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Received July 11, 1941

Accession No. 53562

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EMBRYOLOGY OF INSECTS AND MYRIAPODS

*The developmental history of insects, centipedes, and
millepedes from egg desposition to hatching*

BY

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FIRST EDITION

MCGRAW-HILL BOOK COMPANY, INC.

NEW YORK AND LONDON

1941

EMBRYOLOGY OF INSECTS AND MYRIAPODS

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THE MAPLE PRESS COMPANY, YORK, PA.

PREFACE

This text is the outgrowth of a course of lectures on the embryology of insects given by the senior author over a period of twenty years and now being continued by the junior author. It goes without saying that more is offered here than is presented in the time allotted to the subject in Cornell University. From year to year new topics were introduced and old ones laid by so that now from the accumulated subject matter the material for this book has been selected. It may well be, in the opinion of some readers, that certain phases of the subject have been overemphasized and others have not been sufficiently stressed. To this can be said only that an effort has been made to present as balanced a treatment as the available material permits and that research students must of necessity refer to original sources for details that limitation of space prevents being included here.

The authors have endeavored to preserve an impartial attitude on controversial questions—presenting in Part I the chief views on debatable points and in the chapters of Part II reflecting the opinions of the several investigators on the subject of their research. Nowhere in the developmental history of the arthropods has the debate been more lively and at times more acrimonious than that relating to the origin of the mid-gut. The student is therefore warned after reading an account of the development of some species in the second part to turn to the first part for a discussion of points of questionable interpretation.

The subject of embryonic development may be presented in several ways each of which has its advantages and disadvantages. Part I of this text is devoted to a comparative study of the tissues and organs found in the several types of animals considered. In Part II the embryonic history of a number of insects representing most of the orders is described, emphasis being placed on the more characteristic features of the development of each type. By the selection of illustrative species in the second part which are not especially stressed in the first part, undue repetition is avoided. After some experimenting the authors have adopted in their classes the following method of presentation, it being assumed that the students have had training in elementary insect taxonomy and anatomy as well as an introductory course in general biology or its equivalent. After a brief introduction and a review of the activities of the animal cell the development of a generalized insect is described in some detail accompanied by charts and blackboard diagrams. This is followed by accounts of the development of a few forms beginning with

those least deviating from the hypothetical type, as for example, in the order: locust, dragonfly, honeybee, blowfly, *Isotoma*, polyembryonic Hymenoptera. From time to time a comparative study is made of the different types, and controversial topics are discussed.

For the benefit of the research student, reference lists are given at the end of each chapter. No pretense is made as to their completeness, especially those in Part I, but it is hoped that they are sufficiently comprehensive to prove useful to investigators.

The bibliography, though extensive, is restricted chiefly to books and papers dealing with embryology proper. References to borderline subjects such as the physiology and cytology of the embryo and postembryology are included only when referred to in the text. Reviews on the subject of physiology and biochemistry and references relating to them may be found in the texts of Needham (1931) and Wigglesworth (1939). Only the briefest outline is given of spermatogenesis and oögenesis. These subjects are fully treated in the texts on cytology by Agar, Doncaster, Schroeder (Depdolla), Sharp, and Wilson. Because of the increasing attention paid to experimental embryology a chapter is devoted to it. This chapter is largely an abstract of an article by Richards and Miller, to whom credit is due.

The authors have been fortunate in having had at their disposal embryological material of representatives of the major orders, prepared in part by themselves and in part by colleagues and advanced students. Figures taken from the works of others have all been redrawn and in many cases conventionalized. Those not acknowledged in the legends are from the following sources: Butt, Figs. 234-242, 246, 255, 258, 313-326; Escherich, 329, 330, 331*B*, 333-336; Fernando, 167-174; Heymons, 109-112; Johannsen, 295-312; Knower, 133-135; Leiby and Hill, 259-264; Muir and Kershaw, 197-201; Noack, 327, 328, 331*A*, 332; Noskiewicz and Poluszyński, 217-233; Patten, 286-294; Patterson, 265-275; Philiptschenko, 63-99; Roonwal, 137-166; Schölzel, 175-180; Seidel, 202, 203, 207, 209-211; Strindberg, 215, 216; Toth, 182-187; Uzel, 100-108; Webster and Phillips, 190-196. Figures in Part I not otherwise acknowledged are copies of diagrams used in the authors' classes. Permission to use Figs. 128*B*-132 from an unpublished paper was given by its author Dr. L. C. Pettit. Figures published for the first time and drawn by the junior author from his own preparations are the following: 113-116, 119-126, 204-206, 208, 212, 243-245, 247-254, 256, 257, 276-280, 284, 285. To the publishers, the Schweizerbart'sche Verlagsbuchhandlung of Stuttgart, we are indebted for permission to use Figs. 337-361 from the work of Prof. Heymons on *Scolopendra*, and to Dr. R. Wiesmann for permission to use Figs. 136*A-E* from the text of Leuzinger, Wiesmann, and Lehmann.

The sequence of the orders of insects given in the table of contents is not in agreement with that usually adopted in textbooks, but it is felt that it expresses a more natural grouping so far as this is possible in a linear arrangement. In making this arrangement the authors have been guided by the works of Crampton, Handlirsch, Imms, Lameere, Martynov, and Tillyard as well as by suggestions from their colleague Prof. J. C. Bradley. For obvious reasons generic and specific names used in the text are those employed by the authors of the original articles. Only in cases where confusion might result in the use of an older name is another term employed.

Although much work has been done on the embryonic development of insects in general, an examination of the text and references reveal that many problems, both theoretical and factual, have not yet been solved. Future workers, however, are reminded of the words of Nelson, which are still appropriate after twenty-five years:

There is need of further investigation, particularly of the more generalized types. Superficial study, however, would be worse than useless; the type of investigation demanded is of the highest, requiring the delicate and precise methods of the cytologist, the best fixation and staining possible, a complete series of stages, a study of the origin of the rudiments cell by cell, and finally an eye single to the facts and regardless of preconceived theoretical considerations.

In conclusion it may be said that great activity in experimental embryology recently manifested both in Europe and America has stimulated interest in normal embryology. Therefore we may look forward to further work on controversial questions that have arisen in the last seventy years, and on the later development stages that involve the formation of the exoskeleton, the individual muscles, and the sense organs.

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CORNELL UNIVERSITY,
ITHACA, N. Y.,
January, 1941.

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PART I

CHAPTER I

INTRODUCTION

ONTOGENETIC DEVELOPMENT

In its broadest sense the ontogenetic developmental history of an animal not only embraces all stages from that of a fertilized egg (ovum) to that of the sexually mature adult but includes also a period of senescence. That a final stage of decadence must be included is obvious when one reflects that even during the earliest (embryonic) period provisional structures arise only to degenerate after functioning for a shorter or longer time. We therefore recognize for the majority of animals four periods of development, not sharply marked to be sure, that in general are recognizable by certain external characteristics.

The first period is that of embryonic development that begins with the fertilized egg or the first cleavage stage and ends at hatching or at the birth of the animal. The transition from this stage to the next is a gradual one even among the Eutracheata which for the most part are oviparous. For example the eggshell, or chorion, among the Myriapoda and the Collembola and some other insects is ruptured some time before the completion of the embryo, whereas in other cases a fully formed insect larva may lie dormant within the eggshell without emerging for a period of several months.

The second, or adolescent, period is a period of growth, during which the reproductive organs become mature. It is an interval of marked change in the outward appearance of many animals, notably among amphibians and hemimetabolous and holometabolous insects. Designated as the "postembryonic period" in insects, it is here frequently much prolonged, lasting in some instances for months or even years. The third period is that of sexual maturity and reproduction. Among vertebrates and some invertebrates it may extend through a number of years, but among the Eutracheata the period is usually much shorter, lasting in the case of the Ephemeridae but a few hours. The final stage is that of senescence, or a period of decadence and death. Phylogenetically it has no significance. It is the first of these stages, the embryonic period of development, with which we are here concerned.

Among the ancients, numerous animals, including amphibians and many insects, were thought to arise spontaneously, and it was not until

the seventeenth and eighteenth centuries that Spallanzani, Redi, Swammerdam, and Rösel von Rosenhof, attempted to demonstrate by experiment the error of the theory of spontaneous generation. With the publication of the work of Von Baer the modern phase of embryology begins. It was Von Baer who elaborated Pander's idea of the three germ layers in the early embryo from which the later organs are developed. He also called attention to the greater similarity that exists between embryos of related groups than between adults and thus suggested what later became known as the "recapitulation theory," or "the biogenetic law," which is attributed to F. Müller and E. Haeckel.

Among the earlier works dealing with the embryology of insects may be mentioned that of Herold (1815) on the Lepidoptera, of Hummel (1835) on the roach, and of Kölliker (1843) on a comparative study of the development of insects and vertebrates. These researches were followed by Weismann's (1863) work on the Diptera which represents for its time an outstanding contribution to our knowledge of the embryology of this group of insects. The work of Meeznikow and Bütschli on the honeybee belongs to this period. In the year 1871 a paper on the embryology of worms and arthropods by Kowalewsky appeared, a work of great merit, in which the method of cutting sections of tissues, previously fixed and embedded in paraffin, was used. During the thirty years that followed, numerous and important contributions to the subject of arthropod embryology were made by both European and American investigators. Among prolific European writers of this period may be mentioned Carrière, Cholodkowsky, Graber, Heider, Heymons, Korschelt, and Nusbaum. For the same period the works of the American zoologists Ayers, Claypole, Knower, Packard, Patten, Ryder, Wheeler, and Woodworth are noteworthy. Wheeler's papers on the development of the Orthoptera are especially outstanding.

The strong interest that has been aroused in vertebrate embryology by the recent experimental work on the amphibians by Spemann and his associates is reflected in a greatly increased activity in the study of the normal embryonic development of insects, which is a prerequisite to experimental work. The pioneer experimental studies of Wheeler, Megušar, and Hegner have been followed up by those of Reith, Seidel, Pauli, and others in Europe and by those of Brauer, Child, Howland, King, Shull, Slifer, Weiss, and others in the United States.

All these investigations cannot fail to impress one with the necessity for a study of the developmental processes from the standpoint of genetics, physiology, and cytology in order to obtain an adequate conception of what is involved. A consideration of the first and second of these extensive topics lies outside the scope of this text. As for the third, only so much of it will be included here as may be required for an understanding

of the cellular activities involved in fertilization and growth. We shall therefore begin with a brief account of the structure of the cell to obtain an idea of the condition of the zygote from which the individual arises.

THE CELL

The structural unit of the animal or plant body is called the "cell." The concept of the cell has undergone change since the term was first used. When first introduced it was applied, as the name signifies, to the wall of the little compartment containing the protoplasm. As the contents of this "cell" were studied, it became evident that the small mass of protoplasm contained a protoplasmic nucleus in which complicated changes took place during the growth of the organism; and in time the word "cell" came to mean not only the wall but its entire contents.

The Cell (Fig. 1).—The protoplasm within the cell wall consists of two primary components: nucleoplasm, composing the nucleus (*nu*); and the cytoplasm, or the extra-nuclear portion. The nucleus, containing nuclear sap, or karyolymph, is bounded by the nuclear membrane (*nm*). In the karyolymph is the nuclear reticulum composed of linin (*l*), an achromatic supporting material, and chromatin (*cm*). One or more plasmosomes (true nucleoli), a reservoir of nutritive material, is usually found in the nucleus (*nu*). In addition, karyo-

FIG. 1.—An animal cell. (*c*) Chromidia. (*ch*) Chondriosome. (*cm*) Chromatin. (*ct*) Centrosome. (*ec*) Ectoplasm. (*en*) Endoplasm. (*k*) Karyosome. (*l*) Linin. (*nm*) Nuclear membrane. (*nu*) Nucleolus within the nucleus. (*pl*) Plastid. (*v*) Vacuole.

somes (chromatin nuclei), which are accumulations of chromatin on certain points of the reticulum, may be present (*k*). A centrosome (*ct*) is usually found in animal cells, occupying the center of a differentiated region—the centrosphere, or attraction sphere—which at the time of cell division is the focus of a system of radiating astral rays collectively known as the "aster." Minute bodies having the form of granules, rods, or threads, known as "chondriosomes" or "mitochondria," are present in the cytoplasm, as well as metaplastic inclusions, passive accumulations of food materials, and differentiation products. The cell wall itself is regarded by many as a secretion of the protoplast, or cell proper.

Cell Division.—Cells multiply by direct or indirect division. By direct division (amitosis) the cell including the nucleus is merely pinched in two. This process is characteristic of aging cells. Indirect division (mitosis), the usual method of nuclear division, is a series of complex processes which may be arranged in several phases (Fig. 2). In the resting stage (*A*) of the cell the so-called “chromatin granules,” composed of a dark staining substance, are apparently scattered through the nucleus. When about to divide, this chromatin material takes on the form of threads or a long single strand, or spireme (*B*), which later separates into

FIG. 2.—Mitosis. *A*, resting stage. *B-D*, prophase. *E*, metaphase. *F*, anaphase. *G*, telophase. *H*, late telophase returning to resting stage.

several pieces. This is the prophase stage. The nuclear wall breaks down when the spireme segments into a number of bodies called “chromosomes” (*C,D*). These bodies become arranged in a plate at the equator of a spindle halfway between the centrosomes. In the next stage—the metaphase—the chromosomes split in such a manner that each of their parts contains an approximately equal amount of chromatin (*E*). In the next, or anaphase stage, the chromosomes formed after splitting appear to be drawn along the spindle fibers (*F*) to the centrosomes. Every chromosome present at the end of the prophase sends half its chromatin to either end of the spindle. The next is a reconstruction stage, or the telophase, wherein the nuclei return to the resting condition (*G*). The chromatin apparently again becomes scattered through the nucleus; a new nuclear wall is formed; and the cell itself constricts between the nuclei, producing two daughter cells (Fig. 2*H*). Growth in all animal

and plant tissues takes place by cell division, and most cell division involves these changes in the nucleus.

The number of chromosomes, in general, is constant for each species, there being 4 to 30 or more in the body cells of insects. An even number is usual in most animals, but in some forms, especially in the males of certain insects, there may be an odd number.

FIG. 3.—Maturation and fertilization. *A*, female cell. *B*, male cell. (*a*) Oöcyte of the first order. (*a'*) Spermatocyte of the first order. (*b*) Oöcyte of the second order. (*b'*) Spermatocyte of the second order. (*c*) Egg. (*c'*) Spermatid. (*d*) Sperm. (*1p*) First, (*2p*) Second polar body. (*e*) Egg and sperm. (*f*) Fertilized egg.

That the chromosomes maintain their individuality (genetic continuity) throughout the life cycle has long been held by cytologists. In some plants and animals the chromosome boundaries do not entirely disappear during the resting stage, from which it is evident that the morphological identity of the chromosome is not lost between mitoses. Chromosomes are the carriers of hereditary qualities from parent to offspring.

Sex Cells.—During embryonic life the primordial germ or sex cells give rise to numerous cells that migrate into the male or female gonad. The male cells, at this stage known as “spermatogonia,” after a period of

repeated normal mitotic division cease dividing and have a period of growth when they are known as "spermatocytes." They then undergo a maturation period during which two maturation divisions rapidly succeed each other (Fig. 3*B*). The first maturation division results in two spermatocytes of the second order. These immediately divide again to form four spermatids from each spermatogonium. Each spermatid develops without again dividing into functional spermatozoa.

The female cells, known as "oögonia," after a period of repeated mitotic division also have a growth period with two maturation divisions (Fig. 3*A*). Unlike the male, where all the spermatocytes finally develop into spermatozoa, in the female maturation results in one functional egg which carries all the nutrient material and three much smaller non-functional cells known as "polar bodies." In some cases the second polar body fails to divide, in which case but two polar bodies are formed.

The chromosome behavior during one of the maturation divisions differs from that of normal mitotic division in that the chromosomes of each cell undergo a pairing which is known as "synapsis." It is not a random pairing but is a union of homologous male and female chromosomes descended from parent chromosomes which came together at the time the egg was fertilized. Chromosomes in many cases are sufficiently distinctive morphologically so that homologous pairs are readily recognized. Two of them, one derived from each parent, in the female egg cell before synapsis are known as "*x*-chromosomes"; the others are known as "autochromosomes." We shall now refer to the diagram (Fig. 3) to illustrate what occurs during maturation of the germ cells of an animal in which we shall assume that the male has five chromosomes and the female six. The circle at *Aa* represents an egg before maturation with six chromosomes; the circle *Ba'*, a spermatocyte with five chromosomes. At the first division of the egg nucleus reduction in number of chromosomes occurs (*Ab*), one of each pair going to the first polar body, the others remaining in the egg. The second division is mitotic; hence after division at *Ac* there are still three chromosomes in the egg nucleus as in the second polar body. In the spermatocyte (*Ba'*) we are assuming that there are five chromosomes, two pairs and a single *x*-chromosome, which after reduction would give three chromosomes in one of the spermatocytes of the second order and two in the other (*Bb'*). The second maturation division (*Bc'*), being mitotic, gives three chromosomes in one pair of spermatids and two in the other pair, the same number being preserved in the resulting spermatozoa (*d*). Should the egg (*Ac*) be fertilized (at *e*) by one of the sperms containing an *x*-chromosome, a female animal will develop. Should it be fertilized by a sperm lacking an *x*-chromosome (*i.e.*, having but two chromosomes in our example), a male animal would result.

If the species were such that both male and female had an equal number of chromosomes in their somatic cells (say six for example), the additional male chromosome would be designated as a "*y*-chromosome," and all four spermatocytes of the second order would carry three chromosomes, two with an *x*-chromosome and two with a *y*-chromosome. Should the egg now be fertilized by a spermatozoon with an *x*-chromosome, a female would develop from it; if by one with a *y*-chromosome, a male. In this example the statement is made that reduction occurs in the first maturation division, but it should be noted that reduction in some cases occurs in the second division.

The Spermatozoa.—It has already been stated that the final division of the male cells results in spermatids that develop into spermatozoa. The process of spermatogenesis is a complicated one which need not be discussed here; suffice it to say the mature spermatozoon, in many animals, is an elongated organism with an enlarged head containing the nucleus, a short middle piece, and a long flexible tail. By means of the lashing motion of the tail the sperm immersed in fluid moves rapidly about. Spermatozoa are very minute, although there is a considerable range in size, those of *Amphioxus* being but 0.02 mm. in length; those of the orthopteran *Gryllotalpa vulgaris*, 0.5 mm.; whereas those of the amphibian *Discoglossus* attain a length of 2 mm. Wilson states that it would take 400,000 to 500,000 sea-urchin spermatozoa to equal in volume the egg of the same species. As Hegner (1914) says, it is not surprising, therefore, to find that the number of spermatozoa produced by a single male may be hundreds of thousands of times as great as the number of eggs developed in a female.

The Egg.—The egg of the animal is relatively very much larger than the sperm; in fact the winter egg of the aphid may be nearly as long as the body of the insect itself. Among animals that lay many in rapid succession, the eggs are naturally relatively smaller than among those depositing but few eggs. The amount of yolk in the egg is an important factor in determining the manner in which the egg divides to form the embryo.

TYPES OF CLEAVAGE IN ANIMAL EGGS

After fertilization, which will be discussed farther on, the egg cell divides rapidly in 2, 4, 8, 16, etc., cells which continuously grow smaller with repeated divisions. Two primary types may be recognized: holoblastic eggs with total cleavage and meroblastic eggs with partial cleavage.

Holoblastic eggs may have a very small amount of yolk which is distributed uniformly among the approximately equal-sized blastomeres, as in *Cerebratulus*; or the yolk may be more abundant but not sufficient to prevent cleavage as in amphibians. In the latter case the cleavage

is unequal, the cells at the animal pole are small with but little yolk, and the cells at the vegetative pole are larger and rich in yolk.

Meroblastic eggs also are of two kinds: those in which cleavage is discoidal and restricted to a small disk at the animal pole, whereas the great mass of yolk at the vegetative pole does not divide, as with birds and reptiles; and those in which the cleavage nucleus is a cytoplasmic area located in the egg center surrounded by yolk, as with the arthropods. In the second case a protoplasmic layer, the periplasm, covers the surface and is connected with the central mass by a fine plasmic reticulum; the cleavage nuclei as soon as they form, migrate to the surface to form a superficial layer.

Animals having holoblastic cleavage are the porifera, most coelenterates, echinoderms, worms, mollusks except cephalopods, ascidians, *Amphioxus*, amphibians, and the mammals except monotremes. Animals having meroblastic cleavage are the cephalopods, the bony fishes, reptiles, birds, monotremes, arthropods, and a few coelenterates, of which the last two have superficial cleavage, the others discoidal.

Based on the amount of yolk present, eggs have also been divided into alecithal, telolecithal, and centrolecithal. Alecithal eggs are those in which the small amount of yolk is uniformly distributed throughout the egg and in which cleavage is equal and holoblastic, as with the eggs of echinoderms. Telolecithal eggs have considerable yolk and may be either holoblastic, in which the entire mass undergoes unequal cleavage as in the frog's egg, or meroblastic, in which only a disk at the animal pole undergoes cleavage, as in the eggs of reptiles and fish. Centrolecithal eggs, which are restricted to arthropods (exclusive of scorpions) and a few coelenterates, are meroblastic, rich in yolk, and have superficial cleavage. It is evident from what has been said that the type of cleavage has no great significance so far as the systematic grouping of animals is concerned, save that centrolecithal eggs with few exceptions are restricted to the Arthropoda.

References

Doncaster (1920), Hegner (1914a), Hertwig (1912), Korschelt and Heider (1936), Richards (1931), Schröder (Depdolla, 1928), Sharp (1934).

CHAPTER II

A TYPE OF EMBRYONIC DEVELOPMENT IN INSECTS

Before taking up other topics pertaining to the embryology of the Insecta we believe that a clearer conception of the various steps in their natural sequence can be gained by first following through a brief outline of the development of a typical insect from the time of maturation of the egg nucleus to the emergence of the larva from the egg. Exceptional types of development are not considered here but will be treated in the chapters of Part II.

This account does not apply to any specific insect but rather to a generalized type that possesses characteristics common to many insects in most particulars. The writers herein visualize an insect embryo that possesses features that relate it to both generalized and specialized forms, having an oval egg, a superficial germ band of moderate length forming on the ventral side of the egg, with the germ cells making their appearance before the formation of the germ layers, with bipolar development of the mid-gut epithelium, with complete amnion and serosa, and with well-developed coelomic sacs.

The Egg (Fig. 4).—The oval egg, slightly flattened on the dorsal side, is covered by a tough shell, or chorion (*ch*), beneath which is the thin vitelline membrane. Its contents consist of a thin layer of protoplasm (*pr*) at the surface (periplasm) and an internal protoplasmic reticulum (*r*) in the meshes of which the food yolk is held. The egg nucleus (*nu*) is at or near the center.

Entrance of Sperm.—Before an egg is deposited, one or more spermatozoa may pass from the spermatheca of the female into the egg through the micropyle, an opening or a group of openings in the shell in many species located at the anterior end of the egg.

Maturation.—About the time a sperm enters the micropyle, the female nucleus migrates to the periphery of the egg where it undergoes two maturation divisions, throwing off two or sometimes three polar bodies (in case the first body divides again) (Fig. 5, *pb*).

Fusion Nucleus.—The female nucleus, now with the reduced, or haploid, number of chromosomes, migrates back toward the center of the egg, uniting on the way with the nucleus of the sperm producing the zygote, or fusion nucleus, in which the diploid number of chromosomes has been restored.

Division of the Nucleus.—On reaching the egg center, or before it has been reached, the zygote nucleus undergoes mitotic division, the daughter nuclei (cleavage nuclei) migrating toward the egg periphery. In their outward migration the nuclei acquire a cytoplasmic envelope derived from the protoplasmic reticulum, thus becoming amoeba-like cleavage cells (Fig. 6).

Germ Cells, or Sex Cells, and Germ-track Determinant.—Before the primary epithelium is complete, some of the cleavage cells migrating

FIG. 4.—Insect egg. FIG. 5.—Maturation. FIG. 6.—Cleavage. (cc) Cleavage nucleus. (ch) Chorion. (mi) Micropyle. (nu) Nucleus of egg. (os) Oösome. (pb) Polar bodies. (pr) Periplasm. (r) Protoplasmic reticulum. (sp) Sperm. The chorion has been omitted in Figs. 5 and 6.

toward the posterior pole of the egg pass on their way through a protoplasmic substance variously designated by writers as "oösome," "germ-track determinant," "Keimbahn determinant," or "polar plasm" (Fig. 6, *os*). The cells in passing through this oösome cause it to break up the fragments accompanying them as they form a clump at the posterior pole of the egg (Fig. 7). This mass of cells are the germ cells (*gc*), also called "polar globules" or "pole cells" by earlier writers.

The Primary Epithelium, or So-called "Blastoderm."—The cleavage cells now penetrate the periplasm (Fig. 8), undergo one or more mitotic divisions, and then acquire distinct cell walls. The yolk is thus now

surrounded by a cellular wall, the so-called "blastoderm," or primary epithelium, which lies immediately below the vitelline membrane (Fig. 9).

Yolk Cells, or Vitellophags.—After the formation of the primary epithelium (blastoderm) some cells migrate back into the yolk where they increase in size and change in appearance (Fig. 9, *yc*). These are the yolk cells, or vitellophags, which some embryologists regard as the primary entoderm. In the more highly specialized insects the yolk cells,

FIG. 7. FIG. 8. FIG. 9.
 FIG. 7.—Cleavage stage. FIG. 8.—Blasteme stage. FIG. 9.—Blastoderm formation.
 (*bld*) Blastoderm. (*cc*) Cleavage cells. (*gc*) Germ cell. (*y*) Yolk. (*yc*) Yolk cell.

instead of reaching the periphery and then reentering the yolk, remain behind in the yolk while the cleavage cells continue their outward migration.

The Germ Band, or Germ Disk, or Embryonic Rudiment, and the Primary Dorsal Organ.—The primary epithelium (blastoderm) now thickens along the midventral longitudinal line, forming the germ band (Fig. 10). The cells on the dorsal and lateral sides of the blastoderm which do not take part in the formation of the germ band become flattened, later to form the serosa (*ser*), or embryonic envelope. In some insects, as in some of the Lepidoptera, the cells while forming the primary epithelium (blastoderm) differentiate immediately into the ventral columnar cells of the germ band and the pavement cells of the serosa.

On the dorsal side a small group of cells invaginates slightly and later is absorbed in the yolk. This small group of cells constitutes the primary dorsal organ (*do*). Similar structures, apparently homologous, have been

FIG. 10.—Germ-band formation. A, sagittal section. B, cross section. (*do*) Dorsal organ. (*gb*) Germ band. (*ser*) Future serosa. (*yc*) Yolk cells.

FIG. 11.—Formation of embryonic envelopes. A, sagittal section. B, cross section. (*am*) Amnion. (*am.cav*) Amniotic cavity. (*gb*) Germ band. (*gc*) Germ cells. (*hl*) Head lobe. (*ser*) Serosa. (*yc*) Yolk cell.

described for the embryos of *Endromis* (Lepidoptera), the honeybee, and other insects.

The Embryonic Envelopes (Amnion and Serosa).—After the germ band is well defined and with well-developed head lobes (*hl*), the caudal

end pushes into the yolk carrying with it the adjacent primary epithelium. A pocket is thus formed at the posterior end of the egg, the inner wall of which is the tail end of the germ band, the outer wall the amnion, and the invagination itself the amniotic cavity (Fig. 11, *am.cav*). A fold next appears on each side which later extends to the head end. These amniotic folds (*amf*) including the tail fold increase in width, the edges approaching each other (Fig. 12) until they meet, thereby closing over the germ band. The outer surface, composed of pavement cells, constitutes the serosa (*ser*), the cover over the ventral face of the germ band (embryo rudiment), the amnion, the space between amnion and germ band, the amniotic cavity (*am.cav*). The amnion, which is regarded as a derivative of the germ band and has a similar structure, later becomes membranous (Figs. 13, 14). As the tail of the germ band invaginates, it carries with it the germ cells.

