidea, 273, 297.
 Spatangus, 297.
 Species, 140.
 Species:—Cuvier's definition of, 149; Mutability of, 144; Origin of, 144, 149.
 Species, Relation of to genera, 149.
 Speckkäfer, 590.
 Sperm, 97.
 Spermatophores, 99.
 Spermatozoon, 33, 97.
 Sphæridia, 272.
 Sphærodorum, 372, 379.
 Sphæroma, 460.
 Sphæronectes, 250.
 Sphæronites, 289.
 Sphærophyra, 205.
 Sphærotherium, 521.
 Sphærozoum, 191.
 Sphæricularia, 356.
 Sphex, 552, 596.
 Sphingina, 584.
 Sphinx, 584.
 Sphyrocephalus, 311.
 Spicula of Nematoda, 347.
 Spiders, 498.
 Spindle-tree moth, 382.
 Spinning glands, 532.
 Spinning mite, 495.
 Spio, 382.
 Spiodea, 381.
 Spio-Nephthys larva, 378.
 Spionidæ, 381.
 Spirälzooids, 241.
 Spirillum, 206.
 Spirochaeta, 206.
 Spirographis, 382.
 Spiroptera, 348.
 Spirorbis, 372, 382.
 Spirostomum, 205.
 Sponges calcareous, 222; glassy, 221; gelatinous, 221; horny, 222; levantine, 221.
 Sponge type, 210.
 Spongia, 221.
 Spongiadæ, 221.
 Spongiaria, 214.
 Spongilla, 218, 221.
 Spontaneous generation, 10.
 Spores, 97.
 Spores 128; of Trematoda, 129.
 Sporocyst, 129, 319.
 Spring-flies, 564.
 Springkäfer, 589.
 Spring-tails, 554.
 Spumella, 195.
 Squama, 572.
 Squilla, 472.
 Stag-beetle, 589.
 Staphylinus, 590.
 Star coral, 232.
 Star-fishes, 290, 292.
 Stauridæ, 230.
 Staurocephalus, 379.

- Stechfliege, 576.
 Stelleridea, 292.
 Stemmata Arthropoda, 408.
 Stenorhynchus, 478.
 Stentor, 205.
 Stephanoceros, 404.
 Stephanosphæra, 195.
 Sterile polyp, 237.
 Sternum, 525.
 Stigmata, 71.
 Stiletfliegen, 576.
 Sting, 592.
 Stipes, 523.
 Stomatopoda, 470.
 Stomobranchium mirabile, 239.
 Stomoxys, 576.
 Stone canal, 272.
 Stratiomys, 577.
 Strepsiptera, 565.
 Stridulandia, 571.
 Strobila, 125, 255, 256.
 Strongylidæ, 347.
 Strongylocentrotus, 296.
 Strongylus, 352.
 Struggle for existence, 145.
 Stutzkäfer, 590.
 Stylaria, 386.
 Stylasteridæ, 241.
 Stylochus, 316.
 Stylonychia, 205.
 Stylops, 566.
 Suberites, 229.
 Subgenital pits of Discophora, 260.
 Submentum, 524.
 Suboesophageal ganglion, 82.
 Sub-species, 141.
 Succession of similar types, 171.
 Suctoria, 205, 446.
 Summer eggs of Phyllopora, 418.
 Summer eggs of Rotifera, 403.
 Summer eggs of Turbellaria, 313.
 Supra-oesophageal ganglion, 80.
 Swallow tail, 585.
 Swammerdam, 133.
 Sweat glands, 77.
 Sycaltis, 222.
 Sycandra, 222.
 Sycetta, 220.
 Sycilla, 222.
 Sycon, 221, 222.
 Syconidæ, 212, 217, 222.
 Sycortis, 222.
 Syculmis, 222.
 Sycysa, 220.
 Syllis, 379.
 Syllis prolifera, 372.
 Symbiotes, 492.
 Sympathetic, 82.
 Synapta, 278, 283, 298, 299.
 Synaptidæ, 283.
 Syrphus, 576.
 System, Meaning of, 150.
 System of Aristotle, 132.
 " Cuvier, 136.
 " Linnaeus, 135.
 " Pliny, 132.
 " Present day, 138.
 Tabanidæ, 574, 576.
 Tabanus, 577.
 Tachina, 576.
 Tachinæ, 541.
 Tactile corpuscles, 47.
 Tænia, 327, 330, 331, 335.
 Tænia cucumerina, 329.
 Tæniadæ, 334.
 Talitrus, 455.
 Tanais, 459.
 Tanystomata, 576.
 Tanzfliegen, 576.
 Tapetenmotte, 582.
 Tapeworm, 326.
 Tarantula, 504.
 Tardigrada, 496.
 Tarsus, 527.
 Taste, 92.
 Tegenaria, 504.
 Tegmina, 528.
 Tegulæ, 591.
 Teleas, 594.
 Teleas, larva of, 549.
 Telephorus, 589.
 Telepsavus, 382.
 Telepsavus-Chætopterus larva, 378.
 Telolecithal, 112.
 Telotrocha, 378.
 Telson of thoracostraca, 461.
 Tenebrio, 589.
 Tentredo, 594.
 Teratology, 51.
 Terebella, 382.
 Terebra, 592.
 Terebrantia, 594.
 Terga of Cirripedia, 439.
 Termes, 561.
 Termites, 559.
 Terricolæ, 385.
 Tesselata, 289.
 Testis, 97.
 Tetracoralla, 230.
 Tetranychus, 495.
 Tetraphyllidæ, 338.
 Tetraplasta, 194.
 Tetrapneumones, 504.
 Tetrarhynchus, 327, 338.
 Tetrastemma, 341, 342.
 Tettigonia, 571.
 Tettix, 558.
 Textularia, 187.
 Thalamophora, 183.
 Thalassemia, 392.
 Thalassicolla, 190.
 Thalassina, 477.
 Thamnocnidia, 241.
 Theca of Actinozoa, 228.
 Thecla, 585.
 Thecodontidæ, 175.
 Thelyphonus, 508.
 Thereva, 576.
 Theridium, 502, 506.
 Theriodonta, 175.
 Thomisus, 504.
 Thoracostraca, 460.
 Thread cells, 212.
 Threadworms, 344.
 Thrips, 559.
 Thysanopoda, 475.
 Thysanozoon, 316.
 Thysanura, 553.
 Tibia, 526.
 Ticks, 493.
 Tiger-beetles, 590.
 Tillodontia, 173.
 Tillotherium, 173.
 Tima, 242.
 Tinea, 582.
 Tipula, 578.
 Tipulariæ, 577.
 Tissue, 29.
 Todtengräber, 590.
 Tomopteris, 380.
 Tornaria, 300.
 Tortoiseshell butterfly, 585.
 Tortrix, 582.
 Touch, 84.
 Toxodon, 170.
 Toxodontia, 173.
 Toxopneustes, 296.
 Tracheæ, 70, 410.
 Trachelius, 204.
 Trachymedusæ, 239, 242.
 Trachynema, 239, 242.
 Trachys, 589.
 Transverse plane of Ctenophora, 262.
 Trap-door spider, 504.
 Trematoda, 316.
 Trepan, 299.