FIG. 12.—Sagittal section of germ band. (*am*) Amnion. (*am.cav*) Amniotic cavity. (*amf*) Amniotic folds. (*gc*) Germ cells. (*ser*) Serosa.

Gastrulation and Formation of the Inner Layer.—While the embryonic envelopes are forming, gastrulation of the germ band takes place. A furrow-like invagination forms which begins anteriorly at the point where

FIG. 13.—Gastrulation. Cross section of germ band. (*am*) Amnion. (*ect*) Ectoderm. (*gastr*) Gastrula furrow. (*il*) Tubular inner layer. (*ser*) Serosa. (*yc*) Yolk cells.

the stomodaeal invagination will arise and extends posteriorly to the caudal end of the germ band, or "embryo," as we shall now term it. The invagination does not form in its entire extent at once, and it may in some

cases begin in the middle and extend caudally and finally to the head end. The invaginated part is in the form of a tube which later flattens, obliter-

FIG. 14.—Cross section of germ band after completion of serosa (*ser*). (*am*) Amnion. (*am.cav*) Amniotic cavity. (*ect*) Ectoderm. (*il*) Inner layer. (*neur*) Neuroblasts. (*neurg*) Neural groove. (*yc*) Yolk cell. (*ysp*) Yolk spherule.

ating the cavity (Figs. 13, 14). The flattened tube represents the inner (or so-called "lower") layer which differentiates into a median, or middle, strand which ends anteriorly and posteriorly in a cell mass (the so-called "secondary entoderm") and the two lateral mesoderm bands. To what extent we are justified in considering the longitudinal furrow as a gastrular invagination and in regarding the inner layer as composed of a middle entoderm strand and two lateral mesoderm bands is discussed in Chap. VI of this text.

FIG. 15.—Ventral aspect of embryo. (*ant*) Antenna. (*cly*) Clypeus. (*lb*) Labium. (*lr*) Labrum. (*m*) Mouth. (*md*) Mandible. (*mx*) Maxilla. (*p*) Thoracic legs. (*pleur*) Pleuro-podium.

embryo. Later segmentation occurs, 6 segments eventually forming in the head, 3 in the thorax, and 11 in the abdomen with a telson in addition.

Blastokinesis, Segmentation of the Embryo, and Formation of Appendages.—When the lateral and anterior amniotic folds have formed, the embryo pushes still further into the yolk. This shift in position with respect to the yolk and change in length is termed "blastokinesis" (Fig. 12). Meanwhile there may now be recognized, first, the protocephalon, *i.e.*, the cephalic lobes of the embryo comprising the labrum, eyes, antennae, and usually the postoral somite of the second antennae; and, second, the protocorm, or the remaining part of the

Gradually appendages appear on the segments, the antennae arising posteriorly but later migrating forward. In front of the stomodaeal opening which has formed in the first segment is the labrum. The hypopharynx which develops from the fusion of two small elevations near the median line behind the stomodaeum belongs to the intercalary segment; the basal

FIG. 16.—Cross section of embryo. (*am*) Amnion. (*coel*) Coelomic cavities. (*ect*) Ectoderm. (*mes*) Mesoderm. (*mst*) Median nerve strand. (*neur*) Neuroblasts. (*neurg*) Neural groove.

part of the hypopharynx, however, is formed from the sternal regions of the jaw segments. The jaws and the legs at first appear as short, broad elevations (Fig. 15). The second maxillae later fuse along the median line to form the labium. As development proceeds, the appendages become segmented. On the first abdominal segment they are glandular embryonic structures (pleuropodia).

FIG. 17.—Cross section of embryo. (*am*) Amnion. (*coel*) Coelomic cavity. (*ect*) Ectoderm. (*eps*) Beginning of epineural sinus. (*f*) Fat body. (*gr*) Genital ridge. (*mds*) Median derm strand. (*neur*) Neuroblast. (*nc*) Developing nerve cord. (*yc*) Yolk cell.

Differentiation of the Mesoderm.—The first indication of mesoderm segmentation occurs when the intersegmental parts of the lateral bands become thinner or actually rupture. The segmental parts (somites) acquire in each lateral half a lumen (Fig. 16, *coel*), which in section is more or less triangular or circular in the thoracic and in at least some of

the appendage-bearing segments of the head but often transversely oval or slit-like in the abdominal segments. Thus the coelomic sacs (coel) are formed, whose dorsal walls will later in part form the splanchnic (visceral) mesoderm; the lateral and ventral walls, which are contiguous to the ectoderm, will form the somatic mesoderm. In *Donacia* Hirschler (1909) found coelomic sacs in the intercalary and second maxillary segments as well as in the three thoracic and the first nine abdominal segments. In some primitive insects more sacs are present in the head, and sacs are also found in the tenth and eleventh abdominal segments, whereas in the thorax the coelomic cavities extend deeply into the legs. Laterally, the yolk recedes from the mesoderm, resulting in the formation

FIG. 18.—Cross section of embryo. (*am*) Amnion. (*bl*) Blood cell. (*cbl*) Cardioblasts. (*coel*) Coelomic cavity. (*ect*) Ectoderm. (*eps*) Epineural sinus. (*f*) Fat body. (*gr*) Genital ridge. (*neur*) Neuroblast. (*neurg*) Neural groove. (*som.m*) Somatic mesoderm. (*spltm*) Splanchnic mesoderm.

of a longitudinal cleft on each side, the beginning of the epineural sinus (Fig. 17, *eps*). The dorsal part of the inner layer now splits medially into two lamellae; the dorsal lamella in contact with the yolk becomes the splanchnic layer (Fig. 18, *spltm*); the ventral lamella which passes outward to join the fat body (*f*) becomes the genital ridge (Figs. 17, 18, *gr*). The lateral- and ventral-lying somatic mesoderm (*som.m*) likewise differentiates into two parts; the part in contact with the ectoderm (Fig. 18, *ect*) is the anlage which will form the musculature of the body; the mediodorsal part, which has become more loose and spongy, will form the fat body (Fig. 18, *f*). The large-nucleate cardioblasts, which are found laterally at the junction of splanchnic and somatic layers, will give rise to the heart (Fig. 18, *cbl*). On the middle line is the median secondary entoderm strand (Fig. 17, *mds*) which later will break up into free cells but which now still abuts laterally the anlage of the muscles and fat. Later the lateral margins of the embryo begin to grow around the yolk.

Meanwhile the yolk has receded along the medial line, establishing a connection between the lateral sinuses, thus forming the single definitive

FIG. 19.—Parasagittal section of embryo. (*am*) Amnion. (*amf*) Amniotic fold. (*br*) Brain. (*ch*) Chorion. (*ect*) Ectoderm. (*eps*) Epineurial sinus. (*f*) Fat. (*mes*) Mesoderm. (*mge*) Anterior (*a*), posterior (*p*), mid-gut epithelial rudiments. (*nc*) Nerve cord. (*neurp*) Neuropile. (*proct*) Proctodaeum. (*r*) Mid-gut epithelial ribbons. (*ser*) Serosa. (*splm*) Splanchnic mesoderm. (*stom*) Stomodaeum.

epineurial sinus (Fig. 18, *eps*). The cells of the middle strand are then liberated into the epineurial sinus, some perhaps to share later in the

formation of the mid-gut epithelium, some to disintegrate in the yolk, and some to form the blood cells (*bl*). It is probable that those which are destined to form the blood cells really arise from the lateral median margins of the coelomic sacs. This liberation of cells takes place in the gnathal head segments as well as in the thorax and abdomen. The genital ridges are not found in the head or the two anterior thoracic segments, and cardioblasts are lacking in some head segments and in the last two abdominal segments. Later the genital ridges degenerate anteriorly and posteriorly, remaining only in those intermediate abdominal segments where the germ cells will later lodge and the gonads develop.

FIG. 20.—Cross section. (*cbl*) Cardioblasts. (*f*) Fat body. (*mge*) Mid-gut epithelial ribbon. (*mus*) Muscles. (*nc*) Nerve cord. (*splm*) Splanchnic mesoderm.

The Alimentary Canal.—When the posterior end of the embryo has invaginated into the yolk to the maximum extent and the segmentation of the mesoderm has begun, the stomodaeal invagination begins to form in the head at about the level of the future preantennal segment. A little later the beginning of a proctodaeal invagination is to be seen in the last abdominal segment. These two invaginations will give rise to the fore- and hind-gut. The inner layer, as already stated, is made up of three longitudinal strands, the laterals of mesodermic tissue, the middle one regarded by some writers as the secondary entoderm. The extremities of the middle strand, which remain in position when its middle section breaks down, are here designated as the “mid-gut epithelial rudiments” (*i.e.*, secondary entoderm, or mesenteron rudiments). The stomodaeal and proctodaeal invaginations deepen; their inner ends impinge upon the mesenteron rudiments (Fig. 19, *mge*). Through active proliferation each rudiment sends out a pair of ribbons (*r*) which run lateroventrally of

the yolk and above and upon the splanchnic mesoderm bands (Figs. 19, 20, *splm*). From both fore and aft the paired enteron ribbons grow toward each other toward the middle of the embryo where they fuse. In some insects at the same time numerous cells that were set free into the epineural sinus from the middle strand attach themselves to the yolk between the ribbons. By growth in width of the ribbons and by tangential division of the cells liberated from the middle strand that now lie between the ribbons, a single median sheet is formed which late in embryonic life grows around the yolk on both sides and over the top to form the tube that constitutes the mid-gut epithelium. According to Hirschler, not all of the anterior cell mass is used up in the formation of the mid-gut epithelial ribbons; the anterior part migrates forward and

FIG. 21.—Cross section of developing heart. (*cbl*) Cardioblast. (*div*) Dorsal diverticulum. (*ect*) Ectoderm. (*eps*) Epineural sinus. (*f*) Fat. (*mes*) Remains of coelomic wall. (*mge*) Mid-gut epithelium. (*pd*) Pericardial septum. (*sin*) Blood sinus of gut.

becomes paired to form a spherical mass on each side of the stomodaeum. This pair of spherical masses is the subesophageal body which most embryologists believe to be of mesodermal origin. At the blind end of the proctodaeum three pairs of evaginations arise which elongate to become the Malpighian tubules. Shortly before hatching, the blind ends (limiting membrane) of the stomodaeum and proctodaeum break down, and thus continuity of the alimentary canal is established.

Circulatory System, Pericardial Cells, Pericardial Septum, and the Paracardial Cell Strand.—Laterodorsally, where the splanchnic and somatic mesoderm meet, the cardioblasts (Fig. 20, *cbl*), or heart cells, develop. These strands of cardioblasts, one right and one left, are pushed dorsad by the dorsad growth of both the ectodermal body wall and the mesoderm until the two strands meet and fuse into a tubular heart (Fig. 21). The cardioblasts do not all meet simultaneously; but in some instances, as in *Donacia*, the tube first closes ventrally and later dorsally at the posterior end of the heart, whereas elsewhere the tube fuses first dorsally and then ventrally. The aorta is not formed by cardioblasts but from the median walls of the antennal coelomic sacs. The aorta thus develops independently of the heart; the dorsal blood vessel in its

entirety, therefore, first develops at each extremity and later is formed in the middle.

As has already been stated, blood cells arise from cells liberated along the midventral line above the inner neural ridge. By some embryologists

FIG. 22.—Section of ventral nerve cord. (dt) Daughter cells. (ect) Ectoderm. (mst) Median nerve strand. (neur) Neuroblast. (neurp) Neural groove. (neurp) Neuropile. (From Wheeler.)

these are regarded as coming from the inner lateral margins of the coelomic sacs adjacent to the middle strand and therefore mesodermic; other writers, Hirschler (1909) among them, say that these cells come from the middle strand itself and therefore, like the mid-gut epithelium, are entodermic.

The pericardial cells, likewise regarded by some embryologists as mesodermic and probably derived from the middle section of the pericardial septum (Fig. 21, *pd*), are said by Hirschler (1909) to arise from those cells of the posterior mesen-

teron rudiment which are not used in the formation of the posterior part of the mid-gut epithelium.

The paired structure found in the pericardial septum in metameric arrangement at the sides of the dorsal blood vessel in *Forficula* and some other insects, and known as the paracardial cell strand, arises from the dorsal part of the coelomic sacs.

Nervous System.—Shortly before the appearance of the stomodaeal and proctodaeal invaginations the neural groove (Fig. 16, *neurp*) forms along the mid-ventral longitudinal line, extending at a little later stage from near the stomodaeum to the proctodaeum. On each side of the groove outwardly is an outer neural ridge which later develops into the paired nerve strands. The outer neural ridges become segmented. The ectoderm adjacent to the neural groove becomes two-layered, the outer layer consisting of ordinary body-wall cells, the inner layer composed of large nerve cells, or

FIG. 23.—Cross section of posterior end of an early embryo. Germ cells (*gc*) lodged between the primary epithelium and the yolk. (From Hirschler.)

the pericardial septum in metameric arrangement at the sides of the dorsal blood vessel in *Forficula* and some other insects, and known as the paracardial cell strand, arises from the dorsal part of the coelomic sacs.

neuroblasts (Fig. 16, *neur*). The daughter cells of the neuroblasts nearest the neural groove develop into the median nerve strand (Fig. 22, *mst*). The number of neuroblasts in any section is fairly constant for a given species, most numerous in the region of the head lobes. Active proliferation of the neuroblasts gives rise to numerous

FIG. 24.—Blastokinesis. Successive stages A-D. (*am*) Amnion. (*do*) Secondary dorsal organ. (*fu*) Fusion area of amnion and serosa (*ser*).

daughter cells (nerve cells), which in cross section appear as a column of cells with a neuroblast (*neur*) at the base of each. Ganglia are formed in the body segments, and later the neural layer of cells separates from the body wall. The neuropile (Punctsubstanz, fibrillar substance, nerve fibers) develops in the ganglia in the older stages, at first free dorsally but later surrounded by nerve cells. Commissures appear before the connectives. In young embryos 6 pairs of ganglia belong to the head, 3 to the thorax, and 11 (more rarely 10 or 12) to the abdomen. In the

later stages there may be a considerable reduction in number owing to fusion of the brain ganglia, the subesophageal ganglia, and, in more highly specialized insects, thoracic and certain abdominal ganglia also.

Tracheal System.—The stigmata of the respiratory system appear shortly after the outer neural ridges have become segmented—a pair each for mesothorax and metathorax and a pair for each of the first eight or nine abdominal segments. Each of the stigmata is the mouth of a tracheal invagination. In most insects this trachea forks, the posterior branch of one fork fusing with the anterior branch of the next succeeding one, thereby forming two major tracheal trunks. Transverse branches arise which connect the right and left sides, and from the minuter subdivisions the tracheoles develop. In the more primitive insects longitudinal trunks are not formed.

FIG. 25.—Sagittal section. Formation of secondary dorsal organ (*do*) from the serosa. (*am*) Amnion forming a provisional dorsal closure. (*y*) Yolk.

Oenocytes.—The oenocytes, a clump of large rounded cells, may be observed in the ectoderm at the time the tracheal invaginations first appear, a little behind and laterad of them. These cells occur in all abdominal segments except possibly the last one or two. As the embryo grows older, the oenocytes extend as a more or less connected strand of cells into the interior adjacent to the tracheal trunks and press into the fat body. Eventually they lose their ectodermal connection.

Migration of Germ Cells. Gonads.—The germ cells are early differentiated as a group of cells located at the posterior pole of the egg. When the posterior amniotic fold develops, they pass through the primary epithelium (blastoderm) and lodge between this and the yolk (Fig. 23). By the time the proctodaeum and the coelomic sacs appear, the germ cells have migrated forward between the entoderm and the yolk and have divided into two masses. In about the ninth or tenth abdominal segment one mass migrates to the right, the other to the left, penetrating the mesoderm. When the coelomic cavities have appeared, the germ cells pass further forward, penetrate into the genital ridge, increase in number, and form a mass of cells surrounded by the tissue of the genital ridge, the anlage of the gonads.

Secondary Dorsal Organ and the Dorsal Closure.—As soon as the embryo has attained its maximum length and is about to begin shortening, amnion and serosa fuse longitudinally for a short distance at the head, as in *Forficula* (Fig. 24A-D), whereupon a longitudinal fissure

appears in the fused area. Amnion and serosa adhere to each other along the edges of the fissure; a shrinkage of the envelopes and a folding back of the amnion cause them to gather on the dorsal side of the embryo where the serosa sinks into the yolk in tubular form (the secondary dorsal organ) and the amnion forms a provisional dorsal closure (Fig. 25, *do*). Finally the ectoderm grows over the dorsal organ which becomes detached and is wholly absorbed in the yolk. With the dorsal growth of the ectodermal wall that replaces the amnion in its progress the definitive dorsal closure is effected. Meanwhile the mid-gut has also closed, and thus the embryonic development is completed.

References

To avoid unnecessary repetition the works noted below are for the most part omitted from the list of references following the chapters in Part I. Either they are comprehensive treatises or they deal in more or less detail with the developmental stages of a single insect from egg deposition to hatching.

Balfour (1880), Berlese (1909), Blunck (1914), Brachet (1921), Brauer (1925), Bruce (1887), Brues (1903), Butt (1934*a*, 1936), Carrière und Bürger (1897), Cholodkovsky (1891*d*), Claypole (1898), Comstock (1924), Dawydoff (1922), Eastham (1927, 1930*a*), Emeis (1915), Evans (1902), Gambrell (1933), Ganin (1869), Gatenby (1917), Graber (1879, 1889*b*, 1890*b*), Hagan (1917), Hammerschmidt (1910), Hardenburg (1929), Heider (1889), Heider (1913), Henneguy (1904), Heymons (1895*a*, 1896*a*, 1897*b*, 1899*b*, 1901), Hirschler (1907*c*, 1909*b*, 1912, 1924), Huxley and DeBeer (1934), Imms (1934), Johannsen (1929), Kahle (1908), Kellicott (1913), Kennel (1884-1886), Kessel (1939), Knower (1900), Korotneff (1886), Korschelt (1912), Korschelt and Heider (1899, 1936), Kowalewsky (1871), Lécaillon (1898*b*), Leuzinger, Wiesmann und Lehmann (1926), Lignau (1911*b*), McBride (1914), Meisenheimer (1917), Melanby (1936), Melnikow (1869), Metschnikoff (1886*a,b*), Miall and Denny (1886), Miall and Hammond (1900), Morgan (1927, 1934), Needham (1931), Nelson (1915), Noack (1901), Noskiewicz und Poluszynski (1927), Nusbaum (1886), Packard (1871*b*, 1903), Paterson (1932, 1936), Patten (1884), Philpitschenko (1912), Richards (1931), Roonwal (1936, 1937), Saito (1937), Sedgwick (1885-1888), Shinji (1919), Snodgrass (1925, 1927, 1935*b*), Spemann (1938), Strindberg (1913*b*, 1914*a*), Tanquary (1913), Tiegs and Murray (1938), Tillyard (1917), Toyama (1902), Uichanco (1924), Uzel (1898), Voeltzkow (1889*a*), Waddington (1935), Weber (1933, 1937), Weismann (1863), Weiss (1939), Wheeler (1889*b*, 1893*a*), Wigglesworth (1939), Will (1888*a*), Willey (1898), Witlaczil (1884), Woodworth (1889), Wray (1937), Zograff (1883).

Krause (1939), Roonwal (1939), Snodgrass (1938).

CHAPTER III

THE EGG, FERTILIZATION, MATURATION, AND CLEAVAGE

THE EGG OF THE EUTRACHEATA

The germ cells are differentiated at an early period, in some cases before the formation of the blastoderm. Dividing into two groups, they migrate forward and become lodged on or near the genital ridges which have meanwhile developed on the splanchnic mesoderm. The genital ridges give rise to the gonads, the embryonic reproductive organs, from which the testes or ovaries later are formed. Within these organs the germ cells develop into eggs or sperms during postembryonic life.

Except in some parasitic forms the egg is outwardly protected by a firm shell, or chorion, in which there are one or more orifices for the passage of the sperms. Immediately within the chorion is the thin, noncellular vitelline membrane. The contents of the egg are composed chiefly of two elements: protoplasm and deutoplasm. The former is the formative yolk; the latter, the food material upon which the developing embryo will live. The formative protoplasm (oöplasm) usually consists of a thin peripheral layer, or periplasm (Keimhautblastem), immediately under the vitelline membrane; and an inner reticulum, or net, in the meshes of which the deutoplasm, or food yolk, is held. The periplasm seems to be lacking in Orthoptera and some Hymenoptera. At or near the center is the nucleus surrounded by a protoplasmic envelope (nuclear cytoplasm).

The chorion, or eggshell, is formed by the follicular cells of the ovarioles of the parent in a manner similar to the formation of the cuticula by the epidermis of the body wall. The chorion, however, is not chitinous, as was formerly believed, but differs in containing sulphur, in having a higher nitrogen content, and in being less resistant to alkalines. Korschelt (1887) states that when first formed it is soft and plastic and that it adjusts itself to the changing form of the developing egg. The chorion does not always develop simultaneously over the egg but may form first at the posterior end, gradually covering the surface. The reticulate or otherwise complicatedly marked egg surface is produced by the impression of the ends of the ovarian follicle cells upon the plastic chorion. The coriaceous substance of which the chorion is composed and to which the term "chorionin" has been applied is secreted not only by the ends of the follicular cells but also by the sides from between adjacent cells resulting in the strange markings characteristic of certain insect eggs.

In some eggs the chorion appears to be homogeneous; in other cases it may be more or less complex, either with an outer thicker exochorion and a thin inner endochorion united by minute perpendicular trabeculae; or more or less felt-like with fibers running in all directions. Miller (1939) states that the chorion of the stone-fly egg consists of two layers: the exochorion, which is hard, thick, and lacunar and the very thin endochorion, the two layers being separated by an interlamellar space traversed by low cylindrical or discoid pillars, or trabeculae.

Korschelt (1887) found that certain cells of the follicular epithelium, the nuclei of which are not in alignment with those of adjacent cells and lying in the region where the micropylar orifices are to form, are provided distally with a pointed protoplasmic process. After secretion of the chorion by these cells at their distal end the withdrawal of the protoplasmic points leaves passages free that constitute the micropylar canals (Fig. 26). In the egg of the flesh fly Verhain

FIG. 26.—Micropyle formation. Section of follicular epithelium (*fol*) and chorion of egg (*ch*). (*mi*) Micropyle. (*x*) Mucous layer.

(1921) ascribes the formation of the micropyle not to a single cell but to a group of follicular cells which push in from the extremity of the nurse chamber between the nurse cells in the form of a cellular clavate process and which probably form the micropylar core. The formation of the micropylar canal in the *Anopheles* egg as described by Nicholson (1921) in principle resembles that of the flesh fly.

Pore canals in the chorion are similarly formed over the protoplasmic processes of cells, but here the processes are, of course, much smaller.

For the entrance of the sperms, micropylar openings, either single or in groups, are in most cases found at or near the anterior end of the egg. But they may also be found lateral in position, as in some Orthoptera; or a group of openings may be found at both ends, as in the eggs of the flea; or they may encircle the egg, as in the stone fly *Pteronarcys*.

Immediately below the chorion is the vitelline membrane, a thin noncellular tissue which Korschelt (1887) says is the hardened surface of the periplasm and in some insects is formed before, in others after, the formation of the chorion. Its elasticity, when it first appears, permits it to conform with the changing shape of the developing egg. The membrane is said to be lacking in some Collembola. According to Emeis (1915) it is also apparently absent in some coccids, but Shinji (1919) states that it is present in the species studied by him. It should, however, not be forgotten that the inner layers of the chorion may in some cases be mistaken for the vitelline membrane (Slifer, 1937).

The oöplasm (formative yolk) and the deutoplasm (food yolk) constitute the egg yolk; the former chiefly albuminoid, the latter composed of fat, lecithin, cholesterolin, glycogen, and inorganic salts, substances derived from the nurse cells of meroistic ovaries or from the follicular epithelium of panoistic ovaries.

A meroistic ovary is one in which the egg tubes (ovarioles) contain nurse cells that may all be restricted to the germarium or apical part of the tube (found in the Hemiptera, polyphagous Coleoptera, and Siphonaptera) or that alternate with the eggs in the vitellarium (in the Dermaptera, Diptera, Lepidoptera, Hymenoptera, and adelphagous Coleoptera) (Fig. 27). A panoistic ovary is one that lacks nurse cells, as in *Machilis* and *Japyx* among Apterygota and in the Odonata, Orthoptera, and Plecoptera. The nurse cells are abortive eggs and together with the functional eggs are derived from the embryonic germ cells. In *Miastor*, however, according to Hegner (1912) the nurse cells are derived from the somatic cells.

The part played in the formation of yolk by certain inclusions such as mitochondria and Golgi bodies is still a matter of controversy. King (1926) maintains that in *Peripatopsis capensis* yolk formation begins before the mitochondria have become distributed. The yolk is fatty, but its source has not been determined. In *Drosophila melanogaster* and *D. simulans*, according to Ephrussi (1925), there is no proof that the mitochondria play any part in the elaboration of yolk.

Payne (1932) describes and figures young oöcytes of a stone fly in which the yolk and fat are at first located around the nucleus and migrate peripherally, but with insects in general they arise in the periphery. Nicholson (1921) found that to some extent yolk material is laid down in the periphery of *Anopheles* eggs in the earliest stages, but undoubtedly the greater part of the nutritive material reaches the egg through the medium of the nurse cells. Although Gresson (1929) asserts that the

FIG. 27.—Ovariole of meroistic ovary. Alternating nurse cells (*nur*). (*egg c*) Egg cells. (*fol*) Follicle. (*ger*) Germarium. (*vtl*) Vitellarium.

the medium of the nurse cells. Although Gresson (1929) asserts that the

fatty yolk of the tenthredinid egg is formed from the Golgi vacuoles of the oöcyte and nurse cell, Payne (1932) in a study of the oögenesis of a number of species of insects representing six orders found no evidence that the Golgi bodies are concerned either directly or indirectly in either yolk or fat formation but that they appear to be the intermediate products of metabolism. Vacuoles and Golgi bodies he considered separate, independent structures. There is a wide divergence of opinion regarding the source of both fat and yolk as the works of Gatenby, Woodger, Harvey, Hirschler, Ludford, Nath, King, and others attest. Payne concluded that since yolk and fats have no relationships to other visible substances in the cell, the assumption is that they arise independently in the cytoplasm, the nuclei playing no visible part in this synthesis. Neither did he find indications in the insect eggs studied of the transformation of mitochondria (chondriosomes) into fats, yolk, fibers, or any other substances or structures.

In the eggs of many animals a special inclusion, associated with the primordial germ cells, was named the "Keimbahnplasma" by Hasper (1911), or the "Keimbahn-" or the "germ-track determinant" by later workers. Other names that have been applied to this inclusion are "oösome," "posterior granular plate," "germ-line determinant," "germinal cytoplasm," "pole disk," "germ plasm," and "polar granules." The term "oösome," first used by Silvestri, because of its simplicity and because its adoption will cause no confusion, we shall use in this text. The substance is characterized by its position near the posterior pole of the egg, its affinity for stains, and its frequently disk- or saucer-like shape (Fig. 6, *os*). The oösome has been demonstrated in the eggs of a number of insects as well as in those of *Sagitta*, *Cladocera*, *Sphaerium*, and other invertebrates.

After fertilization the cleavage cells, as they arise, start their migration toward the periphery of the egg. Of the nuclei that reach the posterior pole of the egg one enters the oösome which then breaks up, either in granular form or in fragments, the particles entering the cytoplasmic envelope of the nucleus. The nucleus that enters the oösome becomes the primordial germ cell. With some insects several nuclei enter the oösome, in which case they all develop into germ cells. The fact that in a number of species of animals the oösome in its association with the germ cells can be traced from the time of the segregation of the germ cells until they are lodged in the gonads gave rise to several of the names applied to the substance. Sachtleben (1918) found that in *Chironomus* the oösome may be traced from the unfertilized egg through to the growth period of spermatocyte and oöcyte of the first order during postembryonic development. Continuity, however, of the oösome through two generations does not exist, the substance being formed anew in the egg. The

association of the oösome with the germ cells has given rise to the assumption on the part of some workers that this substance in some way acts as a stimulus to convert undifferentiated cleavage nuclei into germ cells. Recent writers, however, regard the oösome merely as an *indicator* of the path of the germ cells from their original position at the posterior pole of the egg to their definitive position in the gonad rather than a *determinant*, or causal factor, in the production of germ cells.

It is not the oösome but the cytoplasm lying adjacent to it that is the factor governing the conversion of the cleavage cells into germ cells according to Hegner (1914), all the cleavage cells being qualitatively alike. Furthermore, Huettner (1923) states that the deciding factor that determines whether a nucleus shall become somatic or germinal appears to be the posterior pole plasm, which he regards as a differentiated oöplasm. Any nucleus of the developing egg may be differentiated into a polar nucleus (*i.e.*, germ cell) if it comes accidentally into the region of the posterior polar plasm. If one daughter nucleus enters the posterior polar plasm and the other remains in the general oöplasm, the latter becomes a somatic nucleus, whereas the former, surrounded by polar granules (oösome), becomes a polar nucleus. The posterior polar plasm referred to here is the periplasm (cortical oöplasm) which lies at the posterior pole of the egg.

As for the nature of the oösome substance, Huettner holds that in the egg of *Drosophila* it is a by-product of the posterior pole plasm and is not composed of minute yolk granules, or mitochondria.

Among insects it has been demonstrated in Coleoptera (Chrysomelidae and *Brachyrhinus*), in Diptera (*Miastor*, *Chironomus*, *Simulium*, *Sciara*, *Drosophila*, *Musca*, *Phormia*, *Calliphora*, *Melophagus*), and in Hymenoptera (*Apis*, *Litomastix*, *Ageniapis*, *Encyrtus*, *Oophthora*, *Diastrophus*, and others).

FERTILIZATION AND MATURATION

Fertilization.—With insects in general, after the eggshell has been formed, fertilization takes place. The egg descends from the ovary and in passing the opening of the spermathecal duct receives through the micropyles the sperms that have previously been deposited in the spermatheca (or in some cases in the bursa) by the male. Although polyspermy is the rule with insects, in that a number of sperms enter the micropyles, monospermy has been recorded for *Sciara* (Schmuck and Metz, 1932), *Diacrisia* (Johannsen, 1929), parasitic Hymenoptera (Leiby, Patterson, Silvestri), and some other insects. When polyspermy takes place, the supernumerary sperms degenerate in the yolk. Huettner (1924, 1927) reports that supernumerary sperm in *Drosophila* eggs degenerate, only rarely forming mitotic figures. If, however, the degree

of polyspermy is too great, it may lead to disturbances that prevent further development. These disturbances are usually due to disorganization of the maturation divisions by sperm which enter this region of the egg. Such sperm may form uni-, bi-, or multipolar spindles or even enter normal spindles to form multipolar figures. This condition may or may not become adjusted. In binucleate moth eggs Doncaster (1914) and Goldschmidt and Katsuki (1928) report that each nucleus fuses with a sperm. Genetic evidence shows that the same is true for some binucleate eggs of the wasp *Habrobracon* (Whiting, 1934). In no case is there any evidence of a sperm functioning except after uniting with an egg nucleus, but Huettner (1927) states that such is possible and shows that it might conceivably be followed by normal development.

Fertilization membranes are seldom mentioned for insects. In the silkworm, Bataillon and Su (1931*a*, 1933) report that a strong fertilization membrane is detached from the egg following induced parthenogenesis and in the first brood of two-brooded stocks but not in the second brood or in single-brooded stocks. The significance of this variation is not known.

The chromosome behavior during fertilization and maturation has already been briefly described. As has been stated, the male of certain animals produces two kinds of sperms differing visibly in chromatin content; *i.e.*, the male is heterozygous for sex, whereas the female producing but one kind of egg is homozygous for sex. We have also shown that although the autochromosomes occur in homologous pairs, the accessory chromosomes in the male may either occur singly as an *x*-chromosome (Fig. 3) or, if in pairs, as an *x*-chromosome and a *y*-chromosome; *i.e.*, the male is heterogametic (digametic). The accessory chromosome is single in the Orthoptera, Homoptera, some Heteroptera (*Protenor*, *Hydrometra*), some Diptera (*Tephritis*), some Coleoptera, and Neuroptera. The diploid cells of the females of these forms have two similar *x*-chromosomes instead of one. At fertilization, eggs receiving an *x*-chromosome will produce females; others receiving none will produce males. The accessory chromosomes are double in the diploid cells of the males of most Heteroptera, Diptera, and Coleoptera. In this case at fertilization some eggs will receive an *x*-chromosome and therefore produce a female, whereas others that receive a *y*-chromosome will produce a male. In some species of animals conditions are reversed, and it is the female that is heterozygous for sex, as in certain Lepidoptera (*Talaeporia*, *Fumea*).

More detailed accounts on this subject may be found in texts on cytology (Doncaster, Sharp, 1934; Wilson, Schröder, 1928). Schröder's text deals especially with cases among insects.

Maturation.—In the insect egg maturation begins immediately after the entrance of the sperm, so that the transformation of the head of the

sperm into a male pronucleus takes place at the same time as the formation of the female pronucleus. Although several sperms may have entered the egg, only one male pronucleus unites with the female pronucleus to form the fusion nucleus (syngaryon).

The maturation spindles lack the asters, although centrosomes may be either present as in *Miastor* (Kahle, 1908) or absent as in *Apis* (Nachtsheim, 1913) and Lepidoptera (Seiler, 1924). The first polar body may again divide mitotically so that three polar bodies are formed, as has already been described in Chap. I; but in some cases it either does not again divide, as in *Pseudococcus citri* (Schrader, 1923), or only partially divides, as in *Diacrisia virginica* (Johannsen, 1929). With *P. citri* the diploid chromosome group of the first and the haploid group of the second polar body unite into a triploid group, which then divides mitotically, resulting in nuclei that become surrounded with cytoplasm and thus give rise to giant cells which will later associate with the symbionts of the egg. When the process has been completed, the giant cells are known as "mycetocytes."

During the first maturation division chromatin elimination may take place in the eggs of a number of species of Lepidoptera (Seiler, Johannsen, 1929), in Diptera (*Miastor*, Kahle, 1908; *Sciara*, DuBois, 1932), and other forms. The elimination takes place in the form of an equatorial disk (Fig. 295), the amount eliminated being variable, leaving a constant amount in the daughter cells.

Hegner (1917) in his account of the organization of the insect egg concludes that the insect egg at the time of maturation is a mosaic of differentiated cytoplasmic areas predetermined to develop into definite parts of the embryo. This organization results from the interaction of nucleus and cytoplasm during the germ-cell cycle. Such interaction is taking place at all times but is visible only when such processes as the protrusion of chromidia or chromatin diminution occur.

The point in the egg where the maturation divisions take place is not constant. In *Simulium* and some other Diptera and in *Diacrisia* it is not far from the anterior pole; in *Melophagus* it is below the middle on the dorsal side; in *Pteronarcys* it is midventral. It has been pointed out that since the point of entrance and path of the sperm are probably constant in any one species owing to the position of the micropyle, it is uncertain whether or not they bear any relation to the origin of the orientation of the embryo. The only cases in which any part of fertilization is thought to have a bearing on development, other than initiating completion of the maturation divisions, is in incompletely determinate eggs. In this type of egg Reith (1931b, 1935) reports that induction of the visible zonation of the cortical layer of the ant egg and a similar but not visible determination in the beetle egg start immediately after the

beginning of cleavage. How this activation of the activation center is brought about and whether it is caused by the entrance of the sperm, the fusion of the pronuclei, or some other factor are unknown.

CLEAVAGE IN EGGS OF THE EUTRACHEATA

Although the eggs of most arthropods undergo superficial cleavage, there are a number of exceptions. The following groups may be recognized.

1. Eggs with a Purely Superficial Cleavage.—This type, which is the usual form, has already been described in the account of the development of the generalized insect in Chap. II. The fusion nucleus divides into daughter cells which by repeated division and migration to the periphery give rise to a layer of cells or primary epithelium commonly known as the "blastoderm." This type occurs with eggs rich in yolk, but it also occurs exceptionally in certain cases where there is a deficiency in yolk as in the eggs of aphids, some *Platygastridae*, and *Hemimerus*.

2. Eggs with a Combination Cleavage—First Total, Later Superficial.—Combination cleavage that is total at first and later becomes superficial has been observed in the group *Collembola*, and even among them *Anurophorus* and *Tetrodontophora* undergo a purely superficial cleavage. The combination type is well exemplified in *Isotoma cinerea* described in Chap. XIII in which the entire egg mass divides until it forms the 32- or 64-cell stage, each nucleus surrounded by a protoplasmic envelope which in turn lies in the center of a yolk spherule (Fig. 65). The nucleated cell-like bodies now migrate, first to the surface of the yolk spherules and then to the periphery of the egg, leaving the yolk spherules in the center (Fig. 67), thus forming the blastula. The early development of *Anurida maritima* as described by Claypole (1898) does not essentially differ. In the genus *Tomocerus* (*Macrotoma*) the development starts with the division of the nucleus, but it is not until the third or fourth division that the yolk also begins to divide. At the 32-cell stage the yolk-cell walls disappear, and the yolk nuclei pass to the periphery of the egg, where through tangential division of the nuclei the blastoderm is completed. In the forms mentioned cleavage is equal; but in *Achorutes armatus*, according to Uzel, an unequal cleavage takes place with the formation of micro- and macromeres. A possible case of combination cleavage has been briefly described by Strindberg for an ant of the genus *Azteca*.

3. Eggs with Purely Total Cleavage.—Purely total cleavage occurs in the eggs of several parasitic Hymenoptera and is associated in most cases with polyembryony. As the process of cleavage in these forms is complicated and is described in Part II in the section dealing with the Hymenoptera, it will not be given here. Suffice to say it occurs among

the Proctotrupidae (*Platygaster*, *Polygnotus*), Chalcidae (*Copidosoma*, *Paracopidosomopsis*, *Ageniaspis*), and some others.

References

Arthropoda, etc.: Blochmann (1887, 1888), Brandt (1880), Claus (1864), Claypole (1898), Dohrn (1870), Hegner (1917), Huettner and Rabinowitz (1933), Korschelt (1884, 1887*a*), Leuchart (1855), Leydig (1848), Ludwig (1874), Payne (1932), Sharp (1934), Will (1884).

Myriapoda: Balbiani (1883), King (1926), Nath and Husain (1926), Stuhlmann (1886).

Apterygota: Brandt (1878), Weismann (1882).

Orthoptera and Dermaptera: Bezrukow (1923), Blochmann (1887), Brandt (1878), Brauns (1913), Carothers (1931), Giardina (1897), Gresson (1931), Henneguy (1890), Husian (1927), Korschelt (1885, 1886), Leydig (1889), McNabb (1928), Müller (1825), Murray (1926), Rau (1913), Slifer (1931*b*, 1937, 1938), Stuhlmann (1886), Weismann (1882), Williams and Buxton (1916), Zakolska (1917).

Minor Orders: Miller (1939), Zaddach (1854).

Hemiptera: Brandt (1878), Emeis (1915), Henking (1888–1892), Hirschler (1912), Jordan (1909), Korschelt (1885, 1886), Lawson (1939), Leydig (1889), Ries (1932), Wielowiejski (1885), Zacharias (1884).

Lepidoptera: Doncaster (1914), Foa (1924, 1937), Grandori (1921), Henking (1888–1892), Meissner (1855), Sehl (1931), Seiler (1924), Umeya (1937), Waldeyer (1870).

Coleoptera: Brandt (1878), Hegner (1908, 1911*b*), Henking (1888–1892), Hirschler (1932), Hughes-Schrader (1924), Korschelt (1885, 1886), Leydig (1889), Meissner (1855), Saint-Hilaire (1895), Tur (1920), Wieman (1910).

Diptera: Blochmann (1887), Branch (1931), DuBois (1932), Ephrussi (1925), Henking (1888–1892), Huettner (1924, 1927, 1934, 1935), Korschelt (1886), Meissner (1855), Metcalf (1935), Metz (1938), Nath (1925), Nicholson (1921), Rabinowitz (1937), Ravetta (1931), Strasburger (1933, 1934), Stuhlmann (1886), Verhain (1921), Waldeyer (1870), Weismann (1882).

Hymenoptera: Blochmann (1884–1889), Brandt (1878), Doncaster (1906), Hegner (1911*b*, 1914, 1915), Henschen (1929), Korschelt (1886), Marshall (1907), Meissner (1855), Nachtsheim (1913), Patterson (1917), Silvestri (1906*a*), Stuhlmann (1886), Weismann (1882), Weyer (1928), Whiting (1924, 1934), Whiting and Gilmore (1932).

See also the list of general works cited in Chap. II.

CHAPTER IV

EARLY DEVELOPMENT

THE BLASTODERM

In the egg before cleavage begins one may distinguish a central nucleus surrounded by protoplasm; a cytoplasmic reticulum with food yolk in its meshes, forming most of the contents of the egg; and a peripheral cytoplasmic layer, the periplasm. The periplasm is of variable thickness and seems to be very much reduced or entirely lacking in certain Orthoptera, Odonata, and Hymenoptera. The cleavage nuclei which migrate toward the surface are surrounded by a layer of cytoplasm and thus may be called "cells." In some cases, at least, it appears that these cells are not independent but are connected by cytoplasmic strands to the reticulum which, in turn, is joined to the periplasm. In some Orthoptera the blastoderm is formed from cleavage nuclei migrating in the periphery from an egg nucleus near the surface of the egg. The first few cleavage divisions are synchronous in Coccidae, Siphonaptera, *Drosophila*, *Phormia*, *Diacrisia*, *Brachyrhinus*, and numerous other forms. *Calandra oryzae* (Tiegs and Murray, 1938), however, offers an exception in a complete absence of synchronization. There is a lack of uniformity also in the orders of insects as to when and where the cleavage nuclei reach the periphery (Marshall and Dernehl, 1905). In the Holly Tortrix moth (Huie) all cleavage nuclei reach the periphery simultaneously; in *Pieris* (Eastham, 1927) the blastoderm is first formed at the anterior pole; and in *Diacrisia* (Johannsen, 1929) it is first formed at both poles. Apparently the exact region of the periplasm at which the cleavage nuclei first reach the surface is conditioned in part by the shape of the egg and in part by the position of the egg nucleus at the time when cleavage first begins rather than by phylogenetic considerations. The reason for the peripheral movement of the nuclei toward the surface is not clear. Miller (1939) regards it as a passive drifting without intrinsic movement due to local changes in and around the cells themselves, the synchronous migration being due merely to a summation of simultaneous, local, nuclear influences. Sehl (1931) suggests that the movement is caused by the attraction that the periplasm exerts upon the nuclei.

The cleavage nuclei, each surrounded by a layer of cytoplasm, enter the periplasm where they may undergo one or more tangential divisions. The nucleated periplasm before the formation of cell walls has been

designated the "blastema" by Weismann. When the definitive number of peripheral nuclei have been formed, cell walls appear, first between the nuclei and then on the side toward the yolk, thus completing the cells and with them the blastoderm. Some writers who regard the yolk cells as the primary entoderm substitute for the term "blastoderm" as used here the term "primary epithelium" on the ground that an entoderm being already present, the stage itself is really a gastrula. In the formation of the blastoderm in *Calliphora*, *Diacrisia*, and many other insects the cells at the time they reach the periplasm are closely spaced; in other forms, as in *Carausius*, they are far apart except those in one area that forms the small embryonic rudiment. In the stone fly *Pteronarcys* and in the centipede *Scolopendra* the blastoderm arises from isolated cell groups which have developed from the outward-migrating cells. The examples given here represent extremes between which intermediate types may be found in several orders.

YOLK CELLS

In the outward migration of the cleavage cells toward the periphery some remain behind in the yolk and form the so-called "vitellophags," or primary yolk cells. This intravitelline separation, as it was termed by Heymons, occurs in *Machilis*, *Lepisma*, Heteroptera, Homoptera, Lepidoptera, Coleoptera, Diptera, most Hymenoptera, and some Orthoptera (*Locusta*, *Gryllus*, *Oecanthus*, *Gryllotalpa*). With some other insects all cleavage cells reach the periphery, but some to return later into the yolk as secondary yolk cells. This may occur either by a centripetal migration of cells from the peripheral layer or by a division of a peripheral cell. The centripetal migration has been recorded in *Campodea*, *Pteronarcys*, *Neophylax*, and several genera of Orthoptera (*Periplaneta*, *Blattella*, *Gryllotalpa*, *Mantis*, *Carausius*). In some cases it seems that both types may occur as in *Gryllotalpa* among Orthoptera, *Calliphora* and *Melophagus* among Diptera, and *Brachyrhinus* (Butt, 1936) among Coleoptera. Although numerous writers record amitotic (direct) division of yolk cells, mitotic division has been observed in *Pieris* (Eastham, 1927), *Ephestia* (Sehl, 1931), *Calandra* (Tiegs and Murray, 1938), *Apis* (Dickel, Nelson, 1915), and some others. It is probable that all yolk cells may undergo amitosis during senescence.

The function of the yolk cells is to liquefy the yolk, rendering it readily assimilable by the embryo; hence the names "vitellophags" and "trophonuclei" are also applied to them. Uichanco (1924) calls them "mycetoblasts" because of the part that they play in the development of the mycetom in aphids. Toward the close of embryonic life they disintegrate in the yolk, only exceptionally being present in post-embryonic life. Because of their early appearance they have been

regarded by some writers as the primary entoderm. This matter is discussed in the chapter on gastrulation. Certain cells, termed "paracytes" by Heymons (1895*a*), liberated into the yolk from the germ band are not likely to be confused with secondary yolk cells. They are derived from both ectoderm and mesoderm and disintegrate during embryonic life. In sections of an early embryo they have the appearance of supernumerary cells that are crowded out of the tissues.

SECONDARY YOLK CLEAVAGE

During gastrulation or later the yolk undergoes a cleavage into large polyhedral or spherical masses, each with one or more yolk nuclei within. This type of cleavage begins anterior to or in the immediate vicinity of the embryo and also under the serosa, but later it extends to the rest of the yolk. Each spherule is surrounded by a delicate yolk membrane. Yolk cleavage of this type occurs in the Orthoptera, Dermaptera, Coleoptera, Lepidoptera, and Mallophaga. Kessel (1939) would limit the use of the term "yolk cell" to what is here designated as "yolk spherule," but the term "yolk cell" is so firmly fixed in existing literature as a synonym of "vitellogophag" that it will be difficult to eliminate.

GERM CELLS

The early history of the germ cells in the Eutracheata has been studied in a number of orders, especially the Diptera, Coleoptera, and Hymenoptera. Robin (1862) and Weismann (1863) described them under the name of "polar globules" or "pole cells." A few years later Leuckart (1865) and Metschnikoff (1866) identified the pole cells in the cecidomyid *Miastor metraloas*, and Ritter (1890) those in *Chironomus*, as the true primordial germ cells (Fig. 313). Since then they have been found in numerous species of insects. In certain chrysomelid beetles and nemocerous flies, by reason of the presence of the oösome (germ-track plasma), the primordial germ cells are easily distinguishable from the somatic cells and therefore can be traced from the time of their appearance until they become mature eggs and sperms. To some writers this is considered a clear demonstration of the early differentiation of the germ cells set apart for the preservation of the race as distinguished from the somatic cells set apart from the maintenance of the individual, as postulated by Weismann in his theory of the continuity of the germ plasm. Some writers believe that the areas of the periplasm into which a cleavage nucleus enters determine what that particular nucleus will later produce. As Hegner (1917) expresses it:

The kind of tissue which develops from any part of the egg depends upon the kind of cytoplasm encountered by the cleavage nuclei. The distribution of the nuclei is entirely adventitious. They are potentially alike, that is, toti-

potent. That they may play a part in the differentiation of the cortical layer of cytoplasm during the cleavage period is highly improbable, since definite cytoplasmic organization already exists before cleavage begins.

Two general types of germ-cell differentiation in insects are illustrated by *Miastor* and *Drosophila*, respectively. In *Miastor*, as shown by the studies of Metschnikoff (1866), Kahle (1908), and Hegner (1912, 1914), a single primordial germ cell gives rise to all the germ cells of the organism. In *Drosophila*, on the other hand, a variable number of cleavage cells migrate into the posterior polar plasm, and each is constricted off as a primary germ cell (Huettnner, 1923). In this case the germ cells are of polynuclear origin.

With those pterygotes in which the primordial germ cells are early distinguishable, they are found in a little mass at the posterior end of the egg (Fig. 313), a position from which they are pushed forward at the tip of the caudal end of the developing embryo and into the interior. They then migrate forward, perhaps passively, dividing into two groups, one going to the right, the other to the left, until they reach their definitive position on the mesodermic genital ridges which are to form the gonads. In those pterygotes in which the germ cells are not recognizable as such until they have reached their definitive position after the formation of the coelomic sacs, it is possible that they have a similar early history, but this has not been demonstrated because of their probable similarity to the somatic cells. In the apterygote *Isotoma* the primordial germ cell is differentiated either at the 16- or at the 32-cell stage and develops into a cluster. This cluster divides into two groups which pass from the yolk into the tissue of the visceral wall of the mesodermic somites of the third and fourth segments. From here they migrate to their definitive position in the first to the third segments.

Although there are many families and some orders of Eutracheata in which the time of the segregation of the germ cells is not known, nevertheless the data on a sufficient number are available to make an attempt at generalization, adopting the following divisions of Nelsen (1934):

1. In the Diptera, Siphonaptera, parasitic Hymenoptera, *Isotoma*, and certain Coleoptera (some chrysomelid beetles and the curculionid *Calandra granaria*) the germ cells are distinguishable as such some time during the formation of the blastoderm. In the midge *Chironomus* the primordial germ cell appears at the time of the second cleavage division; in *Isotoma* it is 1 cell in the 16- or 32-cell stage; in *Miastor metraloas* and *Phytophaga destructor* it is differentiated at the 8-cell stage.

2. In the Dermaptera, some Homoptera (certain Aphidae), a lepidopteran (*Euvanessa*), and certain Coleoptera (some chrysomelid beetles, the curculionids *Calandra callosa*, *C. coryzae*, and *Brachyrhinus ligustici*) the germ cells are apparent immediately after the blastoderm is formed.

3. In the centipede *Scolopendra*, in the Thysanura (*Lepisma*), some Homoptera (coccids, certain aphids), Heteroptera (*Rhodnius prolixus*), and some Lepidoptera (*Endromis*, *Ephestia*, *Solenobia*) the germ cells are recognizable shortly after the germ band is differentiated but before the formation of the inner layer.

4. In some Orthoptera (*Gryllus*, *Periplaneta*, *Blattella*, *Melanoplus*), some Coleoptera (the tenebrionids *Tenebrio* and *Tribolium*), and some Heteroptera (*Pyrhcoris*) the germ cells are apparent during gastrulation but before the formation of the coelomic sacs.

5. In the Orthoptera (*Xiphidium ensiferum*, *Locusta migratoria*), Lepidoptera (*Bombyx mori*), Coleoptera (*Hydrophilus piceus*), and Hymenoptera (*Apis mellifica*) the germ cells are first apparent after the coelomic sacs are formed. Roonwal (1937) questions the correctness of the position of *Melanoplus differentialis* in Section 4 above where it is placed by Nelsen (1934) on the ground that a fundamental difference in the origin of the germ cells is hardly to be expected in such closely related species as *L. migratoria* and *M. differentialis* and that cardioblasts in the latter species were probably mistaken for germ cells by the describer.

The origin of the germ cells has not been described in the Odonata, Ephemerae, Neuroptera, and some smaller orders.

Nelsen (1932) has attempted to correlate the various germ-cell origins in insects by making the following assumptions: (1) The germ plasm, embryologically, is composed of two components, *viz.*, the nucleus containing its complete genic constitution and a rudimentary organization contained in the cytoplasm of the egg; (2) the cytoplasmic component is similar to other organ-forming rudiments; (3) the entire developmental history of this rudiment from the egg to the gamete is considered epigenetic; and, finally, (4) the germ-plasm rudiment located in the germ cytoplasm may pass directly from the egg with the nuclear component in the form of "pole cells," or it may take a more circuitous route together with other organ-forming rudiments until it is ultimately segregated and differentiated in the form of recognizable germ cells.

Nelsen's view concerning the origin and segregation of the germ cells does not sustain the idea of germ-plasm continuity and the "germ-cell track" in a Weismannian sense, nor does it concur in the belief that germ cells may be derived from a somatic origin.

Seidel (1924) has endeavored to show that with the following insects in the order given, *Japyx*, *Lepisma*, *Pyrhcoris*, Orthoptera, *Hydrophilus*, *Calligrapha*, Aphidae, *Isotoma*, and Diptera there is a continuous series from the nondeterminative to the determinative type and that the variation in the time of the appearance of the germ cells is directly correlated with the general character of the development. With the non-determinative type the differentiation of the germ cells occurs after the

blastoderm formation; with the determinative type it occurs before blastoderm formation.

The differentiation of sex cells from the soma in general represents one of the first of the differentiations of organs to take place in the germ band, even though in some cases the germ cells appear later than in others.

GERM BAND

The length of the germ band, or germ disk, either when it first appears or when it has reached its greatest length as an embryo, is not correlated with the length of the insect at the time of emergence. In a comparative study the relation of length to breadth of the embryo should be considered with reference to the form of the egg. In general, it may be said that the form of the egg has but little relation to the form or length of either the early or the late germ band. Graber (1890) attempted a classification of the types of germ bands on the basis of maximum length and degree of flexure, but it will be seen that only within rather narrow limits is it of phylogenetic significance. He recognized three types: (1) long (tanyblastic) and flexed (ankyloblastic), (2) short (brachyblastic) and straight (orthoblastic), and (3) intermediate. In the first group he placed some Coleoptera (*Lina*, *Donacia*, *Lema*, *Telephorus*), Lepidoptera, Phryganidae, and some Hemiptera; in the second group, Libellulidae and some Orthoptera (*Blatta*, *Stenobothrus*, *Mantis*, *Oecanthus*); and in the third group some Coleoptera (*Hydrophilus*, *Melolontha*), some Orthoptera (*Gryllotalpa*), and Hymenoptera (*Apis*, *Formica*, *Hylotoma*). Of other orders not mentioned by Graber the Diptera and Collembola would find a place in the first group to which the Myriapoda may be added. The maximum length of the embryo bears but little relation to its initial length, however, as may be seen in comparing the minute disk-like early rudiment of the walking stick *Carausius* with its definitive form.

In some insects the blastoderm consists of a layer of deep cells uniformly distributed over the entire surface after which there is a thinning out of the nonembryonic part, as in the Mallophaga (Strindberg, 1916), *Apis* (Nelson, 1915), the muscids (Graber, 1889). In other insects the cells at the time of formation of the blastoderm are already differentiated into germ band and extraembryonic tissue, as in *Diacrisia* (Johannsen, 1929) and *Ewanessa* (Woodworth, 1889). The germ-band formation in *Pteronarcys* as described by Miller (1939) is unusual. Here compound "primary nuclear aggregates," which seem to represent the prospective embryonic cells, appear after the time of the outward migration of the cleavage cells; they presumably arise by clumping of cells that migrate inward from the periphery. The embryonic rudiment is formed evidently from the nuclear aggregates in the yolk and by individual plump cells scattered near or in the ventral primary epithelium and perhaps else-

where. When the time for differentiation of the embryo is at hand, all these elements presumably move to the center of the yolk and stream down en masse to the middle of the venter, where they pile up to form a more or less oval multinucleate mass which is the material of the embryonic rudiment.