- Triænophorus, 338.
 Trichina, 347, 348, 353, 354, 355.
 Trichocephalus, 348, 353.
 Trichodectes, 336, 568.
 Trichodes, 589, 599.
 Trichodina, 205.
 Trichomonas, 194.
 Trichoptera, 564.
 Trichosomum, 353.
 Trichotrachelidæ, 353.
 Trigonía, 599.
 Trilobita, 483.
 Triphæna, 583.
 Tristomum coccineum, 323.
 Trivium, 269.
 Trochal disc of Rotifers, 401.
 Trochanter, 526.
 Troctes, 559.
 Trogus, 595.
 Trombidium, 495.
 Trypeta, 576.
 Tube-spinners, 504.
 Tubicinella, 446.
 Tubicolæ, 380.
 Tubicolaria, 401, 404.
 Tubifex, 385.
 Tubipora, 231.
 Tubitelæ, 504.
 Tubularia, 239, 241.
 Tubulariæ, 241.
 Turbellaria, 309.
 Turbinolia, 232.
 Tylenchus, 357.
 Type, 52.
 Type of Desor, 341.
 Typhis, 456.
 Typhlosole of Lumbri-
 cus, 383.
 Tyroglyphus, 492.
 Umbellula, 231.
 Upper lip of Crustacea, 412.
 Uroceridæ, 594.
 Uropoda of Crevettina, 454.
 Uterine bell of Acantho-
 cephalæ, 361.
 Uterus, 99.
 Vagina, 99.
 Vampyrella, 194.
 Vanessa, 553, 585.
 Variability, 145.
 Varieties, 141.
 Variety, Relation of to
 species, 149.
 Vascular pore of Nema-
 toda, 346.
 Vascular system, 59.
 Vas deferens, 99.
 Vein, 62.
 Veins, 528.
 Velarium, 252.
 Velarium of Scypho-
 medusæ, 252.
 Vellella, 246, 250.
 Vellellidæ, 244.
 Velia, 572.
 Venous, 73.
 Ventral plate, 545.
 Ventriculitidæ, 221.
 Veretillum, 231.
 Vermes, 302.
 Vesiculæ seminales, 99.
 Vesiculata, 239, 241.
 Vespa, 597.
 Vexillum, 266.
 Vibrio, 206.
 Vine-lice, 570.
 Vinegar worm, 357.
 Visceral nerves, 82.
 Vitellarium of Turbel-
 laria, 312.
 Vocal organs, 552.
 Volvox, 195.
 Vortex, 313.
 Vortex viridis, 310.
 Vorticella, 205.
 Waffenfliegen, 577.
 Wallace, 147.
 Warm-blooded, 74.
 Wasps, 597.
 Wasserläufer, 572.
 Water-bugs, 571.
 Water-fleas, 419.
 Watermites, 495.
 Water-scorpions, 572.
 Water-spiders, 504.
 Water-vascular system,
 308, 311.
 Water-vascular vessels
 of Platyhelminthes 75.
 Wax glands, 532.
 Weevils, 588.
 Weizenfliege, 576.
 White ants, 559.
 White butterflies, 585.
 White coral, 232.
 Wickler, 582.
 Wings, 528.
 Winkelspinne, 504.
 Winter eggs of Rotifera,
 403.
 Winter eggs of Turbel-
 laria, 313.
 Winter-sleep, 74.
 Wolf-spider, 504.
 Wood-bees, 598.
 Wood-wasps, 594.
 Worm, Paste, 357.
 Worm, Vinegar, 357.
 Wotton, 133.
 Xantho, 478.
 Xenos, 566.
 Xiphosura, 480.
 Xylocopa, 598.
 Xylophaga, 589.
 Xylophagus, 577.
 Xylotomæ, 576.
 Yolk, 111.
 Yolk-cord, 543.
 Yolk, Effect of, on de-
 velopment, 120.
 Yponomeuta, 582.
 Zerene, 583.
 Zoæa, 466.
 Zoantharia, 231.
 Zoanthus, 232.
 Zoogloea, 200.
 Zoological provinces, 160.
 Zoophytes, 209.
 Zoosperms, 209.
 Zoospores, 194, 197.
 Zoothammium, 205.
 Zünsler, 582.
 Zygæna, 584.

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