Eggs of insects in many cases are more or less elongated, sometimes convex on one side and straight or even concave on the other. In such cases the embryo usually forms on the convex side. This, however, is by no means a criterion, since in *Hydrous*, as Heider has shown, eggs are as often curved ventrally as dorsally and in some instances even laterally. Where the germ band forms at the end rather than the side, it is almost always near the posterior pole.

SEGMENTATION

Superficial segmentation of the germ band in insects begins about the time that the germ layers develop. Metamerism is apparent in the transversely divided mesoderm and usually later in the transverse grooves formed in the ectoderm. In some cases the ectoderm exhibits segmentation before the mesoderm, as pointed out by Eastham (1927) in the butterfly *Pieris*. Soon after forming, the germ band shows a broader head region and a narrow posterior portion; the former is the protocephalon, the region of the procephalic lobes which will bear the labrum, the mouth, the eyes, the antennae, and the rudimentary post antennae (Figs. 28, *pro.c.*, 29). The posterior part, or protocorm (*ptc*), is the portion that will give rise to the gnathal (jaw) segments of the head, the thorax, and the abdomen. In most insects the protocorm divides immediately into its definitive segments beginning with the anterior end. Division of the abdomen is retarded in some instances, as in parasitic Hymenoptera, until postembryonic life. In *Brachyrrhinus*, *Stenobothrus*, etc., segmentation begins in the thorax and proceeds both forward and backward.

Less frequently the protocorm is first divided into a few major divisions, or macromeres, which later subdivide into the definitive segments. In *Locusta migratoria*, Roonwal (1936) describes the germ band as first dividing into a protocephalic and three protocormic elements, wherein the inner layer has undergone a segmentation into four parts roughly corresponding to the external primary segmentation. Hirschler (1909) has described a similar segmentation in the chrysomelid beetle *Donacia*. Early segmentation of germ band in *Isotoma*, according to Philipschenko, occurs by the formation of the head lobes, the three gnathal segments, and the first thoracic segment, the remainder of the body not becoming segmented until later. Other examples of primary segmentation have been described for *Oecanthus*, *Stenobothrus*, *Melasoma*, *Meloe*, and the Platygastreae. In *Xiphidium* Wheeler (1890) found that

macrosomitic segmentation sets in only after the germ band has split up into about eight segments, and he therefore concluded that, as opposed to the view of Graber (1890), macrosomitic segmentation has no phylogenetic significance.

In primitive insects 12 abdominal segments may be present, the terminal anus-bearing segment without appendages being the twelfth. In malacostracan Crustacea this terminal segment, or periproct, is the telson. Insects in which a twelfth segment has been described are,

FIG. 28.

FIG. 29.

FIGS. 28, 29.—Two stages of embryos representing two periods in evolutionary history of insects. (*abd*) Abdomen. (*ant*) Antenna. (*ant 2*) Second antenna. (*lb*) Labium. (*lr*) Labrum. (*md*) Mandible. (*mx*) Maxilla. (*p*) legs. (*pleur*) Pleuropodium. (*pro.c*) Protocephalon. (*ptc*) Protocorm. (*stom*) Stomodaeum. (*th*) Thorax. (From Snodgrass.)

among others, *Lepisma*, *Gryllotalpa*, *Eutermes*, and *Chalicodoma*. In the embryos of most Pterygota, however, 11 represents the maximum number, as found in *Locusta* (Roonwal), *Calandra* (Tiegs), *Diacrisia* (Johannsen), *Siphonaptera* (Kessel), *Apis* (Nelson), etc.

The question as to the number of segments that enter into the composition of the head of an insect or indeed of an arthropod generally has been the subject of much controversy. Since the segments of the gnathal (jaw) region are distinct in the embryo, the question centers on the number of segments involved in the procephalic region of insects. Until recently workers have also been in general agreement as to an antennal and an intercalary segment lying immediately in front of the

mandibles. The part lying in front of the antennae, however, has been variously interpreted: as a primary head segment by Weismann (1864), Heymons (1895*a*), and Heider (1889); as an ocellar segment by Viallanes (1891) and Packard (1898); as an ocular segment by Holmgren (1908); as the acron plus the preantennal segment by Heymons (1901); as the brain and labral segments by Patten (1884), Wheeler (1889), and Carrière (1898); as an acron, labral, and preantennal segment by Wiesmann (1926); and as labral, clypeopharyngeal, and frontoocellar segments by Verhoeff (1905). Furthermore, Folsom called the part in front of the antennae the "oral segment" but recognized an interpolated superlingual segment between the mandible and maxillae. Finally, Janet accounted for four in front of the antennal segment, or nine in all. The earlier investigators, whose works have been reviewed by both Wiesmann (1926) and Eastham (1930), used the appendages, the mesoblastic somites, and the neuromeres as the criteria indicative of segments. The attempts at homologizing have been based on a study of both the embryo and later stages; but since in certain cases some of the parts are purely embryonic and in other cases much reduced or represented in varying degree in different species of insects, it is small wonder that there are such diverse opinions and that the number of segments attributed to the head of an insect by the different workers should vary between six and nine.

A departure from the former approach to the problem is found in the comparative studies by Holmgren and Hanström on the annelid and arthropod brain and in Solland's study on the crustacean genus *Leander*. These workers strongly maintain that the postoral segment of the second antennae is the first true somite, a view also shared by Snodgrass (1935, 1938). The principal ground for the generally accepted belief that the acronal region of the arthropod embryo contains one or more "cephalized somites" is the occurrence of temporary coelomic sacs in this region. To this Snodgrass (1938) replies:

It has not been shown that the presence of cavities in the cephalic mesoderm is necessarily indicative of somites, and it would seem that the burden of proof should be on the positive side of this question. . . . Coelomic cavities formed in the cephalic region . . . being radial in position the cephalic sacs cannot represent "somites" in the manner of the paired sacs lying posterior to the mouth, which are transversely opposed to each other. Hence, the assumption that these anterior sacs represent "cephalized somites" is inconsistent with the anatomical conditions that arise in the acronal region. Moreover, as may be seen in a study of the annelids, the coelomic sacs themselves do not determine metamerism; the segmentation of the postoral parts of the mesoderm bands is secondary to metamerization of the primary somatic muscular system, and the coelomic cavities are later formed. . . . The usual absence of well-differentiated coelomic sacs in the annelid prostomium and the fact that the fullest development of the

head sacs is found in the higher arthropods indicate that the formation of the cavities in the cephalic mesoderm is a temporary accompaniment of advancing organization in the prostomial lobe, but the temporary nature of the head cavities might equally suggest that they are purely ontogenetic structures as claimed by Faussek, for coelomic cavities in general.

Snodgrass says further:

The principal reasons for regarding the oculo-antennal region of the arthropod head, here defined as the acron, as representing a primarily unsegmented archi-cephalon corresponding with the annelid prostomium may be summarized as follows: (1) There is never any external division of the acronal region into segmental areas; (2) there is no specific evidence of the cephalization of primarily postoral somites, except in the case of the tritocerebral somite; (3) the embryonic coelomic sacs of the first antennae, the preantennae, and the labrum are formed directly where they occur in the cephalic mesoderm and give no evidence of having been drawn forward from behind the mouth; (4) coelomic sacs of the acronal region, so far as known, are best developed in the higher arthropods and thus do not appear to be primitive structures; (5) the protocerebral and deutocerebral parts of the brain are always connected by preoral commissures, the only postoral cerebral commissure being that of the cephalized tritocerebral ganglia; (6) the mouth and labrum are innervated from the tritocerebral ganglion, which would not likely be the case if several other postoral ganglia preceded the tritocerebral ganglia; (7) paired appendages, sense organs, and primarily discrete nerve centers pertain both to the annelid prostomium and to the arthropod acron; (8) the first antennae of the arthropods never have the structure or musculature of the following appendages; in the Crustacea they are never truly biramous.

Snodgrass (1938) gives a brief review of the facts now known concerning the development of the procephalic mesoderm and nervous system of the arthropods wherein he maintains that the facts are not inconsistent with the idea that both the coelomic sacs and the multiple nerve centers may be formed directly in the otherwise unsegmented acronal region and that the phenomena of embryonic development pertaining to the head are most easily understood if they are taken approximately at their face value for phylogenetic recapitulations.

The theory proposed by Snodgrass (1938) assumes that the archi-cephalic nervous system of the arthropods, as that of the annelids, has been built up from groups of ganglionic cells centering upon a fibrous commissural tract arched forward around the mouth and continuous posteriorly with the ventral nerve cords of the somatic system (Fig. 30). The primary cephalic ganglion included a median anterior ganglion, paired protocerebral and optic ganglia, paired preantennal ganglia, and paired first antennal ganglia. "That these ganglia belong to the preoral acron (*acr*) is shown by the fact that the paired ganglia are always con-

nected by preoral commissures. The cephalic mesoderm extends forward from the somatic mesoderm bands and, in its fullest development, surrounds the mouth anteriorly; it may become excavated by cavities corresponding with the first antennae (*ant*), the preantennae (*pren*), and the labrum (*lr*)."

Roonwal (1939), however, is not convinced of the soundness of Snodgrass' interpretation on the ground that not sufficient stress is given to embryological evidence. He concludes that on developmental criteria we must accept the existence of both the labral and preantennary segments in insects and these, together with the five following segments, indicate a seven-segmented nature of the insect head.

APPENDAGES

It is probable that the early ancestors of the Arthropoda had a pair of appendages on each of the somites between the prostomium and the anus-bearing terminal segment. Although typically segmented in postembryonic life, in the embryo these appendages appear as lateral or lateroventral evaginations of the body wall, simple and lobe-like, which only

later secondarily may become segmented. The antennae and post-antennae were regarded by most embryologists, at least until recently, as parts homologous with the gnathal appendages and the thoracic legs. Preantennal appendages have also been described in *Scolopendra* (Heymons, 1901) and *Carausius* (Wiesmann, 1926). Even the eyes of arthropods were by some believed to be homologous with the appendages, on the basis that the stalks bearing the eyes in Crustacea are segmented and movable and that when an eye is removed under certain conditions an antenna-like structure is regenerated.

Embryologists in general consider the labrum not as an appendage but as an unpaired lobe of the head that has arisen medially to the neural

FIG. 30.—Diagram of relation of coelomic sacs of an arthropod to the central nerve ganglia and associated appendages. (*acr*) Acron. (*ant*) Antenna. (*ant. 2*) Second antenna. (*coel*) Coelomic sac. (*com*) Commissure. (*con*) Connective. (*ggl*) Ganglion. (*mes*) Mesoderm. (*pren*) Preantenna. (*tel*) Telson. (From Snodgrass.)

swellings. In some insects it arises as a pair of faint swellings, but later the bifid condition is lost. In view of the paired origin in certain cases and the occurrence of an independent pair of coelomic cavities lying in the labrum in *Carausius morosus* and *Locusta migratoria*, some writers are inclined to regard the labrum as homologous with the gnathal appendages.

Recently Snodgrass (1935, 1938) has expressed the view that the antennae of insects are not true segmental limbs but are to be regarded as organs analogous to the prostomial tentacles of the annelid worm, since neither in their segmentation nor in their musculature do they resemble the limbs of the postoral somites, and their nerve centers are preoral in position. The second antennae, which are rudimentary in insects but functional in the Crustacea, without doubt represent the first pair of appendages. Morphologically they are postoral, since they are innervated from the postoral tritocerebral lobes of the brain. Rudiments of the second antennae have been recorded in adult *Campodea*, *Machilis*, *Dissosteira*, and *Geophilus*, and embryonic vestiges of them occur in the representatives of several orders where they are usually referred to as "second antennal," "intercalary," or "premandibular appendages." Well-developed articulated appendages provided with muscles, designated as "premandibles," are found in the larvae of some Chironomidae, Chaoborinae, Bibionidae, and other nemocerous Diptera and, although they have not been studied in the embryo, may represent appendages of the intercalary segment. As Wheeler, Claypole, and Folsom (1900) have already pointed out, there are anlagen of premandibular appendages on the intercalary segment in *Anurida maritima*. Folsom furthermore demonstrated the presence of an independent nerve ganglion in this segment.

In the gnathal region Folsom maintained that a nerve ganglion exists between the mandibular and the maxillary ganglion together with a corresponding head segment and a pair of appendages which he termed "superlinguae." Later authors (Philipstchenko *et al.*) for the most part disagree with Folsom regarding the presence of an additional head segment, believing Folsom in error regarding the corresponding nerve ganglion and considering that the superlinguae are solely lateral processes of the hypopharynx. The hypopharynx itself represents the fused sternites of the mandibular and first maxillary segments in the roach (Riley, 1904) or of the sternites of the mandibular and both maxillary segments in *Locusta* (Roonwal, 1937). Such origin of the hypopharynx also occurs in *Forficula* and several Hemiptera (Heymons, 1895a, 1899). In other insects it seems to be associated with the intercalary region, and Hirschler suggests (1924) that the segment also shares in the formation of the hypopharynx.

The gnathal appendages, representing rudiments of the mouth parts, developed in the embryo as distinct pairs of evaginations with the corresponding nerve ganglia and coelomic sacs are well marked and distinctly separated (Fig. 29). The second maxillae late in embryonic life fuse along the median line to form the labium. It has been shown by Heymons (1899), Muir and Kershaw (1911), and others that the very specialized mouth parts of the Heteroptera develop from the usual embryonic outgrowths such as are formed in the embryos of insects with biting mouth parts. Shinji (1919) made a similar observation regarding the mouth parts of the Coccidae. The ventrolateral, thoracic, embryonic evaginations which develop into legs together with the corresponding nerve ganglia and coelomic sacs likewise are clearly differentiated and cannot be misinterpreted.

Attention has been called to paired evanescent, embryonic, ventral evaginations of the first abdominal segment in insects by Graber (1889a), Wheeler (1889a,c, 1892b), Carrière (1891a), and others. Hussey (1926) has given in addition to her own contribution a review of the work of earlier writers, which may be summarized as follows: The pleuropodia of insect embryos are paired appendages of the first abdominal segment which arise from foot-like organs and which tend, as they develop, to take up a position on the pleural wall of the embryo. They are serially homologous with the appendages of the head, thorax, and abdomen. In the orders Dermaptera, Hymenoptera, and Lepidoptera they are present for a very brief period as minute, papillate, evanescent evaginations and probably are as short-lived in the orders Isoptera, Strepsiptera, Embiidæ, Megaloptera, and Trichoptera. They develop as bulbiform evaginations with a reniform or subreniform outline in the Orthoptera. They occur as pyriform or digitiform or conical evaginations in the orders Mantoidea and Blattoidea. In the order Coleoptera they may be evaginated, flattened, bag-like, and very large; bulbiform, digitiform; or calyculate with their distal ends invaginated; or they may be quite submerged with a large orifice at the surface of the body. In the order Hemiptera they arise before the revolution of the embryo as ectodermal evaginations. In *Belostoma* and *Ranatra* they soon sink into the body and become bowl-shaped structures, greatly increasing in size to the time of hatching.

The pleuropodia probably serve as organs of excretion or secretion during embryonic life. Blunck (1914), Slifer (1937), and others have found that they furnish a hatching enzyme. In *Hesperoctenes*, where they are unusually developed, Hagan (1931) considers them to be important nutritive organs for which he proposes the term "pseudoplacenta," which he would also apply to the nutritive structure described by Heymons (1909) in *Hemimerus*. Hagan (1939) has also described an analogous structure occurring in a viviparous roach, *Diploptera dytiscoides*.

Polypody finds expression in the development of appendages that may appear on all abdominal segments except the telson. In the myriapods they are segmented and functional; in insects they are usually reduced or lacking, though in the embryos anlagen of as many as 11 pairs may be found with corresponding metameres and nerve ganglia. Among Apterygotes abdominal appendages are found in postembryonic stages though modified in function, as are also some posterior appendages of certain Orthoptera and other primitive pterygotes. The prolegs of the larvae of Lepidoptera and Tenthredinidae, generally regarded as serially homologous with the thoracic legs, are well developed in the embryos. In the case of the embryos of the Lepidoptera the appendages appear on segments one to ten, but later they persist only on segments 3 to 6 and 10, in the more typical forms (Eastham, 1930; Friedmann, 1934; *et al.*).

Appendage rudiments are commonly present in the Orthoptera on all the abdominal somites of the embryo, but in the male those on somites anterior to the ninth disappear before hatching. The appendages of the ninth segment of the male, however, are retained in many families as a pair of small, nonmusculated styli borne on the posterior margin of the definitive ninth sternal plate, their coxopodites supposedly in most cases being incorporated in the sternal plate. According to Else (1934) the embryonic appendages of the ninth abdominal segment of the male of *Melanoplus differentialis* merge completely with the posterolateral parts of the primitive sternum of this segment, even the styli being thus obliterated in Acrididae. It is only in the Grylloblattidae that the ninth-segment appendages retain a two-segmented structure, the coxopodites being here large, free lobes bearing styli. According to Else appendage rudiments of the tenth segment in *Melanoplus* persist and continue their migration toward the median line until they take a position at the sides of the point where the ejaculatory duct invagination is being formed. Here they grow out into lobes that unite about the mouth of the duct and eventually form the complex phallic organ of the adult which contains the gonopore. According to Wheeler (1893) the embryonic tenth appendage rudiment in the male of *Conocephalus*, after the ampullae have withdrawn from them, disappear. Embryonic appendages of the tenth segment are retained as larval "legs" in the Neuroptera, Trichoptera, Lepidoptera, and the lower Hymenoptera.

Regarding the homologies of the appendages of the abdominal segments in the Apterygota and the primitive Pterygota it must be admitted that in the embryo the outgrowths of the body appear so much alike that their similarity offers but little proof of their identity. Whether the part that develops into an unsegmented stylus or the valve of an ovipositor or a clasper represents a reduced abdominal leg or only an appendage of a completely obliterated leg is difficult to say.

Grassi and others on comparative anatomical grounds and Heymons (1895a, 1898b) on ontogenetic evidence considered that the gonopophyses represented specially developed structures which could not be referred to former limbs. Later writers with few exceptions, in agreement with Verhoeff, believe that the lateral divisions of the eighth and ninth sternal plates in the Thysanura represent flattened leg coxae, the gonocoxites, whereas the ovipositor lobes borne mesally by these structures, a pair each by the eighth and ninth gonocoxites, represent modified distal leg segments. In the pterygote insects, then, the anterior ovipositor valves of the eighth segment and the inner valves of the ninth are believed to be serially homologous structures and to correspond to the telopodites of Thysanura, the lateral ovipositor valves of the ninth segment being gonocoxites. The recent work of Nel (1929) on the development of the terminalia of orthopterous females seems further to substantiate this view. Nel also maintains that the common oviduct originates as an unpaired ectodermal (epidermal) invagination and that there is no evidence that part of the common oviduct is of mesodermal origin or that it has a paired origin in the Orthoptera and in insects in general.

References

Reviews of the literature dealing with the *germ cells* of the Eutracheata, especially of insects, have been published by Hasper (1911), Hegner (1914), and Nelsen (1934). Some works which include this subject are the following:

- Myriapoda, Chilopoda*: Heymons (1901).
- Collembola*: Claypole (1898), Philpitschenko (1912).
- Thysanura*: Heymons (1897).
- Orthoptera*: Heymons (1895a), Nelsen (1934), Roonwal (1936), Wheeler (1893).
- Ephemera*: Heymons (1897).
- Odonata*: Heymons (1897), Tillyard (1917).
- Dermoptera*: Heymons (1895a).
- Homoptera*: Balbiani (1870), Metschnikoff (1866), Shinji (1919), Strindberg (1919), Tannreuter (1907), Todt (1933), Uichanco (1924), Walczuch (1932), Will (1884, 1888), Witlaczil (1884).
- Heteroptera*: Mellanby (1936), Seidel (1924).
- Lepidoptera*: Eastham (1927), Johannsen (1929), Lautenslager (1932), Sehl (1931), Schwangert (1905), Toyama (1902), Woodworth (1889).
- Coleoptera*: Brauer (1925), Butt (1936), Friederichs (1906), Hegner (1908, 1914), Heider (1889), Hodson (1934), Hirschler (1909), Inkmann (1933), Lécaillon (1898), Paterson (1931, 1936), Saling (1907), Tiegs and Murray (1938), Wray (1937).
- Siphonaptera*: Kessel (1939), Packard (1872).
- Diptera*: Butt (1934), DuBois (1932), Escherich (1900), Gambrell (1933), Grimm (1870), Hasper (1911), Hegner (1914), Huettner (1923), Kowalewsky (1886), Lassman (1936), Metcalfe (1935), Metschnikoff (1866), Noack (1901), Pratt (1900), Ritter (1890), Sachtleben (1918).
- Hymenoptera*: Gatenby (1918), Hegner (1915), Henschen (1928), Leiby (1922), Nelson (1915), Petrunkevitch (1903), Silvestri (1907).
- Blastoderm, Germ-band Formation, Yolk Cells, Segmentation, and Appendages*: Auten (1934), Brandt (1878, 1880), Carrière (1891), David (1936), Fernando (1933), Folsom

(1900), Giardina (1897), Graber (1888, 1891), Grandori (1914), Grimm (1870), Heathcote (1886), Heymons (1895*b*, 1897*c*, 1898*b*, 1899*a*), Hirschler (1912), Hottes (1928), Hussey (1926), Krause (1938*a*), Leydig (1848), Mansour (1927), Marshall and Dernehl (1905), Mellanby (1936), Muir and Kershaw (1911), Murphy (1922), Murray (1864), Nusbaum (1889), Pflugfelder (1932), Riley (1904), Robin (1852), Schmidt (1889), Sehl (1931), Smreczynski (1931, 1932), Snodgrass (1928, 1932, 1935*b*, 1937), Wagner (1894), Wheeler (1889, 1890*b*, 1892*b*, 1893*a*), Will (1883, 1888).

See also the list of general works cited in Chap. II.

CHAPTER V

EMBRYONIC ENVELOPES, DORSAL ORGANS,
AND BLASTOKINESIS

THE EMBRYONIC ENVELOPES

During the course of early embryonic development there are formed in most insects two protective envelopes, or membranes: an outer serosa and an inner amnion, the former a derivative of the extraembryonic primary epithelium (blastoderm), the latter developing from the margin of the embryonic rudiment. The steps in the development of these membranes in the most typical case is represented in the accompanying figures. In initiating the development of amnion and serosa an amnio-serosal fold appears in the periphery of the germ band (Fig. 31*B,amf*), the inner part of the fold forming the amnion, the outer part (extraembryonic primary epithelium) forming the serosa. With the extension of these membranes the lips close on each other so that finally the serosa lies at the surface immediately under the vitelline membrane and covers the entire egg while the amnion covers the ventral face of the developing embryo (Fig. 31*C*). At a later period just before the reversal of the embryo, when their development has well advanced, the serosa and amnion become fused in the head region (Fig. 31*D,am.ser*). A rent appears in this fused area, the margins of the rent, however, remaining fused so that the edges of the amnion and serosa adhere to each other (Fig. 31*E,amf*). The membranes then contract (Figs. 31*E,F*) toward the dorsal side of the embryo where the amnion (*am*), turning inside out in the process, forms a provisional dorsal wall and the serosa a tubular so-called "secondary dorsal organ." Both these structures thereupon undergo degeneration (Fig. 32, *do*). Another structure, known as the "primary dorsal organ," which develops early behind the head in the Collembola and some other insects, will be referred to later. The description given above of the position and origin of the germ band is that of a generalized type which is subject to many modifications. These variations may be traced back to the shape of the egg, the amount and distribution of the food yolk, and the manner in which the embryo grows.

Certain features in embryological development occur to which terms have been applied that may here be defined. When the yolk penetrates between the amnion and the serosa, the germ band is said to be immersed,

as in the *Lepidoptera* and in some *Odonata*. In the case of the latter the germ band, instead of sinking beneath the surface to become immersed, invaginates into the yolk. This is the invaginated type of immersed

FIG. 31.—Development and fate of the embryonic envelopes. A, gastrulation. B, formation of amniotic fold. C, completion of serosa (*ser*). D, fusion of amnion and serosa (*am. ser*). E, rupture of amnion and serosa. F, shrinkage of envelopes. (*am*) Amnion. (*am. cav*) Amniotic cavity. (*amf*) Amniotic fold. (*ect*) Ectoderm. (*gastr*) Gastrula furrow. (*ggl*) Ganglion. (*il*) Inner layer. (*lp*) Lateral ectodermal plate. (*mge*) Mid-gut epithelium. (*ser*) Serosa. (*y*) Yolk.

germ band. The embryos of many insects remain at the surface during development, in which case we have the superficial type. Certain forms are intermediate in type, as with some *Coleoptera* in which the anterior part of the embryo remains superficial but the caudal end is invaginated

The question as to the homologies of the amnion and serosa with reference to structures existing in the Arthropoda lacking these envelopes has frequently been raised by embryologists. With the Collembola there is no unanimity of opinion. Heymons thought that the primary dorsal organ of the Onychophora, Myriapoda, and Apterygota was a structure homologous with the serosa of the Pterygota; but as Philpitschenko (1912) has pointed out, this is impossible, since in the beetle *Donacia* there is a serosa as well as a rudimentary primary dorsal organ. Willey (1899) regarded the dorsal organ of the Onychophora and of the Collembola as being homologous with the indusium, a structure exceptionally found among pterygotes, and believed that the serosa and the dorsal organ among these arose independently. Hirschler (1909) found a cell mass appearing early in the embryo of *Donacia* which he identified with the dorsal organ in *Isotoma*. Philpitschenko (1912) held that the envelope-like extra-embryonic part of the primary epithelium (blastoderm) in *Isotoma*, which we shall call the "amnioserosa," is the homologue of the combined amnion and serosa of the pterygotes. Finally, Strindberg (1913b) suggested the use of the term "proserosa" for the dorsal organ in *Isotoma* and "proamnion" for the extraembryonic lateral walls, thus indicating his opinion of the homologies.

Heymons' interpretation of the homologies of the amnion, serosa, and secondary dorsal organ among the Onychophora, Myriapoda, Thysanura, and Pterygota, however, seems to rest upon a firmer basis. He points to the occurrence in the neck region of the embryo of *Peripatus capensis* of a thickened area of vacuolated cells which Sedgwick designated as the "ectodermal hump" and which corresponds in position to the secondary dorsal organ of the Pterygota. It is doubtless the same type of structure that Willey (1899) described as the trophic vesicle in *P. novae-britanniae* and that corresponds both as to position and fate to the secondary dorsal organ of the higher insects. In *Scolopendra* the elongated germ band of an intermediate stage embryo occupies the ventral side, the *membrana ventralis* (*vm*), the dorsal side of the egg. Immediately behind the head there is a small disk, which, as development proceeds, thickens and becomes several-layered. Later the lower layers of the disk degenerate in the yolk while the surface layer, together with the *membrana dorsalis*, forms the definitive dorsal closure of the animal. Comparing the stage just described with that of a pterygote insect that has just undergone

FIG. 32.—Provisional closure of dorsal wall by the amnion (*am*). Serosa sinks into the yolk (*y*) to form the tubular secondary dorsal organ (*do*). (*ect*) Ectoderm. (*ggl*) Ganglion. (*mge*) Mid-gut rudiment.

revolution, one will note that here also the dorsum is covered by the thin amnion and that in front of this is the more or less thickened contracted serosa in the form of the secondary dorsal organ (Fig. 24C). The origin, position, and fate of the secondary dorsal organ of insects correspond so closely with that of the cephalic disk of *Scolopendra* that one can scarcely question that these structures are homologous. The only real difference lies in the fact that the *membrana dorsalis* of *Scolopendra* will later form the definitive dorsal closure, whereas in insects the amnion forms only a provisional one. If one accepts the foregoing interpretation of Heymons, then the cephalic disk and the *membrana dorsalis* of *Scolopendra* are respectively homologous with the serosa and amnion of the pterygote insects. The position, time of origin, and fate of the dorsal organ of

FIG. 33.—*Machilis alternata*. (gb) Germ band. (pra) Proamnion. (prs) Proserosa. (From Heymons.)

the Diplura (*Campodea*) and the cephalic disk of *Scolopendra* so closely resemble each other that Heymons considered them likewise homologous structures.

To account for the formation of the amnioserosal folds Heymons points to the condition found in *Machilis* and *Lepisma*, both thysanurans. The germ band in the laterally compressed egg of *M. alternata* is small and lies at the posterior pole of the egg (Heymons, 1905), its lateral walls merging into the primary epithelium which covers the egg (Fig. 33). Two zones are to be distinguished in the epithelium: a small-nucleate smaller zone immediately surrounding the germ band (*pra*) and a second much larger zone (*prs*) with large nuclei. The smaller zone Heymons designated as the "proamnion," the larger as the "proserosa." In the course of development the germ band sinks into the yolk and is carried

toward the center of the egg. Simultaneously the proamniotic zone (*pra*) is stretched and occupies the posterior half of the egg (Fig. 34) with a corresponding reduction in the size of the proserosa (*prs*). The egg of *Machilis* being laterally compressed, the furrow that carries the embryo inward is not in the nature of an invagination, since it is open at the sides, exposing the lateral margins of the embryo. The furrow is not precisely comparable to an amniotic cavity, for its walls are made up of a part of both proserosa and proamnion, for which reason Heymons chose the terms "proserosa" and "proamnion" rather than "serosa" and "amnion" for the membranes in this group of insects.

In *Lepisma saccharina* the form of the envelopes shows a further advance toward the development of an amnion and serosa. Here the minute embryonic disk has sunk into the yolk, carrying with it the amniotic epithelium which joins the periphery of the disk with the serosa. The germ band forms the bottom of a sac (Fig. 109) whose sides

FIG. 34.—*Machilis alternata*. (*emb*) Embryo. (*pra*) Proamnion. (*prs*) Proserosa. (From Heymons.)

constitute the amnion. The sac remains open, communicating with the exterior by the amniotic pore. Were this pore to close, we should have the normal pterygote structure. When the second stage of blastokinesis occurs, the sac turns inside out, without the necessity of the fusion of the envelopes at the head end or of their rupture (Fig. 111). When blastokinesis is completed, the amnion, serosa, and embryo form the walls of a closed yolk sac as in the Pterygota. In the process the amnion becomes extended, with a corresponding shrinkage of the serosa (Fig. 111).

Turning now to the Pterygota, we shall find that in the most generally encountered types both amnion and serosa are developed and that the other more specialized types may in most cases be readily derived from them.

The following synopsis of the Eutracheata will indicate the variations that occur. Too great a reliance should, of course, not be placed on a tabulation of this sort, since the developmental history of the members of too few families among the orders are known to admit of broad generali-

zations. Connecting links and exceptions are certain to be found, especially among the smaller and more aberrant families.

- a. Lateral and dorsal sides of the egg covered by an envelope which represents the amnion and serosa, the ventral face of the embryo not covered by either amnion or serosa during the course of development (Fig. 74).....
 -I. *Myriapoda*, *Collembola* (*Isotoma*), *Diplura* (*Campodea*)
- aa. Ventral face at least in part covered by either amnion or serosa, or amnion wholly lacking and the serosa rudimentary (some ants), or parasitic or viviparous forms in which the envelopes have a nutritive function.
 - b. Amnion wholly lacking, serosa rudimentary, represented by but few cells.*Some ants*
 - bb. At least one envelope more or less developed.
 - c. Parasitic or viviparous insects in which the envelopes have a nutritive function.
 - d. Envelope a trophamnion (Fig. 263A).....
 - X. *Parasitic Hymenoptera* (*Proctotrupidae*, *Chalcididae*, *Bracnidae*)
 - dd. Amnion and serosa present.
 - e. No blastokinesis. Amnion and serosa disintegrate.....(?) *Psocidae*
 - ee. With blastokinesis.
 - f. Amnion and serosa rupture at revolution.....*Hesperoctenes*; some *Aphididae*
 - ff. Envelopes remain unbroken at revolution.....*Hemimerus*
 - cc. Envelopes membranous, chiefly protective.
 - d. Dorsal wall of the embryo represented by primary epithelium, the cells forming a serosa-like covering; amnion present in rudimentary form slightly covering either both cephalic and caudal ends as in *Melophagus* or only the caudal end (Fig. 331)..XI. *Muscoidea*
 - dd. One or both envelopes fully developed.
 - e. One envelope fully developed, the other absent or rudimentary.
 - f. The amnion alone present (Fig. 226).....*Strepsiptera*
 - ff. Serosa present, amnion rudimentary or wholly lacking (Fig. 281B).....IX. *Aculeate Hymenoptera*
 - ee. Two fully developed envelopes except in the Thysanura where they open to the exterior.
 - f. Embryo drawn into a furrow (*Machilis*) (Fig. 34) or into a sac which opens to the exterior by a pore (*Lepisma*) (Fig. 109).
 -II. *Thysanura*
 - ff. The serosa fully covers the egg below the chorion, the amnion covers the ventral face of the embryo (Fig. 215).
 - g. Amnion and serosa fuse either at the head end or along the midventral line, where a rupture occurs just before revolution; after revolution a secondary dorsal organ is formed in most cases.
 - h. No yolk between amnion and serosa before final revolution, at least in anterior half (Fig. 215).....
 - III. *Orthoptera*, *Dermaptera*, *Neuroptera*, *Trichoptera*, *Coleoptera* in part (*Hydrophilus*, *Dytiscus*, *Tenebrio*, *Meloe*, *Donacia*), *Heteroptera* in part (*Corixa*), *Eutermes*, and some *Odonata*

- hh. Yolk between amnion and serosa; lacking in some cases at the head end before final revolution (*i.e.*, germ band immersed).
- i. Embryo completely immersed shortly before fusion of amnion and serosa (Fig. 193).....
V. Anoplura, Mallophaga, Plecoptera (Pteronarcys), Thysanoptera, Heteroptera (Pyrrhocoris, Rhodnius), Homoptera in part, Corrodentia, Orthoptera in part (Stenobothrus), Coleoptera in part (Photurus), Orthoptera in part
- ii. Embryo immersed except at head end (Fig. 117C).
IV. Homoptera (in part), Ephemera, Odonata, in part
- gg. Amnion and serosa do not fuse shortly before revolution; tubular secondary dorsal organ normally lacking.
- h. A fold of the amnion forms a temporary dorsal closure (Fig. 311).
- i. Embryo wholly immersed in the yolk; amnion in some cases at least does not completely cover the ventral face of the embryo until completion of the serosa.....*VI. Lepidoptera*
- ii. Embryo not immersed (Fig. 255).....
VII. Tenthredinidae (Hylotoma), Coleoptera in part (Leptinotarsa, Clytra, Chrysomela, Euryope, Corynodes, Bruchus, Calandra, Brachyrhinus)
- hh. No fold of the amnion forms a temporary dorsal closure..*VIII. Siphonaptera, Nemoceros Diptera*

Of the groups given in the foregoing table we may recognize several types of which the following are more or less distinctly marked. Some aberrant forms are omitted.

- I. Ventral face of the embryo not covered by a membrane (Fig. 74).....
Myriapoda, Collembola, Diplura
- II. Membranes not completely closing over the ventral face of embryo (Fig. 109).
Thysanura
- III. Serosa and amnion fully developed, fusing either ventrally or at head end just before revolution; secondary dorsal organ formed; germ band superficial....
Orthoptera, Eutermes, Dermaptera, Neuroptera, Trichoptera, Coleoptera (in part), Heteroptera (Corixa), Odonata in part
- IV. Like III but germ band is immersed except at the head end.....
Odonata, Ephemera, Embiidina, Homoptera (in part)
- V. Like IV but head is also immersed until just preceding revolution.....
Anoplura, Mallophaga, Corrodentia, Thysanoptera, Homoptera (in part), Heteroptera (in part)
- VI. Amnion and serosa fully developed, although in some cases at least, the amnion does not form until the serosa is completed; envelopes do not fuse at the head end just before revolution; germ band immersed; no dorsal organ; a part of the amnion forms a provisional dorsal closure.....*Lepidoptera*
- VII. Serosa and amnion fully developed and do not fuse at the head end just before revolution nor do they rupture at revolution; germ band not immersed except

- in some cases at the posterior end.....
Coleoptera (in part), *Hymenoptera* (*Tenthredinidae*)
 VIII. Amnion and serosa fully formed, do not fuse at head end; no well-formed
 secondary dorsal organ; germ band not immersed.....
Siphonaptera, *Nemoceros Diptera*
 IX. Serosa fully developed; amnion rudimentary or lacking.....
Aculeate Hymenoptera
 X. Embryonic envelope having a nutritive function....*Parasitic Hymenoptera*
 XI. Dorsal wall of the embryo represented by the primary epithelium, the cells
 forming a serosa-like covering; amnion present in rudimentary form.....
Diptera (*Muscoidea*, *Melophagus*)

The type represented by group III might have been derived from one resembling type II. Type III is quite generalized, its development described in the account of a typical insect given on page 9. From this with slight modifications types IV to IX may be derived. Types X and XI are highly specialized. A few groups given in the analytical table are so modified by reason of some peculiar type of development (parasitic or viviparous) that their relation to the other types is not obvious.

DORSAL CLOSURE

Three different types of structures are concerned in closing the embryo on the dorsal side, two of them provisional, the other definitive. Roonwal (1937) states that in the embryo of *Locusta migratoria*, at about the time the proctodaeum appears, a thin membranous provisional dorsal closure is formed. It arises from the lateral edges of the embryo at a point slightly above the origin of the amnion and covers the entire dorsum. By its formation it cuts off the yolk from contact with the embryonic inner side and encloses, for the first time, an epineural sinus which contains a few blood cells but no yolk particles. It is probably of ectodermal derivation and quite independent of the amnion in origin, although it resembles it in structure. Graber (1888b) noticed an analogous structure in *Stenobothrus variabilis* which arises from the lateral edges of the germ band as two flaps that spread medially toward each other and ultimately fuse into a single membrane. Miller (1939) has described a similar membrane which he designates as the "eetal membrane," occurring in the embryo of *Pteronarcys proteus*, which serves as a base for the spread of the definitive mid-gut epithelial cells. A similar structure is also present in the head louse (Schölzel, 1937). The yolk-cell membrane in *Carausius* described by Leuzinger (1926), though apparently having a different origin, has a similar function. In *Locusta*, as described by Roonwal, the portion of the provisional dorsal closure lying between the blind ends of the stomodaeal and proctodaeal invaginations snaps at the edges and grows around the yolk. Middorsally it fuses with the amnion which

now forms the second provisional dorsal closure of the embryo (Fig. 152). At this stage the first dorsal closure thus forms a temporary mid-gut epithelium. Afterward the splanchnic mesoderm grows around and separates the first dorsal closure from the amnion. The former dorsal closure then degenerates, leaving the inner layer of the splanchnic mesoderm as the second temporary mid-gut epithelium until the definitive mid-gut epithelium is formed.

The second type of provisional dorsal closure, which takes place at the time of revolution, is formed either by the combined amnion and serosa or by the amnion or the serosa alone. Here the membranes, instead of separating yolk from embryo, form an envelope consisting of the membrane (or membranes) on the dorsal side and the embryo on the ventral and lateral sides to enclose the yolk. Both envelopes are involved in members of the groups III, IV, and V described on page 55 and include many orders, among them the Orthoptera, neuropteroids, Hemiptera, and some Coleoptera. Only a small section of the amnion (Fig. 311) forms the provisional dorsal closure in the members of groups VI and VII which include the Lepidoptera, some Hymenoptera (Tenthredinidae), and some Coleoptera (*Brachyrhinus*, etc.). In the aculeate Hymenoptera (group IX) a strip of the primary epithelium (*Apis*) or of the serosa (*Formica*) forms the provisional dorsal closure, whereas in the chilopod *Scolopendra* the *membrana dorsalis* performs this function.

The third, or definitive, dorsal closure is formed by the ectoderm. In *Eutermes*, a member of group III, as described by Strindberg (1913b), both amnion and serosa after rupture form a dorsal covering, the serosa becoming the secondary dorsal organ. The dorsad growth of the body wall gradually forces these membranes into the yolk, without either of them taking part in the formation of the definitive wall. In *Chrysomela*, a member of group VII, the provisional dorsal closure consists of a longitudinal strip of the amnion. With the dorsad advance of the edges of the body wall the strip becomes narrower by compression and finally sinks into the yolk, the definitive body wall being formed by the ectoderm. In *Formica*, a member of group IX, it is a serosal strip that is crowded into the yolk by the advancing edges of the definitive body wall. In the apterygote genus *Isotoma*, Philpitschenko likewise found that the primary epithelium which forms a provisional dorsal closure is not transformed into the definitive ectoderm but is replaced by the dorsad growing body walls of the insect.

CUTICULAR ENVELOPES

After the embryonic envelopes have formed, Slifer (1937) and Cole and Jahn (1937) point out that in various grasshoppers (*Melanoplus*, *Chortophaga*, *Romalea*, and *Locusta*) two membranes are secreted on the

outer surface of the serosa. These consist of a very thin yellow cuticular layer, or cuticulin, and a white chitin-like cuticular layer which is within the first, also secreted by the serosa. The white cuticle shortly before emergence is dissolved by an enzyme; the yellow cuticle persists unchanged to the end. According to Slifer the enzyme noted above is secreted by the pleuropodia. In the yellow cuticle of *Melanoplus* there is a small, circular, specialized area through which water enters or leaves the egg and which has been called by Slifer (1938) the "hydropyle." Wheeler has called attention to a similar cuticle secreted from the surface of the serosa and of the indusium in *Xiphidium*. The cuticle which is molted during the embryonic life of the centipede and the crenated membranes which are cast off by the embryo of *Isotoma* present analogous cases.

THE PRIMARY DORSAL ORGAN

Attention has already been called to the primary dorsal organ, a specialized structure which is most highly developed in the Collembola. As has been stated, although some of the earlier writers regarded both the primary and the secondary dorsal organs as the homologues of the serosa, more recently it has been shown that the primary organ differs from the secondary organ in structure, origin, function, and time of appearance. In *Isotoma* it appears early at the anterior pole of the egg immediately after the formation of the inner layer and the appearance of the germ cells. Cells from the anterior pointed end of the egg become differentiated from the adjacent epithelial cells. As they become deeper, the cells of the inner layer immediately below are dislodged and disappear in the yolk. As development proceeds, the cells penetrate more deeply into the yolk, progressively changing in appearance (Fig. 75), the cluster assuming the character of a gland. The organ in *Isotoma* remains a conspicuous structure until after the revolution of the embryo, when it rather suddenly disappears entirely. To judge from its appearance there can be little doubt of its glandular nature. Similar structures have been described for *Anurida* and *Podura*.

In beetles a vestigial structure has been described that may be homologous with the organ just mentioned. Hirschler (1909) found a structure in the early embryo of the chrysomelid beetle *Donacia* that consists of an oval dorsad-lying area of primary epithelium which sinks down into the yolk and becomes covered by the epithelium. Its component cells meanwhile send out processes into the yolk. This structure, designated by Hirschler as the "primary dorsal organ," finally degenerates completely and is absorbed in the yolk.

In the honeybee, Nelson (1915) has described what he termed the "cephalic-dorsal body," which in position, overgrowth by the primary epithelium, and final absorption in the yolk closely corresponds to the

dorsal organ of Hirschler. It differs in one respect. In the bee the organ develops during the formation of the germ layers; in *Donacia* it is formed prior to that time.

In the dipterous genus *Sciara*, Butt (1934) found a structure which he designated as the "primary dorsal organ" that appears at an early stage before the amniotic folds have closed over the ventral surface of the embryo and consists of a thick saucer-shaped group of cells on the dorsal side projecting toward the yolk. It reaches its greatest size at the fifteenth hour and from then on decreases, until shortly before the thirtieth hour it disappears entirely. The relation that the primary dorsal organ bears to the embryonic envelopes has been discussed in a previous section.

THE SECONDARY DORSAL ORGAN

The term "secondary dorsal organ" is applied to the contracted serosa (in some cases the amnion) after the rupture. As has been described in the account of the amnion and serosa, the amnion forms the provisional dorsal closure; the serosa, the tubular transitional secondary dorsal organ (Figs. 32, 35). It is well developed in many Coleoptera (*Hydrophilus*, *Dytiscus*, *Leptinotarsa*, *Donacia*, *Tenebrio*, *Meloe*), the Orthopteroidea (*Gryllotalpa*, *Phyllodromia*, *Periplaneta*), the Dermaptera, Isoptera, Heteroptera, Homoptera, etc. In the process of the formation of the organ, the pavement epithelium of the serosa becomes columnar, and the development of the cylindrical structure proceeds from behind forward. In the beginning a distinct lumen is present, but this later disappears with a complete degeneration of the cells in the yolk. The destruction of the tubular organ takes place at its posterior end and goes on as rapidly as it is being built up at the anterior end (Fig. 35), so that at any one time the dorsal organ is limited in extent. No part of it goes into the construction of the definitive body wall.

With respect to *Leptinotarsa* (*Doryphora*) Wheeler states that after the rupture of the membranes they shift farther and farther upward toward the middorsal line. When the embryonic area has so far extended around the sides of the egg that its edges have nearly met, the remnants

FIG. 35.—*Tenebrio molitor*. Formation of the secondary dorsal organ (*do*) from the serosa. The amnion (*am*) forms a provisional dorsal closure. (*nc*) Nerve cord. (*proct*) Proctodaeum. (*stom*) Stomodaeum. (*y*) Yolk. (From Saling.)

of the envelopes become invaginated into the yolk, forming the secondary dorsal organ.

Heymons (1895a) found that in *Gryllus*, after rotation, the serosa at first covers the yolk at the head end, then sinks into the yolk to be absorbed. Meanwhile the amnion forms the provisional dorsal closure in the usual manner. As the body wall grows dorsad, the amnion invaginates into the yolk in tubular form and is soon covered over by the ectoderm, later to degenerate. The secondary dorsal organ in *Gryllus*, therefore, owes its origin to the amnion instead of the serosa.

FIG. 36.—*Xiphidium ensiferum*. Development of the indusium (*ind*). Blastokinesis. (*am*) Amnion. (*ch*) Chorion. (*gb*) Germ band. (*ind*) Indusium: (*i*) inner, (*o*) outer. (*ser*) Serosa. (*y*) Yolk. (From Wheeler.)

THE INDUSIUM

The organ named the "indusium" by Wheeler (1893) is found in two species of meadow grasshoppers belonging to the genera *Xiphidium* and *Orchelimum*. It arises as a simple circular thickening of the blastoderm between and a little in front of the procephalic lobes (Figs. 36, 37, *ind*). It divides into an outer and an inner layer and afterward spreads over nearly the whole surface of the egg, leaving the poles uncovered. The outer indusial envelope becomes closely applied to the serosa except at the two poles and remains intact until hatching of the nymph. The inner indusial envelope fuses with the amnion near the head of the embryo

and thereupon takes on the usual functions of the serosa during the revolution of the embryo. The eggs of these grasshoppers thus have the following envelopes, passing from without inward in a median transverse section of the egg: chorion, vitelline membrane, cuticula secreted by the serosa, serosa, outer indusium, cuticula secreted by the inner indusium, a layer of granular substance, inner indusium, and amnion, the last one covering only the embryo (Fig. 37). A complete indusium has been

FIG. 37.—*Xiphidium ensiferum*. The indusium. (am) Amnion. (emb) Embryo. (ind) Indusium: (ci) cuticula of inner indusium, (i) inner, (o) outer. (ser) Serosa. Chorion, vitelline membrane, and cuticula secreted by serosa, omitted from figures. (From Wheeler.)

described by Muir and Kershaw (1912) for the homopteran *Siphanta acuta*. Hagan (1917) found an indusium-like mass of cells in the mantid. It remains attached until rotation, when it becomes free, later to be ingested during the formation of the dorsal body wall. The possible homology of the primary dorsal organ with the indusium of *Xiphidium* has been pointed out by Willey (1898), but this seems unlikely. The structure suggests an abortive twin embryo in its manner of development, the outer layer comparable to the amnion, the inner to the embryo. The *grumorium* described by Miller (1939) seems to be an analogous development. Further investigations are necessary before it is safe to pronounce judgment as to the homologies of these anomalous structures.

THE SUBSEROSEA

About the time the embryo of the snout beetle *Brachyrhinus ligustici* has formed, a substance appears just under the serosa that gradually thickens and hardens until it forms a brown leathery shell around the contents of the egg (Fig. 255). Because of its position during the greater part of its existence Butt (1936) has called it the "subserosa." It is noncellular, nongranular and stains a light brown when haemotoxylin and orange G are used and a deep blue with Mallory's connective-tissue stain. When it first appears as a definite layer next to the serosa at approximately 40 hours, it is not very thick but lies on the inner surface of the serosa cells and extends down between the cell walls. The serosa cells are still columnar in form, as this is the last part of the blastoderm to differentiate. From the appearance of the serosa cells at this time it seems evident that the subserosal substance is secreted by them and possibly also by the cells of the amnion and the cells forming the embryo. Butt suggests that the substance has a protective function. From a figure given by Scheinert (1933) of a snout beetle, *Liparus germanus*, it is evident that the egg of this species is provided with a similar protective coat.

BLASTOKINESIS

By this term Wheeler (1893) designated all the oscillatory movements or flections of the germ band during development. The ascending stage he called "anatrepsis"; the descending, "katatrepsis"; the intervening resting stage, the "diapause" (Figs. 36, 37). Since the flections of the embryo in some cases cannot be sharply distinguished from shifts due to growth in length and to later contraction, the expression is now usually used for all displacements, rotations, or revolutions of the embryo within the egg.

In its broadest sense, blastokinesis then may involve the growth in length of the germ band, the caudal end growing backward, pushing either into the yolk or over the dorsal side, in many cases the embryo becoming reversed in position with the head directed caudad. The diapause then ensues, followed in many instances by rupture of the envelopes and a subsequent reversal of the embryo to its original position with the head again directed forward. In this case the embryo undergoes a revolution about an axis perpendicular to the sagittal plane of the embryo. This occurs in general in the Orthoptera, Dermaptera, Odonata, Ephemera, Heteroptera, Homoptera, Anoplura, Mallophaga, etc. In other cases the rotation is about the longitudinal axis of the embryo, as with some *Lepidoptera* (*Diacrisia*), nemocerous *Diptera* (*Chironomus*, *Simulium*), *Melanoplus* (Slifer, 1933), and the mantid

Paratenodera (Hagan, 1917). In some insects the only movement is that occasioned by growth in length of the embryo which then remains from beginning to end on the ventral side of the egg, the head directed toward the cephalic pole.

Some writers believe that blastokinesis may be due to purely physiological causes, the embryo having "acquired the habit of moving to a different part of the egg where the yolk is as yet unpolluted by the waste products as a result of metabolism. . . ." Tirelli (1931) and others, however, have expressed the view that blastokinesis is due to mechanical and spatial conditions dependent upon the manner of growth of the embryo structure of the insect body and the constricted space within the egg.

In applied entomology it has been shown (Baker, 1921) that the time of revolution is extremely important in interpreting the results of experiments in the control of apple aphids, the overwintering insect undergoing blastokinesis in the spring before a marked rise in temperature, which would be fatal to the insect at this time.

Blastokinesis has been experimentally studied in the grasshopper *Melanoplus*. Here it consists of a reversing of the longitudinal axis followed by a revolution around this axis. Slifer (1932a) shows that this change of position is accomplished by vigorous movements of the embryo itself. These movements originate as contraction waves running along the lateral borders of the dorsally incomplete abdomen and passing rapidly to the head. With the closure of the dorsal wall and the formation of the dorsal vessel they seem to become resolved into the heartbeat, as was suggested by Nelsen (1931). In overwintering eggs, diapause interrupts incipient blastokinesis as well as other developmental activities, these processes being resumed immediately after the end of the diapause period.

Although the embryonic membranes are usually ruptured, Slifer reports one positive case in which blastokinesis was initiated and partly completed without the rupture of the serosa, showing that the contraction of the embryonic membranes cannot be the primary cause of revolution. Hence, in the grasshopper the revolution of the embryo must be due to its own movements. In sections of embryos of this age Slifer (1934) found unicellular, nonstriated, spindle-shaped fibers in the position of the future abdominal muscles. She suggests that these cause the movements (striated muscles do not appear until nine days later).

Concerning the necessity of revolution Slifer (1932a) reports four cases in which it failed to occur and yet the embryos developed more or less normally but were incapable of hatching. But Tirelli (1931) reports that the occasional failure of blastokinesis in the silkworm egg invariably results in death. However, in the latter case blastokinesis brings the

dorsal surface of the embryo into a spatially and mechanically more favorable position, whereas no apparent advantage is attained in the grasshopper. In *Platynemis* Seidel (1929) reports that prevention of blastokinesis by constriction seemingly inhibits development of a posterior part of the embryo beyond the differentiation of the organ systems; whereas if the anterior part of the embryo develops in front of an incomplete constriction, blastokinesis occurs in that part of the egg, and histological differentiation is completed. Accordingly it seems that blastokinesis is prerequisite for the completion of development in *Platynemis*.

References

Baker (1921), Brandt (1869), Butt (1934, 1936), Cole and Jahn (1937), Ganin (1869), Graber (1878, 1888*b*), Grimm (1870), Hagan (1917), Heymons (1894*b*, 1905), Johannsen (1928), Kupffer (1866), Miller (1939), Muir and Kershaw (1912), Nelsen (1931), Nelson (1912), Nusbaum (1890*a*), Poluszynski (1911), Scheinert (1933), Seidell (1929), Slifer (1931*a*, 1932*a*, 1934, 1937, 1938), Strindberg (1915*e*), Tirelli (1931), Waddington (1935), Wagner (1894), Wheeler (1890), Willey (1899). See also the list of general works cited in Chap. II.

CHAPTER VI

GASTRULATION, FORMATION OF GERM LAYERS, AND DEVELOPMENT OF THE ENTODERM

In simple cases, among animals' eggs where there is but little yolk, the cleavage cells (blastomeres) remain associated in a single mass, which, because of its appearance, has been called the "mulberry," or "morula," stage. The morula may become a single-layered hollow sphere of cells

FIG. 38.—An animal egg. *A*, unfertilized egg. *B*, four-cell stage. *C*, blastula stage. *D*, gastrula stage.

(blastula) the cavity of which is the segmentation cavity, or blastocoele (Fig. 38*C*). One side of the hollow blastula then becomes pushed inward, or invaginated, as if one side of a hollow rubber ball were dimpled, resulting in a cup-like structure (Fig. 38*D*). The process of invagination is termed "gastrulation"; the cup with its double wall, the "gastrula." The cavity of the gastrula is the primitive digestive cavity (archenteron); the opening is the blastopore. Of the two layers resulting from the invagination of the blastula, the outer one forms the ectoderm, or epi-

blast; the inner one, the entoderm, or hypoblast; the two constituting the primary germinal layers of the embryo. Excepting among the lowest forms of the Metozoa, there is subsequently formed between these a third layer, the mesoderm (mesoblast) (Figs. 39, 40).

Gastrulation as described above occurs in a number of different sections of the animal series; but in many instances, owing to a relatively large amount of yolk present in the eggs of some animals, it may become modified in various ways so that it is doubtful if in some of these cases true gastrulation occurs.

Cases in which the blastula is a hollow ball of cells, one hemisphere apparently dimpled into the other (Fig. 40), are represented by the eggs

FIG. 39.

FIG. 39.—Section. Mesoderm formation (*mes*). (*bp*) Blastopore. (*ect*) Ectoderm. (*ent*) Entoderm.

FIG. 40.

FIG. 40.—Sagitta (arrowworm). Folds developing from the bottom of the gastrula giving rise to the definitive mid-gut (*ent*) and the coelomic diverticula (*coel*). (*ect*) Ectoderm. (*ent*) Entoderm. (*som. m*) Somatic mesoderm. (*splm*) Splanchnic mesoderm. (From Hertwig.)

of the arrowworms (*Sagitta*), many mollusks (*Paludina*, etc.), sponges, coelenterates, worms, echinoderms, and *Amphioxus*. In this process of invagination (emboly) the outer layer forms the ectoderm; the inner layer, the entoderm. In the medusa *Lucernaria* where a morula is formed, the cavity being absent, the cells of the animal pole (ectoderm) grow over those of the vegetative pole (entoderm). This process of overgrowth is known as "epiboly." A modification of this type is found also in the yolk-laden eggs of birds and reptiles with discoidal cleavage wherein the germ disk overgrows the yolk. In some coelenterates a layer of cells is formed inside the blastula by delamination, the outer layer then constituting the ectoderm, the inner one the entoderm.

The mesoderm has a variable origin. It is represented in the coelenterates and sponges by a gelatinous material, the mesogloea, which appears between ectoderm and entoderm; and into this, cells wander from the two layers. In other Metazoa, the middle layer may arise from a few primary mesoblasts or cells which appear at an early stage

between ectoderm and entoderm or from numerous mesenchyme cells which are separated from the walls of the blastosphere or of the gastrula, as in the Echinoderms. In some forms, as in *Sagitta* and *Balanoglossus*, coelomic pouches—sac-like outgrowths from the entodermic lining of the gastrula-cavity—develop into mesoderm (Figs. 39, 40). The mesoderm comes to lie between ectoderm and entoderm, one layer of the mesoderm which attaches itself to the ectoderm forming the somatic or parietal layer; the other, clinging to the mid-gut, forming the visceral, or splanchnic, layer.

With the Arthropoda, in which, for the most part, the blastula is formed by the outward migration of cleavage cells from the center, the process of gastrulation is obscured by the manner of blastoderm formation and the presence of a large amount of yolk.

The difficulties in interpreting the homologies of the germ layers, especially in insects, are so great that writers from time to time have questioned the validity of the germ-layer theory. According to this theory, which is based on a large number of observations on the development of various animals, the material from which the mid-gut epithelium is formed should correspond to entoderm, and the efforts of many investigators have been bent toward establishing this homology and deriving the conditions found in the insect egg from the typical gastrula. This has proved so difficult a task that Nelson (1915) quoting Weismann says: "It becomes more and more evident that nowhere in the entire animal kingdom is the ontogeny so distorted and coenogenetically degenerate, as in the insects, so that scarcely anywhere are the germ layers so difficult to recognize as here."

The germ-layer theory dates back for much more than a century. Von Baer (1828), who is generally regarded as the founder of the theory, himself assigns the credit for the discovery of germ layers to Pander, although it should be pointed out that he acknowledged the fact that Wolff (1759) had already proposed the theory of epigenesis, a forerunner of the germ-layer theory. Haeckel's biogenetic law, which states that ontogeny, or the development of the individual, is a short recapitulation of phylogeny, or the development of the race, led embryologists to search in the development of individuals for stages that could be regarded as ancestral. It is generally stated that the blastula and gastrula stages at the end of cleavage represent forms that are ancestral to all Metazoa and that one is justified in the assumption that in these two stages there exists a repetition of ancestral forms which are common to all Metazoa (Korschelt and Heider, 1895). Earlier writers saw in the gastrula a form common to all metazoan embryos, but Brachet (1921) points out that there may be no gastrula in the Haeckelian sense in the development of certain forms.

Philippschenko (1912) ventured the opinion that had writers in the past adopted the plan of recognizing only the two primary germ layers (ectoderm and inner, or lower, layer) and then beyond this point treating only of the primitive anlagen of the inner layer, much confusion in description would have been avoided. He thus would go back to the old concept of Von Baer of two primary layers which are further divided into fundamental (or primitive) organs. By this he does not mean to imply that the germ-layer theory is superfluous but, on the contrary, considers it as one of the most useful of all embryological generalizations so far as the homologies of the ectoderm and the inner (lower) layer are concerned. As for the mesoderm and the so-called "secondary entoderm," the two derivatives of the inner layer, these, as at present interpreted, he maintains are not homologous throughout the animal kingdom. Meisenheimer (1917) has made a somewhat similar observation.

Some writers on insect embryology have objected to the use of the term "gastrula" in cases where the invaginated cells are said not to give rise to the entoderm. To this Patten (1884) replied:

I cannot see that it would influence the use of the term in this case, for it seems to me that an inherited tendency to produce an invagination, the sole object of which is to cause a differentiation into germ layers, however successful or unsuccessful the attempt may be should receive the name that was originally applied to the more simple condition, always holding in mind, however, that it is a condition modified by various agents, the nature of which may or may not be known.

In the following discussion the terms "gastrulation" and "gastrula" will be used in the customary manner even in cases where authors have denied that the mid-gut epithelium is an entoderm derivative.

Among the pterygotes, with some exceptions, gastrulation, as usually interpreted by embryologists, takes place soon after the germ band is formed. The middle part of the band sinks inward and may become separated from the part on either side by a slight ridge. There is thus formed a middle plate and the lateral plates (Fig. 41*A*, *mp.lp*). The lateral plates, except for the amniotic (lateral) edges, will form the ectoderm; the middle plate, the strictly internal organs of the future insect. In the more generalized case, as has already been described on page 13, the middle plate continues to sink inward, forming a deep median furrow which is then converted into a sunken tube by the approach and union of the lateral plates beneath it (Fig. 41*B*). The tube now flattens out into a continuous two-layered sheet of cells forming the so-called "inner," or "lower," germ layer (Fig. 41*C*, *il*). This type of inner layer formation is common among flies and beetles (Fig. 329*A*). In other cases, as among certain Lepidoptera and Hymenoptera (Figs. 41*D*, *E*) and some aphids,

the edges of the lateral plates separate from the middle plate and then grow together beneath it, the middle plate being thus cut off from the lateral plates to form, at first, a single-layered inner germ layer. In still other forms, as among Orthoptera and some Lepidoptera, the cells along the middle part of the germ band, without forming a distinct middle plate and either with or without the formation of a gastral furrow, multiply by horizontal (tangential) division and give off cells from their inner ends that constitute the inner layer (Fig. 41*F*). The method of inner layer formation is probably of no great phylogenetic significance,

FIG. 41.—Types of gastrulation. (am) Amnion. (ect) Ectoderm. (il) Inner layer. (lp) Lateral plate. (mp) Middle plate. (ser) Serosa.

since different types may be found in different sections of the germ band of a single individual, as in the Siphonoptera (Kessel, 1939) and other forms.

Among some of the more primitive arthropods gastrulation is not accompanied by the formation of a furrow. The furrow in insects appears to be merely an ontogenetic adaptation which may be present or absent in closely related forms. In *Isotoma*, according to Philpitschenko (1912), gastrulation consists of multipolar migration under the entire blastoderm with the invagination and other gastrulation processes derived from it. In agreement with Metschnikoff (1866) he believes this to be the more primitive, the formation of a furrow being derived from the primitive form. Examples of multipolar gastrulation are found in Collembola,

Scolopendra, *Polydesmus*, *Phyllodromia*, and *Gryllotalpa* (Heymons, Nusbaum, and Fulinski) and *Eutermes* (Knower).

Philipstchenko preferred to speak of an upper, or outer (ectoderm), and an inner, or lower, layer, believing that a sharp line cannot be drawn from the further derivatives of the inner layer, *i.e.*, secondary (entoderm and mesoderm) layers. He contended that in *Isotoma* the unpaired median part of the inner layer is a mixed one, giving rise to both entoderm and mesoderm.

Thus far the ectoderm is accounted for. The question of the derivation of entoderm and mesoderm now arises. In descriptive embryology of arthropods we are confronted with the difficulty of a terminology in

FIG. 42.—Germ disk of *Peripatopsis*. (an) Anus. (bp) Blastopore. (m) Mouth. (From Snodgrass after Balfour.)

which one group of writers uses the term “entoderm” for one of the two components of the inner (lower) layer while another group uses it for the yolk cells. Prior to the time of the appearance of a paper by Grassi (1884) nearly all investigators of insect embryology were divided into two groups; either they followed Dohrn (1866) in deriving the mid-gut epithelium from the yolk cells, or they followed Kowalewsky in deriving it from the inner wall (splanchnic layer) of the mesodermic somites. In 1884 Grassi demonstrated the bipolar origin of the mid-gut epithelium from the inner (lower) layer in the honeybee. This was followed by a brief paper of Kowalewsky (1886) in which he devised a theory wherein he regarded the insect egg at the time of the formation of the germ layers as comparable to a gastrula so stretched out that the mid-gut epithelial rudiment (mesenteron or entoderm) was pulled into two halves. The stretching of the gastrula resulted in a much elongated blastopore, extending along the whole ventral surface as far as the point at which, later, the proctodaeum develops, and the edges of the furrow forming

the lips of the blastopore (Fig. 42). The cellular layer derived from the gastrular invagination (the inner layer) according to Kowalewsky's theory represents the anlage of the entoderm and mesoderm; the former (Fig. 43A, *mge*), having been pulled apart, is restricted to an anterior and posterior entoderm rudiment, the latter constituting the major portion of the inner layer. Some recent writers (Hirschler, Fulinski) hold that in some embryos the two entoderm rudiments are connected by a median

FIG. 43.—Sagittal section of embryo. Development of the mid-gut epithelium. (*am*) Amnion. (*ect*) Ectoderm. (*mes*) Mesoderm. (*mge*) Mid-gut epithelial rudiment: (*a*) anterior, (*p*) posterior. (*proct*) Proctodaeum. (*rb*) Mid-gut epithelial ribbon. (*stom*) Stomodaeum.

strand, coming back to Rabl's idea of the inner layer being composed of a median entoderm band and paired mesoderm bands. Kowalewsky has compared the formation of the germ bands in insects with their formation in *Sagitta* where the archenteron becomes divided by the appearance of two folds into a median enteric rudiment and two lateral coelomic sacs (Fig. 40). The views of Grassi and Kowalewsky were later accepted by Wheeler, Cholodkowsky, and others.

A number of writers, on the other hand, following Heymons (1895a) maintained that the mid-gut epithelial rudiments arose from the blind ends of the stomodaeum and proctodaeum in the Orthoptera and some other orders. They came to the conclusion that the functional mesenteron of pterygote insects is of recent origin and that the original entoderm

was represented by the yolk cells which therefore constituted the vestigial mesenteron. Support for this view was found in *Lepisma* and Odonata where what seem to be yolk cells appear to form functional mesenteron. Followers of this view consider the definitive mid-gut epithelium as an ectoderm derivative and that entoderm derivatives are wholly lacking in postembryonic life. Under this assumption the formation of the so-called "gastral furrow" is a secondary acquisition, since it does not involve an entoderm.

Eastham (1930a) maintains that there is no essential difference between a mid-gut that develops from rudiments arising directly from the germ band and one that arises from anterior and posterior cell proliferations at the blind ends of the stomodaeum and proctodaeum. In the former case cell proliferation to form entoderm begins *before* the stomodaeal and proctodaeal invaginations, whereas in the latter case entodermal proliferation begins later, *after* the invaginations have occurred. Heymons (1895a, 1905), who seems to be in agreement so far as the facts are concerned, states that the divergent views of authors are largely a matter of interpretation. However, since he regards the yolk cells as the entoderm, he interprets the mid-gut epithelium as ectoderm. Nusbaum and Fulinski (1909) in summarizing their views list seven different ways in which the mid-gut may develop:

Type I. Entoderm rudiments are first cut off from the germ band. This is followed by the invagination of stomodaeum and proctodaeum carrying the entoderm into the yolk. Noack (1901) in *Muscids*; Hirschler (1909) in *Donacia*.

Type II. Entoderm rudiments form from the germ band, but the stomodaeum invaginates before these are cut off from the ectoderm. Karawaiew (1893) in *Pyrrhocoris*.

Type III. In anterior region as type II. In posterior region as type I. Nusbaum and Fulinski (1909) in *Gryllotalpa*.

Type IV. Stomodaeum and proctodaeum develop immediately in front of and behind the entoderm rudiments, respectively. Nusbaum and Fulinski (1906) in *Phyllodromia*.

Type V. Stomodaeum, proctodaeum, and entoderm rudiments develop concurrently, and inner layer contributes to mid-gut formation. Hirschler (1909a) in *Gastroidea*.

Type VI. As in type V, but no inner layer contributes to entoderm formation. Carrière and Bürger (1898) in *Chalicodoma*.

Type VII. Growth areas of entoderm rudiments remain dormant till the stomodaeum and proctodaeum appear. Heymons (1895) in *Forficula*. In this type the latent, or dormant, rudiments being indistinguishable from the ectoderm cells of the invaginations have led Heymons and his followers to regard the mid-gut epithelium as an ectoderm derivative.

Several authors who on theoretical grounds are not willing to admit the ectodermal origin of the mid-gut epithelium in Orthoptera, Dermaptera, and some other insects where the epithelium appears to be of

ectodermal origin have adopted the view of Heider of a "latent entoderm." Heider, contending that the mid-gut epithelium originates from the entoderm, suggested that in the groups mentioned above, the anlagen of stomodaeum and proctodaeum contained latent or dormant entoderm cells. These latent cells later became distinctly differentiated. This idea was more fully elaborated by the senior author (Johannsen, 1929). Tiegs and Murray (1938) object, however, saying that

. . . it is evident that the notion of "latent entoderm" is in direct conflict with the very essence of the (gastrulation) theory, *viz.*, the occurrence of visibly distinguishable layers of cells in the very early embryo.

In response to the last statement it may be asked what constitutes "visibly distinguishable layers"?

From time to time efforts have been made to reconcile the opposing ideas. Heider (1897) quoting Braem tabulates three different views held by morphologists relative to the homologies of the germ layers. (1) The germ layers are purely topographical concepts, and they are solely determined by their relative positions. (2) The germ layers are homologous in origin. (3) The germ layers are only analogous structures and only comparable physiologically. They have, as Driesch says, the same prospective significance.

In most cases the discussions of embryologists have been based on the second assumption that the germ layers are homologous in origin. The first thing that is necessary to reconcile the several theories is the determination of the status of the yolk cells. Are they to be recognized as primary entoderm, or are they merely nongerm-layer derivatives?

Because of their early differentiation the yolk cells were considered by Dohrn (1866) and other early writers as the primary entoderm. They believed that the mid-gut arose as a sac surrounding the yolk enclosed anteriorly by the stomodaeum and posteriorly by the proctodaeum, its walls being formed by the free cells or by cleavage. If the yolk cells really represented the entoderm, it was thought that with insects some representatives, at least among the more primitive forms, would show this type of development. Heymons (1897) in a brief paper on the development of *Lepisma* and *Campodea* held that in these forms the yolk cells play a part in the formation of the mid-gut epithelium, but according to Tschuproff (1903) in *Epitheca* and *Calopteryx* the middle section of the mid-gut originates from yolk cells. More recently Stuart (1935) has described for *Melanoplus differentialis* the development of the definitive mid-gut epithelium from yolk cells (vitellophags) which move peripherally to form a lining upon the inner surface of the primitive mesenteron (muscle and connective tissue components of the definitive mid-intestine).

About the time of hatching, each vitellophag nucleus divides in a dozen or more smaller nuclei, which are designated by Stuart as "presumptive mid-gut epithelial nuclei," each of which appropriates a portion of the vitellophag cytoplasm and thus forms the definitive mid-gut epithelium cells. At times the vitellophag nuclei may divide while still out in the lumen of the mesenteron.

The junior author, in a still unpublished account of the development of dragonflies (*Plathemis*, *Erythemis*, *Libellula*), agrees with Tschuproff's statement that the vitellophags take part in the formation of the middle section of the mid-gut epithelium. This is discussed in Chap. XIV.

Attention should be called at this point to the fact that peripheral migration of yolk cells has been reported by a number of investigators for Isoptera, Orthoptera, Plecoptera, and Hymenoptera. Miller (1939) has described a nucleated membrane, presumably derived from yolk cells, which lies in the lumen of the mid-gut and which is shed after hatching of the nymph. The definitive mid-gut epithelium here has apparently been formed by proliferation of cells from the blind end of the proctodaeum. A somewhat similar case is reported by Hoffman (1913-1914) of the development of species of Strepsiptera, wherein the primary mid-gut arises from three vitellophags which surround a lumen. By cell proliferation from the blind ends of the stomodaeum a layer of ectodermal cells grow over the primary mid-gut to form the epithelium of the secondary mid-gut. The primary mid-gut is now absorbed, leaving, according to Hoffmann, a definitive epithelium composed of ectoderm only. The three yolk cells are comparable to the annelid macromeres both in their mode of origin by total cleavage and in their fate. Noskiewicz and Poluszynski (1928) have come to a similar conclusion for *Stylops*. The formation of the yolk-cell membrane in *Carausius* (Leuzinger and Wiesmann, 1926) is also analogous. The membranous cellular sacs that are formed within the lumen of the mesenteron of a psocid described by Fernando may also belong to this category (see Chap. XVI). For lack of sufficient data a positive statement as to the part played by the primary yolk cells in connection with the formation of the mid-gut epithelium in the Apterygota, the Odonata, certain Orthoptera, and other Pterygota cannot be made at the present time. In view, however, of the works cited above, the subject cannot be lightly dismissed. Renewed investigation of the development of yolk cells in apterygotes and in some of the primitive pterygotes is necessary to solve this problem.

Whatever may be the derivation of the mid-gut epithelium it is probable that the majority of embryologists are now agreed that the epithelium develops from the *same* germ layer in most pterygotes. Roonwal (1937) and some others, however, believe that this tissue may originate from ectoderm or secondary entoderm or both.

The following tabulation sets forth the chief points involved in some of the prevailing theories.

1. Primary yolk cells represent the primary entoderm. The entoderm being accounted for, the so-called "blastula" is really the gastrula.
 - a. Gastrulation completed when primary epithelium (so-called "blastoderm") is formed. Formation of a gastrula furrow is a secondary phenomenon. Mid-gut epithelium regarded as an ectoderm derivative in most Pterygota. Inner layer wholly mesodermic. *Heymon's theory*
 - b. Gastrulation biphased, the formation of the gastrula furrow being the second phase. Inner layer with two components—lateral parts mesoderm, median parts (bipolar or with median strand or both) are secondary entoderm. *Hirschler's theory*
 - c. Gastrulation multiphased. Definitive mid-gut epithelium, no matter in what manner arising, is, in the majority of insects, a secondary phenomenon. It may arise from (1) pure ectoderm (as in *Locusta*); (2) inner layer (*i.e.* from secondary entoderm, as in *Carausius*); or (3) ectoderm plus secondary yolk cells (secondary entoderm). *Roonwal's theory*
It is not out of harmony with any of these views to regard the definitive mid-gut epithelium as being derived from primary yolk cells in the apteryotes and the primitive pterygotes.
2. Primary yolk cells nongerm-layer derivatives. The blastoderm stage represents the true blastula. Inner layer with two components, its lateral parts mesodermic.
 - a. Primary entoderm buds off into the yolk from the inner wall of the ventral furrow but gives rise to no larval structures. *Mansour's theory*
 - b. Median part (primary entoderm) of inner layer confined to bipolar mesenteron rudiments, or to a mid-strand, or both. These parts give rise to the mid-gut epithelium. *Extension of Kowalewsky's theory*

It should be noted that the terms "primary and secondary entoderm" and "primary and secondary yolk cells" are used in different ways by the various writers. Cholodkowsky (1891) and others employed the expression "primary entoderm" for the entire undifferentiated inner (lower) layer whose components are mesoderm and "secondary" entoderm (anterior and posterior enteron rudiments). The term "primary yolk cell" usually signifies those cells which are left behind in the outward migration of the cleavage cells during the formation of the blastoderm (primary epithelium). The "secondary yolk cells"—those which return into the yolk after the formation of the blastoderm—are either cleavage cells that had reached the periphery and then turned back into the yolk or cells formed by tangential division of the blastoderm cells. Tiegs and Murray (1938) as well as other writers have taken exception to the application of the term "entoderm" for the yolk cells unless these actually give rise to the mid-gut epithelium. Spemann says that homologizing is possible only after the formation of the anlagen, *i.e.*, at the developmental period when the individual parts of the germ band have become differentiated, if not in their outward appearance, at least in their developmental tendency. To this Tiegs and Murray add: "Homology of an

anlage is therefore determined by its fate rather than its origin. If, then, the gastral epithelium of all Metazoa is homologous, so are also their anlagen whatever their mode of formation."

A brief discussion of the theories tabulated above may be of service.

1a. *Primary yolk cells represent the primary entoderm. Gastrulation completed when the so-called "blastoderm" is formed. Gastrula furrow a secondary phenomenon. Mid-gut epithelium an ectodermal derivative in most pterygotes. Inner layer wholly mesodermic.*

Heymons (1895a) maintains that in the development of Dermaptera and Orthoptera the epithelium of the mid-gut is formed from ectodermal cells of the blind ends of the stomodaeal and proctodaeal invaginations, confirming views previously expressed by Ganin, Witlaczil, Voeltzkow, and others. Subsequently the results of Heymons have apparently been verified by Friederichs (1906), Lécaillon (1898), Roonwal (1937), and a number of other investigators for some of the Lepidoptera, Coleoptera, Hemiptera, and Orthoptera. Heymons' conclusion, that the functional mid-gut epithelium of pterygotes is of comparatively recent origin and is derived from the ectoderm, whereas the original entoderm is now represented by yolk cells constituting a vestigial mesenteron, has been accepted by many though not a majority of workers. In cases where the mid-gut epithelium apparently arises from anterior and posterior rudiments, as in section 1b given below, Heymons (1895a, 1905b) holds that these rudiments develop from the ectodermal (blastodermal) region of the germ band before the appearance of the fore- and hind-gut invaginations and therefore are ectodermal.

Among many Annelida, the ectoderm, strictly speaking, arises from two kinds of cleavage cells: entodermal macromeres and entodermal micromeres, both types occurring among primitive Arthropoda (Myriapoda, Thysanura, Odonata) in the form of yolk cells. A sharp line cannot be drawn between macromeres and micromeres, since the former even in early embryonic life are functioning nutritive cells (trophocytes), the latter are regenerative elements. From the micromeres a portion are transformed into new trophocytes (mid-gut epithelium) which after a period of functioning likewise degenerate to be again replaced by new elements (Heymons, 1901). Among the Odonata (Tschuproff) the yolk cells give rise to the middle section of the mid-gut, but the anterior and posterior extremities of the mid-gut arise from small ectodermal regenerative cells. Other investigators who support the view of the ectodermal origin of the mid-gut epithelium but who may not be in agreement as to the yolk cells are the following: for beetles, Czerski (1894), Deegener (1900), Friederichs (1906), Lécaillon (1898), and Saling (1907); for *Melophagus*, Pratt (1900); for *Mantis*, Rabito (1898); for Lepidoptera, Rizzi (1912), Schwartze (1899), and Toyama (1902).

1b. *Primary yolk cells represent primary entoderm. Gastrulation biphased, the formation of the gastrula furrow being the second phase. Inner layer with two components—lateral parts of mesoderm, median parts of secondary entoderm.*

Hirschler, Nusbaum, Fulinski, and others are in agreement with Heymons in that they consider the primary yolk cells the primary entoderm but differ as to the origin of the mid-gut epithelium which they regard as a derivative of the nonmesodermal component of the lower layer. This component they designate as "secondary entoderm," which corresponds to the enteron (mesenteron) rudiments that Grassi first demonstrated in the honeybee and that since have been described by Wheeler and numerous other writers, most of whom, however, regard the yolk cells as nongerm-layer derivatives.

Hirschler and his followers in general for most pterygotes regard the middle section of the lower layer as consisting of the bipolar mesenteron rudiments together with a connecting median strand or of the bipolar rudiments alone or of the middle strand alone.

1c. *Primary yolk cells represent the primary entoderm. Gastrulation multiphased. Definitive mid-gut epithelium, no matter in what manner arising, is, in most insects, a secondary phenomenon. It may arise from pure ectoderm or from the inner layer or from the ectoderm plus secondary yolk cells (secondary entoderm).*

Among attempts made to reconcile the theories on germ-layer formation and gastrulation processes is one by Roonwal (1936, 1937) which he calls the "multiphased theory."

By the term "multiple-phase gastrulation" Roonwal implies a type of so-called "gastrulation" of which the first phase consists in the formation of a primary epithelial layer (the so-called "blastoderm" in insects) and of yolk cells; the latter at least in part is to be regarded as the primary entoderm, in agreement with Hirschler, Schwangert, *et al.* The second phase, lacking in most insects, leads to the formation of a first primitive furrow (corresponding to a part of the gastrocœle) and of a yolk-cell membrane (also a part of the primary entoderm). In the third phase there is formed a further invagination furrow, and the inner layer (as a part of the secondary entoderm, or entomesoderm) is differentiated from the outer layer. The fourth phase consists finally in the formation of secondary yolk cells, which are to be considered as the secondary entoderm and are transitory. Phases one and four are epibolic; phases two and three, invagination processes. Of this formulation of Roonwal, Weber (1937) expressed the opinion that it is not fundamentally different from the idea stated by Hirschler (1909), the second phase of Roonwal being applicable only in the special case cited by him.

Roonwal's statement that the mid-gut may arise from the ectoderm or from the inner layer (secondary entoderm) or ectoderm plus secondary yolk cells would seem to imply that he, at least in part, supports the views of some experimental embryologists as outlined below by Richards.

2a. *Primary yolk cells nongerm-layer derivatives. Inner layer with two components. Primary entoderm buds off into the yolk from the inner wall of the ventral furrow but gives rise to no larval structures.*

In this group the blastodermal stage corresponds to the blastula stage of other animals. The primary yolk cells are a secondary feature of the developing insect egg. The ventral furrow here is regarded by Mansour (1927) as corresponding to the invagination of the gastrula. Entodermal cells arise from the wall of the ventral furrow or from thickenings in the blastodermal wall. They are budded off into the yolk but give rise to no larval or imaginal structures. The definitive mid-gut epithelium is derived from the inner ends of the stomodaeum and proctodaeum and is therefore of ectodermal origin. Mansour's findings in *Calandra oryzae* (1927) and those of Heymons (1895a) in the Dermaptera and Orthoptera are thus in agreement so far as the origin of the mid-gut epithelium is concerned, but their views differ as to the significance of the yolk cells.

2b. *Primary yolk cells nongerm-layer derivatives. Median part (primary entoderm) of inner layer, which is confined to bipolar mesenteron rudiments or to a middle strand or to both, gives rise to the mid-gut epithelium.*

Embryologists holding this opinion, following Kowalewsky, regard the peripheral layer of cells first formed by the cleavage cells that have migrated outward as the blastoderm and corresponds to the blastula stage of other animals. The primary yolk cells are a secondary feature. The furrow that may be formed along the midventral line of the germ band is looked upon as a true gastrula furrow, the formation resulting in a gastrula. Further support of this view may be found in the development of *Peripatus capensis* in which Sedgwick (1885) has shown that the blastopore divides into two parts by the closure of the middle section (Fig. 42). The two entrances into the gut thus left are spoken of by him as an embryonic mouth and anus. These are subsequently carried inward by the ingrowing stomodaeum and proctodaeum but are never closed.

The essential difference between this theory and that expressed in section 1b is chiefly a matter of opinion as to the significance of the yolk cells. The following statements based upon observations apply to both. The idea that the mid-gut epithelium is derived from bipolar entoderm rudiments was first expressed by Grassi for the honeybee in 1884 and formulated in Kowalewsky's theory two years later. Nusbaum and Fulinski (1906) maintain that in *Phyllodromia*, in addition to the bipolar entoderm rudiments, there is a connecting strand of entodermal

cells which contribute to the formation of the mid-gut epithelium, and Hirschler (1905, 1909a, 1909b) makes a similar claim for some Lepidoptera and Coleoptera (*Catocala*, *Donacia*, *Gastroidea*). Hammerschmidt (1910) asserts that in *Carausius* (*Dixippus*) only the middle strand is concerned in mid-gut formation, the bipolar rudiments being absent, a statement in part confirmed by Leuzinger and Wiesmann (1926). Paterson (1935) found a similar condition in the beetles *Corynodes pusis* and *Euryope terminalis*. A comparative study of these and some other forms indicates that all stages exist in the development of the nonmesodermic component of the inner layer: the bipolar rudiments alone, the bipolar rudiments connected by a middle strand, the middle strand alone, or any or all of these parts breaking down in the yolk. Perhaps a majority of present-day embryologists support this view regarding the development of pterygote insects.

In the foregoing tabulation no mention is made of the old suggestion that the mesoderm may play a part in the formation of the definitive mid-gut epithelium of insects, since the idea is doubtless no longer entertained by embryologists.

Recently there has been an inclination on the part of some workers to follow the lead of experimental embryologists as expressed by Richards (1932) in the words:

So the experimental embryologists, notably the workers on Amphibia, distinguish between "prospective significance" and "prospective potency" and bring the idea in of "time of determination," etc. Pending pertinent experimental data, we are forced to one of two conclusions: either the mid-gut epithelium, despite its final similarity within individual orders of insects, may arise in some cases as an entodermal derivative and in other cases as an ectodermal derivative; or else we must look upon the determination of the mid-gut as a purely physiological process—to borrow Driesch's terminology, "as a function of the position within the whole." That is, that whatever cells in each particular case happen to be appropriately located at the time when the entodermal strands are due to be formed, those cells will be "determined" to form the mid-gut anlage and subsequently differentiate into the structure typical of mid-gut epithelium. The question is purely a matter of the time of the determination of the parts involved. Experimental embryologists are inclined to accept the latter interpretation as superior to the former in the light of the great diversity shown by closely related insects and from the standpoint of modern views of developmental processes in general.

In view of the still prevailing diverse opinions regarding the development of the germ layers as outlined above it is apparent that it would be futile at present to attempt to formulate a theory that will satisfactorily explain all established facts. The endeavors that have been made to reconcile the several existing theories have not proved wholly convincing.

Too much theorizing has already been done on insufficient data. Pending the accumulation of more information, especially with reference to the development and fate of the primary and secondary yolk cells, of the yolk cell and ental membranes, and of the yolk cells as provisional mid-gut epithelium, we deem it wise to withhold judgment.

In concluding this topic we cannot refrain from quoting a paragraph from a recent paper by Dr. Albert Miller (1940), which contains a suggestion that we are most inclined to support:

Perhaps, after all, only the vitellophags may be justly homologized with the entoderm of other invertebrates, using the term "entoderm" in a strictly embryological sense, rather than in a functional or anatomical sense (as it is when the mid-gut tissue is called entodermal by virtue of its definitive position). To extend the embryological concept of the term further, in forms refractory to its application, subjects the germ-layer theory to so severe a strain that it loses its essential characters if not its entire meaning. In our preoccupation with terms there is danger of losing sight of the true nature of living matter—its remarkable adaptability; adaptability that may invalidate our best intentioned attempts to pigeonhole its other manifestations.

References

- Bobretsky (1878), Braem (1895), Brass (1883), Bütschli (1888), Cholodkowsky (1888), Deegener (1900), Eastham (1930*b*), Escherich (1900, 1901), Ganin (1874), Graber (1878), Heider (1885, 1897), Henson (1932), Hertwig (1880), Heymons (1894*a*, 1897), Hirschler (1907*a*, 1909*a*), Iukmann (1933), Jentsch (1936), Jordan (1888), Korotneff (1894), Krause (1938*a*), Lécaillon (1897*a,b*, 1907), Mansour (1927, 1930), Nelson (1911), Nusbaum and Fulinski (1906, 1909), Rabito (1897), Richards (1932), Rizzi (1912), Schwangart (1904, 1907), Schwartz (1899), Sehl (1931), Snodgrass (1933, 1935*a*), Stecker (1877), Strindberg (1913*a*, 1914*a*, 1915*b*), Stuart (1935), Tchang (1929), Thomas (1936), Tichomiroff (1890*a*, 1892), Tichomirowa (1890*a*), Tschuproff (1903), Will (1888*b*), Wagner (1894), Zograf (1882). See also the list of general works cited in Chap. II. The paper by Eastham (1930*b*) is a comprehensive summary.

CHAPTER VII

THE ALIMENTARY CANAL

The alimentary canal of the arthropods has three primary divisions, commonly spoken of as the fore, mid, and hind intestine, or fore-, mid-, and hind-gut. The rudiments of these parts appear very early, the fore and hind parts developing from the ectoderm as anterior and posterior invaginations (Figs. 43*B*, 44) the former constituting the stomodaeum; the latter, the proctodaeum. In general, the stomodaeum forms before the proctodaeum, but in a number of cases the proctodaeum forms first, as in the head louse, the flour moth (*Ephestia*), some chrysomelids, the sheep tick, etc. The esophagus, the proventriculus, the salivary glands, and other annexes have their origin in the stomodaeal invagination. The ileum, colon, rectum, rectal glands, and Malpighian tubules originate in the proctodaeum. The last mentioned arise as evaginations from the blind end of the proctodaeum, either as a single pair of buds which later branch or as two or three pairs depending on the species, three pairs apparently being the primitive number. Henson (1932) only, of recent writers, considers the Malpighian tubules of mesodermic origin.

The stomodaeum is a simple invagination easy to identify. The proctodaeum, on the other hand, by reason of its position may sometimes be confused with the posterior amniotic cavity in cases where the two appear simultaneously and the transition from one into the other is not sharp. The resulting invagination has consequently been termed the "amnioproctodaeal cavity."

Within the lumen of the mid-gut of insects that subsist on solid food, the thin peritrophic membrane is found. Its presence in the embryo has been recorded in but few cases. Strindberg (1913*b*) found it in the embryo of *Formica fusca* in the form of two membranes: an outer and younger membrane closely applied to the mid-gut epithelium and an inner and older membrane in contact with the yolk, the space between them filled with a coagulate. Strindberg argues that since the membrane, at least in the ant embryo, forms a closed sac around the yolk including its posterior end, it cannot develop from a ring of cells in the proventriculus but must be secreted by the mid-gut epithelium.

Gambrell (1933) in her study of the development of *Simulium pictipes* believes that the closing membrane of the stomodaeum after rupture forms the rudiment of the peritrophic membrane. Butt (1934) independ-

ently has made a similar suggestion for *Sciara coprophila*. More work on late embryonic and early larval stages is necessary for convincing proof of the origin of this membrane in Diptera.

As has been described in the foregoing chapter, the origin of the mid-gut epithelium has been the source of much controversy. Whatever may be its origin, among the Hymenoptera and Diptera, as well as some Coleoptera, Lepidoptera, etc., at each extremity of the inner (lower) layer, either united with it or contiguous to it, a cell mass, or

FIG. 44.—Sagittal section of embryo. Development of mid-gut epithelium. (*am*) Amnion. (*br*) Brain. (*ggl*) Ganglion. (*mge* and *mgs*) Mid-gut epithelium. (*proct*) Proctodaeum. (*stom*) Stomodaeum.

mesenteron rudiment (*mge*), is developed, which by many is regarded as an entoderm derivative. From each of these two cell masses or rudiments two ribbons (*rb*) of cells grow out, those from the anterior mass growing posteriorly, those from the posterior mass growing anteriorly, until their tips meet (Figs. 43, 44). After fusion of their tips the ribbons (*rb*) widen until they wholly enclose the yolk. The ribbons usually arise from the ventrolateral angles. In some cases, only a single middorsal ribbon arises from each cell mass; in others instead of a ribbon each rudiment develops in the form of a cup, one covering each end of the yolk, the rims of the cups facing each other and finally fusing. In some insects, in addition to the two ribbons, cells liberated from the middle strand of the inner layer contribute toward building the mid-gut.

Among certain other Coleoptera and Lepidoptera, as well as Orthoptera, the mid-gut epithelium seems to originate directly from proliferating ectodermal cells that lie in the tip of the blind ends of the stomodaeum and proctodaeum. In this case also, ribbons or a middle strand or both may give rise to the mid-gut epithelium.

As has been stated in the preceding chapter, it seems probable that from whatever germ layer the mid-gut is assumed to arise, its origin is the same in the two cases cited above.

Lastly, in the myriapods and apterygotes, as well as with the Odonata and perhaps other primitive pterygotes, the yolk cells are regarded by some embryologists as the source from which at least a part of the mid-gut is derived. In this chapter the terms "entoderm" and "ectoderm" are used as applied by the authors cited.

MYRIAPODA

Chilopoda.—The entoderm cells which are to form the mid-gut epithelium in *Scolopendra* (Heymons, 1901) are set free from numerous points of the inner ventral surface of the blastoderm and then collect in a thin layer on the ventral side of the yolk. This layer soon spreads, apparently by a process of stretching, over the entire yolk as a thin-walled sac, thus forming the epithelium.

Diplopoda.—Pflugfelder (1932) found that the entoderm in *Platyrrhacus* arises by active proliferation of cells at a point where the future stomodaeum will form. Cells liberated here migrate toward the posterior pole; the cells at the seat of proliferation become fewer, leaving an opening at the surface that projects itself into the proliferating cell mass to form a lumen. Later the stomodaeum and the proctodaeum are established, while the entodermal cells arrange themselves epithelial fashion forming the mid-gut. In *Julus*, Heathcote (1886) found that the mid-gut epithelium is derived from yolk cells, some of which collect in the median line just entad of the mesoderm where they arrange themselves between stomodaeum and proctodaeum.

Several workers are in agreement that in the diplopods the mid-gut epithelium arises from a loosely formed strand of cells which is solid at first but later acquires a lumen, the strand extending through (not surrounding) the yolk, a most peculiar mode of development.

COLLEMBOLA

The mid-gut epithelium in *Isotoma cinerea*, according to Philip-tschenko (1912), arises from an anterior and a posterior mesenteron rudiment and a middle strand. The two rudiments each give rise to a pair of entoderm ribbons; the cells liberated from the middle strand migrate to the yolk surface where they later unite with the paired ribbons which

have lengthened and widened and finally cover the yolk. Both the mesenteron rudiments and the middle strand also include mesoderm elements. Philpitschenko believes that the earlier writers on Collembola were in error as to the development of the mid-gut. Uljanin (1885) apparently mistook the germ cells for the mid-gut rudiments. Uzel (1898) for *Macrotoma* and *Achorutes*, Prowazek (1900) for *Isotoma*, and Claypole (1898) for *Anurida* derived the entoderm from yolk cells. Philpitschenko doubts the yolk-cell origin for Collembola generally on the basis of his study of *Isotoma*.

In *Isotoma* as in other Collembola the closing membrane of the proctodaeum widens but does not form Malpighian tubules.

THYSANURA

Heymons (1897) derives the mid-gut epithelium of *Lepisma saccharina* from yolk cells. The yolk spherules retract toward the mesodermal wall of the mid-gut and leave a lumen. Some of the yolk nuclei, each now surrounded by a plasma layer and therefore properly considered yolk cells, migrate out of the spherules and attach themselves to the mid-gut muscle wall, undergoing active mitosis and thus forming small clusters of cells. From these cell crypts, by further proliferation, the mid-gut epithelium is supposed to arise. Some recent writers on theoretical grounds question the yolk-cell origin of the mid-gut epithelium in this species. In the dipluran *Campodea staphylinus*, which was studied by Uzel (1898), the entoderm cells are said to originate from the germ band but later migrate into the yolk where they become distributed. Their further history is in doubt.

ORTHOPTERA AND DERMAPTERA

In the orthopteroid species *Ectobia livida*, *Blattella* (*Phyllodromia*) *germanica*, *Blatta* (*Periplaneta*) *orientalis*, *Mantis religiosus*, *Gryllus* spp., *Gryllotalpa vulgaris*, *Locusta migratoria*, *Melanoplus differentialis*, *Hemimerus talpoides*, as well as the dermapteron *Forficula auricularia*, the anlagen of the mid-gut epithelium are bipolar in position. Although there is an agreement among writers as to location, Heymons and his followers regard these anlagen as ectodermal, whereas other investigators call them entodermal.

In *Stenobothrus*, in addition to paired ribbons and apparently independent of them, there arise from the still intact inner layer, from segment to segment, pointed processes which Graber calls "interpolated mid-gut-epithelium anlagen." They grow laterally and segmentally from the middle strand. Therefore in these insects the mid-gut epithelium arises from the inner layer from more than two points of origin.

In *Carausius morosus*, according to Leuzinger (1926), yolk cells are set free from the median line of the ental surface of the embryonic rudiment, cells that connect with each other by pseudopod-like processes to form a reticulated sheet between the rudiment and the yolk. This sheet is the yolk-cell membrane, or lamella, and is interpreted by Leuzinger as the primary entoderm. From the mesal margins of the segmented inner layer mesodermal cells are liberated which pass by way of pseudopod-like plasma bridges into the yolk cell membrane along the median longitudinal line, a position from which they migrate laterally, and replace the original yolk cells of the membrane, crowding them into the yolk where they undergo degeneration. Although the replacement cells are regarded by Leuzinger as mesodermic, the membrane itself, after substitution, is designated by him as the secondary entoderm. Thomas (1936) states that the definitive digestive epithelium originates from mesenteron rudiments located at the tips of the stomodaeal and proctodaeal invaginations in *Carausius*, but both Hammerschmidt (1910) and Leuzinger and Wiesmann (1926) expressly deny this.

Nelsen (1934) states that in *Melanoplus differentialis* the mid-gut rudiment is derived from the inner layer associated with the blind ends of the stomodaeum and proctodaeum, although he does not deny the possibility of ectodermal material migrating inward with the entoderm. The mid-gut epithelium thus develops from anterior and posterior rudiments.

Stuart (1935), in his study of this species, arrived at a different conclusion regarding the origin of the mid-gut. He maintains that shortly before hatching of the nymph the yolk cells move peripherally to form a temporary lining upon the inner surface of the mesodermic components of the mid-gut. About the time the insect hatches, each yolk-cell nucleus divides into a dozen or more smaller nuclei, which Stuart designates as the presumptive mid-gut epithelial nuclei. Each appropriates a portion of the yolk-cell cytoplasm and then becomes a definitive mid-gut epithelial cell. In *Forficula* the mid-gut epithelium is formed from a median dorsal ribbon with forked end growing out from the stomodaeum and another one from the proctodaeum. They are called "ectodermic" by Heymons (1895), but Strindberg (1915) maintains that the mid-gut ribbons in *Forficula* arise from entodermic rudiments.

NEUROPTEROIDS

Strindberg (1913) states that in the termite *Eutermes rotundiceps* the inner layer is composed of an outer sheet of mesoderm and a thin inner sheet of entoderm which are readily distinguished from each other by their nuclear structure. After the formation of the coelomic sacs both mesoderm and entoderm are interrupted along the median line. Imme-

diately after blastokinesis the inner margins of the two longitudinal entodermal bands approach each other and then fuse below the yolk. The lateral edges then grow dorsad until the yolk is enclosed. Yolk nuclei which have increased in number become attached to the inner side of the entoderm wall and there apparently form a thick cellular layer of cubical cells which is retained during embryonic life. A similar layer is found in the stone fly (*Pteronarcys*) and also in *Periplaneta*, although in the latter it degenerates early. Entad of the yolk-cell layer in *Eutermes* is still another extremely thin layer which appears to represent the much extended limiting membranes of stomodaeum and proctodaeum which have pushed far into the lumen of the mid-gut.

Tschuproff (1903) has described the development of the mid-gut epithelium in the Odonata. According to her the two extremities of the mid-gut are derived from the stomodaeum and proctodaeum, and the middle section develops from the yolk cells. When yolk segmentation starts, the yolk nuclei form the nuclei of the spherules. Some of the nuclei take no part in yolk segmentation but remain distributed in the yolk, are smaller, and divide mitotically. These are the definitive epithelial cells of the middle section of mid-gut. A lumen is formed in later embryonic life by the arranging of the yolk spherules against the mesodermic layer of the mid-gut. The definitive mid-gut epithelial cells noted above, which were distributed till now between the yolk spherules, migrate to the periphery of the yolk and against the muscle layer, where they undergo mitotic division. During early postembryonic life these cells give rise to crypts or nests of cells from which the mid-gut is formed, increasing in number, while the yolk spherules gradually are consumed. This concept of mid-gut formation has been modified by recent investigations by the junior author (see Chap. XIV).

In the stone fly (*Pteronarcys proteus*), Miller (1939) found that the definitive mid-gut epithelium arises solely from a posterior mesenteron rudiment which is composed of cells that at first form the circumferential walls of the terminal part of the proctodaeum, hence presumably ectodermic. The cells of this rudiment spread forward over the yolk side of the entamnion (ental membrane) and increase mitotically, without the formation of proliferating ribbons, until they enclose the entire yolk as a squamous epithelium. A cellular membrane which probably originated from the yolk cells lies entad of the mid-gut epithelium as described by Strindberg for *Eutermes*.

COPEOGNATHA, HETEROPTERA, HOMOPTERA

Fernando (1934) derives the definitive mid-gut epithelium in the psocid *Archipsocus fernandi* from entodermal cells that wander from the anterior and posterior mesenteron rudiments into the central nutritive

mass. From here these cells migrate outward, arranging themselves in a layer outside the nutritive mass and thus forming the mid-gut epithelium. That which remains of the bipolar rudiments later disintegrates after a curious history as described in Part II.

In the head louse (*Pediculus*) and in the biting lice (*Lipecurus baculus*, *Gyropus ovalis*) the mid-gut epithelium develops from bipolar mesenteron rudiments. This is the case also in the bugs *Pyrrhocoris apterus* and *Rhodnius prolixus*. In the summer eggs of the aphid genera *Rhopalosiphum* and *Aphis*, Hirschler (1912) found that anterior and posterior mesenteron rudiments gave rise to a small entodermal strand of few cells without lumen which formed between the ends of the stomodaeum and proctodaeum but later are crowded out by these invaginations. Thus the entoderm is restricted to form a suspensorium, the definitive mid-gut therefore being wholly ectoderm. The yolk cells take no part in the formation of the mid-gut. The anterior and posterior rudiments Hirschler called the "secondary entoderm." No ribbons are formed in this process. This type of development resembles that found in the isopod crustaceans *Porcellio* and *Armadillidium* as described by Goodrich (1939).

Shinji (1919) states that in the coccids *Pseudococcus mcdanieli*, *Lecaniodiaspis pruinosa*, and *Icerya purchasi* the mid-gut arises from rudiments consisting of the entodermal cells situated at the posterior end of the embryo, growing in as two parallel layers extending cephalad from the caudal extremity, where the three germ layers arise. The cells then multiply rapidly and form a coiled tube which pushes forward until its anterior end meets the tip of the stomodaeum.

NEUROPTERA AND TRICHOPTERA

The mesenteron rudiments in the alder fly (*Sialis lutaria*), according to Strindberg (1915), develop at the extremities of the inner layer. From each rudiment two sheets of entodermal cells arise, one on each side, which grow in length and width to enclose the yolk thus forming the mid-gut epithelium.

Tichomirowa (1890) states that in *Chrysopa*, another member of the order Neuroptera, yolk cells give rise to the mid-gut epithelium. This work requires confirmation.

Patten (1884) has described a somewhat similar type of development for the caddis fly (*Neophylax concinnus*). In this species cells do not remain in the yolk while the blastoderm is forming, but later some migrate back from the blastoderm during the formation of the embryonic envelopes. These amoeboid cells with large nuclei, which are gradually distributed through all parts of the yolk, were called by Patten "yolk," or "entoderm," cells. They arise from any point in the blastoderm by

delamination, and this process may continue even after a part of the blastoderm has been converted into the ventral plate. Before the splanchnic mesoderm has completely separated the yolk from the body cavity on the ventral side, some yolk cells migrate into the body cavity where they arrange themselves irregularly along the sides of the body wall. At first the cells are arranged singly and indefinitely along the outer wall of the body, but later, increasing in numbers, they become arranged in distinct groups. These yolk cells (entoderm) are both more distinct and more numerous in the posterior part of the yolk sac; the epithelial lining of the stomach probably is formed first in the neighborhood of the proctodaeum and then extends forward to the stomodaeum. It is certain that the yolk cells (entoderm) do not form a continuous sac until some time after the formation of the mesodermic musculature of the yolk sac.

LEPIDOPTERA

Leaving out of account statements of the mid-gut epithelium derivation from the yolk cells in the Lepidoptera, recent researches seem to indicate that the epithelium may arise from independent bipolar mesenteron rudiments, or it may apparently arise from cells that lie in the blind tips of stomodaeum and proctodaeum. In *Pieris* Eastham (1927) found that the entoderm is formed in anterior and posterior rudiments which develop in the positions of future mouth and anus and therefore belongs to type I of Nusbaum and Fulinski (1909). Sehl (1931) and Drummond (1936) apparently found a similar condition in *Ephestia kühniella*, the entodermal rudiments each developing the usual pair of ribbons, from which the mid-gut epithelium is produced. Bipolar entoderm rudiments have likewise been described for *Catocala nupta* by Hirschler (1906) and for the tusser moth (*Antheraea pernyi*) by Saito (1937). Schwangert (1904) working with *Endromis* and *Zygaena* found an anterior mesenteron rudiment which developed similarly to that of *Pieris* but owing to the complex flexures of the embryo did not find the posterior counterpart.

On the other hand, in *Lasiocampa* (Schwartz, 1899), *Bombyx mori* (Toyama, 1902), *Diacrisia virginica* (Johannsen, 1929), *Diacrisia virginica*, *D. latipennis*, *Estigmene acraea*, *E. congrua*, and *Isia isabella* (Richards, 1932) the mid-gut epithelial ribbons develop from cells lying in the blind ends of the stomodaeal and proctodaeal invaginations. Johannsen (1929) interprets the cells from which the mid-gut originates in *Diacrisia* as latent entoderm, or "dormant," cells in the terminology of Nusbaum and Fulinski (1909) under type VII (see page 72 of text). Schwartz and Toyama, following Heymons' interpretation, regard the mid-gut epithelium in the moths studied by them as derivatives of the

ectoderm. Richards' study of five species of Arctiidae belonging to three genera concludes that

. . . either the mid-gut, despite its final similarity within individual orders of insects, may arise in some cases as an entodermal derivative and in other cases as an ectodermal derivative; or else we must look upon the determination of the mid-gut as a purely physiological process; to borrow Driesch's terminology, "as a function of the position within the whole." . . . the latter interpretation seems much superior to the former in the light of the great diversity shown by closely related insects, and from the standpoint of modern views of developmental processes in general.

COLEOPTERA

In the Coleoptera, development of the mid-gut epithelium from the entoderm as well as from the ectoderm has been described. The following table separates the members of the order according to the supposed origin of the epithelium:

1. Mid-gut epithelium an entoderm derivative: *Doryphora* (*Leptinotarsa*) *decemlineata* (Wheeler, 1889), *Donacia crassipes* (Hirschler, 1909), *Euryope terminalis* and *Corynodes pusis* (Paterson, 1932, 1936), *Tribolium confusum* (Hodson, 1934), *Meloe proscarabaeus* (Nusbaum, 1888), and *Calandra callosa* (Wray, 1937).
2. Mid-gut epithelium an ectoderm derivative: *Chrysomela hyperici* (Strindberg, 1913); *Chrysomela menthastri*, *Clystra laeviuscula*, *Gastrophysa raphani*, *Lina populi* and *L. tremulae*, *Agelastica alni* (Lécaillon, 1898b); *Tenebrio molitor* (Saling, 1907); *Meloe violaceus* (Czerski, 1904); *Hydrophilus* sp. (Deegener, 1900); *Calandra oryzae* (Mansour, 1927).

In *Donacia crassipes* and *Meloe proscarabaeus*, listed in the first group, the mid-gut epithelium is said to arise from a middle entodermal strand as well as from the paired ribbons of the bipolar rudiments. In *Euryope* and *Corynodes*, the species studied by Paterson, also in the first group, the epithelium is built up solely from a middle entoderm strand. *Bruchus quadrimaculatus* (Brauer, 1925) might be placed in either division.

Calandra oryzae, a species in the second group, has been studied by Mansour (1927) and by Tiegs and Murray (1938). The latter do not commit themselves as to which germ layer gives rise to the mid-gut epithelium except to say that it is not entodermal. Mansour (1927) from his study of this species concludes that the entodermal cells of insects are budded off into the yolk from the walls of the ventral groove or from thickenings in the blastodermal wall; further, that in *Calandra oryzae* and most Pterygota the entodermal cells do not give rise to any larval or invaginal structures but that the mid-gut epithelium is derived from the inner ends of the stomodaeum and proctodaeum and is therefore of ectodermal origin.

An examination of the foregoing tabulation reveals that the families Chrysomelidae, Tenebrionidae, Meloidae, and Curculionidae, as well as

the genera *Calandra* and *Meloe*, are represented in both groups and that *Hydrophilus* alone is unrepresented in the first. From this, one cannot escape the conclusion that whatever may be the germ layer from which the mid-gut is derived, it is the same for both groups and that the different opinions expressed by the writers as to the derivation of the mid-gut in the Coleoptera is merely a matter of interpretation.

Hoffmann (1914) showed that in the strepsipteron *Xenos bohlsi* a "primary mid-gut" is formed by three yolk cells which he compares to the annelidan macromeres. The definitive mid-gut epithelium develops from a process arising at the blind end of the stomodaeum. From this process a pair of lateroventral ectodermal ribbons develop which broaden and lengthen to form the epithelium that encloses the yolk. At the blind end of the proctodaeum a small marginal proliferation occurs to which the epithelium from the stomodaeum connects. Noskiewicz and Poluszynski (1928) describe a similar development for *Stylops*. In this insect, proliferating cells at the blind end of the stomodaeum push in under and over the yolk until the epithelial wall is formed. Thus in this group a primary provisional epithelium derived from yolk cells is followed by a definitive mid-gut epithelium made up of ectodermal cells.

SIPHONAPTERA AND DIPTERA

Except for superficial differences the development of the fleas *Ctenocephalides felis*, *Nosopsyllus fasciatus*, and *Hystrihopsylla dippiei* studied by Kessel (1939) is quite similar. The mesenteron rudiments in their embryos originate from near the anterior and posterior extremities of that portion of the blastoderm forming the ventral plate, making their initial appearance before the formation of the inner layer is evident. Each rudiment gives rise to two lateroventral entodermic ribbons from which the mid-gut epithelium is derived. The very few earlier papers relating to the embryology of the flea make little or no mention of mid-gut development.

Among the nemocerous Diptera *Simulium pictipes* studied by Gambrell (1933) and *Sciara coprophila* studied by Butt (1934) exhibit a similar type of development in which the bipolar mesenteron rudiments give rise to paired entoderm ribbons as described above for the fleas. In *Chironomus*, on the other hand, Hasper (1911) states that rudiments from which the mid-gut epithelium is derived appear to arise from the tips of the stomodaeal and proctodaeal invaginations and their cells do not distinctly differ in appearance from the ectodermal cells though sharply distinct from the mesoderm. From each of these rudiments the usual pair of ribbons form that later develop into the mid-gut epithelium. Ritter's account (1890) of the development of the mid-gut of *Chironomus* is not convincing. Another nemocerous species in which the mid-gut

epithelium is said to be derived from the ectoderm is *Miastor metraloas*, a cecidomyiid whose paedogenetic development has been described by Kahle (1908).

Kowalewsky (1886), Graber (1889), Escherich (1900), Noack (1901), and others who have studied the development of the Muscoidea are generally agreed that the mid-gut epithelium arises from an anterior and a posterior mesenteron rudiment which are distinctly separated from the middle plate and each of which gives rise to a pair of entoderm ribbons that develop into the epithelial layer. The species concerned are *Musca (Calliphora) vomitoria* and *M. erythrocephala*, *Lucilia caesar*, *L. sylvarum (illustris)*, and *Phormia regina*. Voeltzkow (1889), however, on the basis of his study on *C. vomitoria* states that lateral proliferations on the blind ends of the stomodaeum and proctodaeum that result in the usual pair of ribbons from which the epithelium is formed are ectodermal.

In the sheep tick (*Melophagus ovinus*), one of the Hippoboscidae, Pratt (1900) found that the first indication of the mid-gut rudiment is a proliferation of cells at the inner end of the proctodaeum. This extends forward, in the form of a single layer of epithelium, along the dorsal surface of the yolk past the stomodaeal invagination and also around the sides of the yolk toward the ventral side of the egg. It appears that most if not all of the mid-gut epithelium comes from the posterior end. If the stomodaeum takes any part in the formation, it seems that it must be only the fusing of the tip of the stomodaeal invagination with the sheet of epithelium that has come from the proctodaeum. The epithelium is regarded by Pratt as an ectodermal derivative.

HYMENOPTERA

Little is known of the embryology of the suborder Chalastogastra. Graber (1890) says that in the barberry sawfly (*Hylotoma berberidis*) entoderm rudiments are present at the blind ends of the stomodaeal and proctodaeal invaginations, each of which develops the usual pair of ribbons that later form the mid-gut epithelium.

Writers who have dealt with the development of the aculeate Hymenoptera are in the main agreed that the mid-gut epithelium is derived from bipolar mesenteron rudiments. Nelson (1915) found that in the honeybee the two rudiments are transferred to the dorsal side of the poles of the egg by the lengthening of the embryo. From the caudal margin of the anterior rudiment and from the cephalic end of the posterior rudiment a thin tongue-like dorsal process, or ribbon, is sent out, these fusing when they meet at the anterior third of the egg. This dorsal strip then widens, growing around the yolk, the lateral margins uniting on the midventral line a short time before hatching. The floor of the stomodaeum, although chiefly ectodermal, is formed also by cells

belonging to the anterior rudiment. Nelson, unwilling to commit himself as to the germ layer's giving rise to the two rudiments, uses for them the term "mesenteron." From Strindberg's account (1914) it appears that the development of the mid-gut in *Vespa vulgaris* is similar.

In the leaf-cutter bee (*Trachusa serratulae*) Strindberg (1914a) found that the mesenteron rudiments each give rise to a broad ribbon on each side, which grow toward each other until they meet and then broaden, first meeting dorsally and then ventrally.

As described by Carrière and Bürger (1897) the mesenteron of the mason bee (*Chalicodoma muraria*) is derived, independent of the mesoderm, from two proliferating areas of blastoderm, one at each end of the germ band, corresponding to the future location of the stomodaeum and proctodaeum, respectively. From each a pair of ribbons arises, as in *Trachusa*. The mesenteron rudiments here differ from those in the honeybee in that the latter are directly continuous with the ventral plate, whereas in *Chalicodoma* they are independent, as they are in the bluebottle fly (*Calliphora*).

The development of the mid-gut epithelium in ants of the genera *Myrmica*, *Formica*, and *Camponotus* differs from that of the other aculeates in that it arises as a sheet of cells that forms on the inner surface of the inner layer, designated by Strindberg (1913a) as "definitive entoderm." Anterior and posterior mesenteron rudiments are not present. Tanquary's account (1913) of the development in *Camponotus herculeanus* and *Myrmica scabrinodis* differs in that the epithelium is said to arise on the dorsal side of the yolk augmented by cells from the posterior end of the germ band as well as scattered cells of the inner layer of peripheral protoplasm.

The literature list given at the end of Chap. VI is applicable to this chapter also.

CHAPTER VIII

ECTODERMAL DERIVATIVES

THE INTEGUMENT

In the later embryonic stages the epidermis secretes at its surface a cuticula which in some cases may be thin and delicate but in other cases, as in the head capsule of many holometabolous insects, may be relatively thick. This cuticula may be shed soon after hatching except in holometabolous forms. Hairs, setae, and scales arise from large epidermal cells (trichogens) which in some instances are very conspicuous. In the late embryo of certain moths (*Diacrisia* and others) they are by far the largest of the ectodermal cells, extending far below the level of the neighboring cells. The setae, scales, and other structures are formed on the attenuated, slender, cytoplasmic processes of the trichogens. Other epidermal cells, either singly or in groups, sometimes deeply invaginated below the surface of the body wall, form the epidermal glands of various sorts.

THE ENDOSKELETON

A system of apodemes—inward invaginations in the form of rods or ridges—is developed for the attachment of muscles and for the support of internal parts. In the head these processes consist of an anterior and a posterior pair of arms which are connected by the transverse bar-like body, together forming the tentorium. The anterior tubular invagination develops on the inner side and somewhat in front of the mandible or behind and near the base of the antenna. The posterior invagination arises behind the base of the first or between the bases of the first and second maxillae. From the posterior arm a transverse branch arises which meets its fellow from the opposite side, thus forming the body of the tentorium. In some insects a pair of dorsal arms are formed as diverticula of the anterior pair. According to Strindberg (1913*b*) two transverse connecting bars instead of one represent the body of the tentorium in *Eutermes*. Epidermal invaginations constitute the apodemes for the attachment of muscles and of the appendages in the head, thorax, and abdomen.

GLANDS

Antennal, mandibular, maxillary, and labial glands all arise as sac-like invaginations of the epidermis. Antennal glands have been described for the roach which presumably originate during embryonic life. Man-

dibular glands occur in many insects; in the case of their appearance in the larvae they begin their development in the embryo. In *Calandra callosa*, Wray (1937) found the invaginations on the inner side of the rudiments of the mandibles and somewhat between them and the base of the maxillae. Maxillary glands occur in some apterygotes as well as among pterygotes. In *Forficula*, Heymons (1895a) described an epidermal invagination at the base of each of the first maxillae from which an irregular system of sacs and tubes develop. They seem to correspond to certain of the head glands of the Chilopoda. The glands that are usually most highly developed in insects are those of the labium. Since they are of variable function, the term "labial glands" is preferable to the usual designation of salivary glands. In the embryo they originate as paired invaginations of the ectoderm just behind the bases of the rudiments of the second maxillary appendages. As development progresses, the two orifices unite medially on the venter of the second maxillary segment. At the same time, the appendages of this segment also come together and unite on the middle line. The median orifice of the glands having moved forward, it comes to lie in the ventral wall of the head anterior to the base of the labium. Although typically these glands are simple or convoluted tubes, they may be branched or provided with terminal vesicles. In the larvae of the Lepidoptera, Trichoptera, Coleoptera, Siphonaptera, and most nemocerous Diptera and Hymenoptera the glands are silk-producing structures.

In the moth *Diacrisia* on the second maxillary segment, in addition to the invagination for the silk gland, there is an outer pair which will form the so-called "hypostigmatic gland" of Toyama (1902). This gland develops as an invagination near the root of the second maxilla (labium). In the embryo at the time the mid-gut rudiment appears, the invaginated cells are larger than those adjacent, the entire invagination spherical in form and gland-like in appearance, with the mouth of the invagination directed cephalad. Shortly afterward the structure has migrated mesad and slightly caudad, coming to lie in front of the prothoracic legs, and has lost its attachment with the surface. Later, its cells can no longer be distinguished from those of the adjacent mesoderm. Nelson (1915) suggests that this structure may represent the corpora allata, though we are inclined to believe that it is the ventral cervical gland, embryonic in this species but highly developed in the caterpillars of *Schizura concinna*, *Dicranura vinula*, and other notodontids though vestigial in many other lepidopterous larvae. In the silkworm (Toyama, 1902) it persists in the larva as branched glands in the first thoracic segment. It may be homologous to the first thoracic Gilson's gland of the Trichoptera.

Heymons (1895a) has called attention to two bodies found in *Forficula* and *Gryllus*, which he named "ganglia allata." Later (1899) he dis-

covered these structures, which he considered part of the stomatogastric nervous system, in the walking stick. Carrière and Bürger (1898) found that in the mason bee (*Chalicodoma*) the ganglia allata have the same origin as in *Forficula*, but these bodies do not later fuse to form a median body as they do in *Forficula*. They remain attached to the ventrolateral margins of the antennal coelomic sacs, as in the honeybee (Nelson, 1915). These authors expressed a doubt whether or not these bodies consisted of nerve tissue. They have since been termed the *corpora allata* and probably are glandular in function. According to Roonwal (1937) the corpora allata of *Locusta migratoria* arise in the stage soon after blastokinesis as a pair of invaginations of the lateral body wall of the embryo on either side of the intersegmental region between the mandibular and the first maxillary segments. The blind ends of these invaginations are directed medio-dorsally. They soon become rounded and are eventually severed from the outer ectoderm. Later this structure moves dorsally and posteriorly and comes to lie on the stomodaeum. Its connection with the stomatogastric nervous system is purely secondary. Its thin mesodermal coat arises from the antennary coelom, as in *Carausius* (Wiesmann), and not from the mandibular coelom, as Heymons claims for *Carausius* (*Bacillus rosi*).

The *corpora allata* are ectodermal in origin according to most writers who have investigated the matter. In *Forficula* (Heymons, 1895) they appear to arise as ingrowths from the anterior angle of the maxilla, a pair of rounded bodies becoming constricted off and eventually finding their way to the antennary coelomic sacs, to the lower ends of which they attach themselves. This appears to be the case also in *Chalicodoma* (Carrière and Bürger, 1898), *Formica* (Strindberg, 1913), *Apis* (Nelson, 1915), and *Pieris* (Eastham, 1930a). In *Silpha* (Smreczynski, 1932) and *Coryodes* (Paterson, 1935) they likewise originate near the base of the mandibular segment or between this and the maxillary segment. In *Calandra oryzae*, however, according to Tiegs and Murray (1938) they arise from the antennary segment; and though they form in intimate association with the *tentorium*, they are, as far as could be ascertained, purely a differentiation of the ventral wall of the antennary coelomic sac; i.e., they are mesodermal.

THE TRACHEAL SYSTEM

The first evidence of the formation of the tracheal system is the appearance of small ectodermal pits, or invaginations, along the sides of the body. These pits deepen into tubes which subsequently fork out into branches. The branches subdivide repeatedly, becoming finer and finer. In the beginning each invagination acquires at its blind end two diverticula of which the posterior one fuses with the anterior of the next

succeeding one, thus forming the two longitudinal trunks. Lateral branches then arise near the junction of the longitudinal trunks with the main spiracular trunk, to form the transverse commissures. Finer branches from the transverse trunks then pass to the alimentary canal and other viscera. In the more primitive insects the longitudinal trunks may be lacking, the tracheae being arranged in segmental clusters the tubules of which may be branched or unbranched. Though most chilopods and the majority of insects have branched tracheae, most diplopods have tracheae consisting of segmental clusters of unbranched tubules.

The apertures at the surface represent the spiracles. The time of the appearance as well as the position and number of spiracular openings varies with the group to which the animal belongs. Tracheal pits are lacking on the head in most cases. Nelson (1915) states that in the embryo of the honeybee tracheal invaginations are found on the anterior part of the second maxillary segment above the bases of the labial rudiments. These give rise to four diverticula which produce the anterior ends of the main tracheal trunks, including the anterior tracheal commissure or loop, and also produce the trachea supplying the head. Later the orifice to the exterior closes, leaving no trace of its existence. In some *Collembola* cervical spiracles are present which may be persisting examples of the second maxillary spiracles, although tracheae are wholly lacking in most members of this group. The presence of tracheal invaginations in the second maxillary segment is an obstacle to the view held by certain writers that the tentorial and some other invaginations of the head are homologous to the tracheae.

Prothoracic spiracles may be present in embryos in some cases, but they usually disappear before hatching. Postembryonic stages of all insects except *Diplura* do not possess more than two pairs of thoracic spiracles. In the embryo of *Lepidoptera* as well as in some other orders, the spiracles are formed on the meso- and metathorax, but in the later embryos the first pair moves forward onto the prothorax whereas the second pair becomes reduced and nonfunctional. A similar condition is found in some *Diptera*. Strindberg (1913b) found that tracheal invaginations in *Isoptera* are formed in the first two thoracic segments but not in the third. In some species of *Diplura* there are three or four pairs of spiracles on the thorax.

Eight pairs of spiracles usually develop on the abdomen; but Chodkowsky (1891) claims to have found a ninth pair in *Blattella*, and Heymons (1897) found in the embryo of *Lepisma* the rudiment of a tenth. Nine pairs of embryonic spiracles have been reported in *Hydrophilus* and *Donacia*. In *Chironomus* (*str. sens*) the tracheal system does not develop until the late larval stages and then only in the thorax. On the other hand, in the subfamily *Orthocladinae* of the same family, the

longitudinal trunks are well developed in the embryo, although the system is a closed one. Tiegs and Murray (1938) found a total of 10 pairs of spiracles in the embryo of *Calandra oryzae* of which all but the first and last pairs later close, a condition normally occurring in the embryos of the muscoidean flies also.

OENOCYTES

Certain large cells found in the body cavities of the pterygote insects and usually associated with the fat cells are the oenocytes. They originate segmentally in the embryo from the ectoderm at points just behind the spiracles of the first eight segments. They have also been observed in the thorax into which they have probably been crowded from the first abdominal segment. Heymons (1895a) has also found them in the eleventh abdominal segment of *Forficula* where they appear after blastokinesis at the time those in the spiracle-bearing segments have come to lie in the fat body as globular groups of cells. Roonwal (1937) states that in the late embryos of *Locusta migratoria* the oenocytes extend into the ninth and tenth abdominal segments, probably as extensions from the eighth. In these last two segments they do not exhibit a metameric arrangement.

THE NERVOUS SYSTEM

The Ventral Nerve Cord.—Shortly after the separation of the inner layer from the ectoderm a median longitudinal neural groove usually forms on the ventral side of the embryo. To the right and the left of this groove, cells, characterized by their larger size, have differentiated from the ectoderm and, sinking below the surface, form the neuroblasts, or primary nerve cells. The presence of these rows of neuroblasts in the form of lateral cords is marked on the embryo by longitudinal thickenings, or neural ridges, one on each side of the groove. The neural ridges thus each have a layer of smaller epidermal (dermatogene) cells outwardly and a longitudinal strip of neuroblasts, a few cells in width, inwardly (Fig. 45). Active division of the neuroblasts now takes place; the repeated division of the neuroblasts in about the same plane results in a column of daughter cells more or less perpendicular to the ectoderm (Fig. 46). These daughter cells are the future ganglion cells. Between the neural ridges, dorsad of the neural groove, a median cord is formed by invagination of the cells and, like the lateral cords, is separated as a neurogene strip from the dermatogene layer. In each interganglionic region, or perhaps in the posterior part of the ganglionic region of the median cord (*mst*), one or more neuroblasts develop from which smaller daughter cells arise as in the lateral cords. When the germ band undergoes segmentation, the lateral nerve cords likewise are metamerically

constricted into segmental divisions. At the time the yolk recedes from the germ band, nerve fibers begin to develop on the ganglion cells that lie on the dorsal side of the lateral cords. These ganglion cells lengthen, the inner ends of each being produced into a plasmic process which elongates and probably in most cases branches, interlacing with the plasmic

FIG. 45.—*Xiphidium*. Cross section of an early stage. (*am*) Base of amnion. (*ect*) Dermatogene ectoderm. (*neur*) Neuroblast. (*neur**g*) Neural groove. (From Wheeler.)

fibers of other cells to form the neuropile, or Punctsubstanz, of the ganglia (Fig. 46, *neurp*). This process of fiber formation proceeds from before backward. Meanwhile the cells that lie more deeply in the lateral cords also develop similar nerve fibers.

The metameric division of the lateral nerve cords at the time of body segmentation results in the formation of nodes of ganglionic cells on each cord.

FIG. 46.—Section of ventral nerve cord. (*dt*) Daughter cells. (*ect*) Ectoderm. (*mst*) Median nerve strand. (*neur*) Neuroblast. (*neur**g*) Neural groove. (*neurp*) Neuropile. (From Wheeler.)

The nodes of one cord, fusing with the corresponding nodes of the other, form the ganglia of the central nervous system. Certain nerve cells in the ganglionic node of each cord send fibers across to the corresponding node on the other side, giving rise to two commissures. Other cells likewise send fibers into the preceding and following nodes to form the pair of connectives. Fibers in the commissures are in some insects also in part derived from the ganglion cells of the median cord. Although there is a close fusion of the ganglionic nodes to produce the defini-

tive ganglia of the ventral nerve cord, thereby obliterating external evidence of the commissures, the connectives usually remain separated, retaining their individuality. For a time the neurogene cells remain in close contact with the dermatogene (ectoderm) cells, but later, as development proceeds, the nerve cord separates from the adjacent tissue and becomes surrounded by the neurilemma, a very thin covering which here

and there has a nucleus. Investigators are not in agreement as to the origin of the neurilemma.

The development of the ventral nerve cord is similar in insects generally, including the apterygotes. Some minor differences to be noted are the following: in *Xiphidium* Wheeler (1893) found four neuroblasts in transverse section of each lateral cord; in *Locusta* (Roonwal, 1937) there are four or, rarely, five; in *Euryope* (Paterson, 1932) there are three in the abdomen but four in the thorax; in *Forficula* (Heymons, 1895a) the number is variable; in *Pieris* (Eastham, 1930a) there are three at first. Baden states that in *Melanoplus* the neuroblasts increase transversely from one to three in the narrower interganglionic portions of each lateral cord and from three to five in the intraganglionic portions. In this form also in each ganglia caudally, from the mandibular to the tenth abdominal inclusive, a typical neuroblast is differentiated. On the other hand, in *Xiphidium*, *Locusta*, and *Apis* one median cord neuroblast differentiates in each intersegmental region, and in *Forficula* (Heymons, 1895a) there are several in this region. Nerve cells (the daughter cells) are formed by unequal division of the large neuroblasts in *Gryllotalpa* (Korotneff), *Xiphidium* (Wheeler), *Forficula* (Heymons) *Eutermes* (Strindberg), *Pieris* (Eastham), and *Musca* (Escherich), but subsequent division does not occur. Subsequent division of daughter cells occurs in *Doryphora* (Wheeler), *Apis* (Nelson), *Calandra oryzae* (Tiegs and Murray), and other embryos.

The total number of nerve ganglia belonging to the ventral chain in insects differs with the species. During the earlier stages in the development in many of the more primitive insects as well as some of the more highly specialized ones, there are 17, one for each segment from the mandibular to the eleventh abdominal inclusive. This is true for *Lepisma*, *Gryllotalpa*, *Periplaneta*, *Gryllus*, *Locusta*, *Leptinotarsa*, *Donacia*, *Calandra*, *Hylotoma*, *Chalicodoma*, *Apis*, and others. In numerous insects, however, the seventeenth, *i.e.*, the eleventh abdominal, is lacking. As development proceeds there is a tendency for some of the ganglia, especially the two or three posterior ones, to fuse. Extreme consolidation (cephalization) occurs in the larvae of the higher Diptera, scarabaeid beetles, etc., in which the entire ventral nerve cord, including the subesophageal ganglion, is consolidated into a single elongate mass lying in the anterior part of the thorax.

The development of the *median cord* (Fig. 46, *mst*), unlike that of the lateral cords, appears to differ considerably in different insects. That it is derived from the median strip of ventral ectoderm, forming the roof of the neural groove, seems to be certain. The ultimate fate of this strip is less uniform. Nelson (1915) states that all investigators of the subject—with the exception of Wheeler—agree with Hatschek that the

intraganglionic sections of the median cord contribute at least in large part, if not all, the median portions of the ganglia, including the transverse commissures. To this opinion, however, Wheeler (1893) took exception. This investigator, although admitting that in *Xiphidium* the intersegmental regions of the median cord, the progeny of the median neuroblasts, are taken up into the central portions of the ganglia to form functional ganglion cells, did not believe that the median cord cells in the intrasegmental regions became ganglion cells but maintained that they are used up in the formation of the neurilemma. In the same group to which *Xiphidium* belongs, the Orthoptera, Heymons (1895a) found that the anterior and central median gangliomeres were actually formed by the median cord, much as in other insects. With this exception, the differences in regard to the development of the median cord center principally about the fate of the intersegmental (interganglionic) sections. Hatschek (1877) stated that these remained in connection with the ectoderm and contributed nothing to the ganglia.

Graber (1890) found that in *Melolontha* the median cord was separated from the epidermis throughout its entire length but that the intersegmental portions later divide transversely, each half being then drawn cephalad and caudad, respectively, into the ganglia adjoining. In *Hydrophilus*, *Lina*, and *Stenobothrus*, on the other hand, the median cord was not observed to separate from the epidermis. In *Lepisma* Heymons (1897) found that a continuous median cord was set free from the epidermis and present in the newly hatched insect, extending the entire length of the ventral cord. The findings of Carrière and Bürger (1898) with reference to the fate of the median cord essentially confirm those of Heymons (1895a) except that the former do not prove that the roof of the neural groove becomes split up into a dermatogenic and neurogenic layer. According to their observations all its cell material goes to form the median cord, and its covering is produced by the union of the epidermis formed in the region of the primitive swellings. The complete sundering of the median cord from the epidermis takes place about the end of development. Its intraganglionic portions separate from the epidermis at about the same time as the delamination of the lateral cords; its interganglionic portions remain in connection with it, after the nerve fibres have become evident in the lateral cords. In *Musca* Escherich (1902) found that a continuous cord is separated from the ectoderm. Within the limits of the ganglion, in this insect, the median cord contributes the median portions, as in other insects; in the interganglionic regions it presents swellings of considerable size, one being situated directly caudad of each ganglion. From each swelling, near its posterior end, a pair of lateral processes regarded as nerves are given off which extend to the neighborhood of the stigmata. This indicates that

in some insects the median cord may form a more or less continuous median nerve and is perhaps a primitive condition.

In *Apis* Nelson (1915) found that the origin and fate of the median cord conforms to Grassi's account and is also similar to that of *Hydrophilus* (Graber, 1890). In both forms the median cord is united with the epidermis in the interganglionic region but is independent in the region of the ganglion. Here, nevertheless, these interganglionic spaces are, up to the time of hatching, of very slight extent in an anteroposterior direction, and the anterior and posterior commissures are close together, so that it is obvious that the anterior and posterior median gangliomeres, as well as the central gangliomeres, are formed from the median cord. The term "gangliomere" as used here designates each of the ganglionic regions of a ventral nerve ganglion—two lateral regions and one in front, one between, and one behind the commissures.

Tiegs and Murray (1938) state that the median cord in *Calandra oryzae* contributes to the formation of the ganglia; its intersegmental neuroblasts attach themselves to the posterior wall of the ganglia, and the intrasegmental (neurogenic) cells form the roof of the completed ganglia, their axons contributing to the formation of the transverse commissures and longitudinal connectives. Baden (1936, 1937), on the other hand, maintains that in *Melanoplus differentialis* all the fibers of the commissures seem to come from the ganglion cells alone and that the median cord does not differentiate into any tissue but apparently degenerates and is absorbed.

The origin of the *neurilemma* in insects has been the subject of controversy. Nusbaum (1883) maintained that this tissue in the roach owes its origin to cells derived from median cord elements that grow around the ventral nerve cord as a cellular membrane. A second membrane from the same source gives rise to an inner neurilemma between the cortical cellular layer and the neuropile strands in each half of the ventral cord. Since Nusbaum (1886) held that the median cord is derived from the provisional yolk-cell membrane which he stated is of yolk-cell origin, the neurilemma itself must therefore be a yolk-cell derivative.

In *Forficula* Heymons (1895a) found that at the time when the neuroblasts begin to disappear the surface of the ganglion is being formed by occasional cells in the ganglion which flatten and spread out to form the outer neurilemma. The inner neurilemma is formed in a similar manner—flattened cells that spread out between the cortical layer and the neuropile. Heymons concluded that the outer neurilemma apparently arises from cells that during the segregation of the neuroblasts from the dermatogenous layer were separated off from the latter. Wheeler (1893) believed that it arose from the intraganglionic sections of the median cord in *Xiphidium*.

In an allied species, *Locusta migratoria*, Roonwal (1937) found that the neurilemma probably arises from the outlying ganglion cells themselves. Baden (1936), however, says that in *Melanoplus differentialis* "the external neurilemma can be traced to the coelom sacs and therefore . . . seems to be mesodermal." As for an inner neurilemma, Baden questions its existence. Eastham (1930a) states that this tissue in *Pieris rapae* probably arises from the outermost products of the neuroblasts. Such neurilemma-forming cells become elongate and insinuate themselves between the epidermis and the nerve cord and also pass above the ganglia underneath the yolk. Tiegs and Murray (1938) assert that in the weevil, *Calandra oryzae*, certain intersegmental median cord cells give rise to the neurilemma. In the honeybee Nelson (1915) admits two possibilities: Either the neurilemma is formed as Heymons suggests for *Forficula*; or, what is more probable, they are merely transformed ganglion cells.

Finally, Strindberg (1913) expresses the view that in *Eutermes* the neurilemma is first formed on the dorsal side of the ganglia and is derived from ganglion cells that unite to form the tissue. Later it is also formed on the ventral side; but since this occurs after the ganglia have separated from the epidermis, it is good evidence that the neurilemma is not formed from the dermatogene layer. The inner neurilemma in this insect develops after the neuropile is wholly covered by the cortical layer of ganglion cells and therefore without doubt owes its origin to the ganglion cells immediately adjacent to the neuropile. Whether or not the cells of the median cord aid in the formation of the outer neurilemma Strindberg did not determine. The development in *Formica* and *Chrysomela* according to Strindberg takes place essentially as in *Eutermes*.

The Stomatogastric System.—Heider (1889) was the first to observe that the frontal ganglion and the recurrent nerve originated in an invagination of the dorsal wall of the stomodaeum, an observation later verified by Graber, Carrière, and Wheeler. Later still, Heymons (1895a) in his studies on the development of the Dermaptera and Orthoptera found that the stomatogastric system in general is derived from three medially lying invaginations in the dorsal wall of the stomodaeum. From these invaginations there arise, first, the frontal ganglion, then an unpaired mass behind the first, which is the common rudiment of the paired ventricular ganglia. These three rudiments then become connected with one another by the recurrent nerve. Roonwal's account (1937) of the development of this system in *Locusta migratoria* agrees in all essential details with that in other Orthoptera and Dermaptera (Heymons, 1895a; Wiesmann, 1926). The only difference is that in all the forms whose development has been studied previously, the ventricular ganglion is unpaired; in *Locusta*, as in all Saltatoria, it is paired. In *Eutermes*

(Strindberg, 1913) it is unpaired, but just before hatching it assumes a lateral position.

The stomatogastric system in *Pieris*, according to Eastham (1930a), arises at two points in the dorsal wall of the stomodaeum in a median line. The stomatogastric (stomogastric) nerve is produced by extension of nerve cells from the two ganglia along the roof of the stomodaeum.

Among the Hymenoptera we have brief accounts of the development of the system in *Chalicodoma* (Carrière and Bürger), in *Formica* (Strindberg), and in *Apis* (Nelson). In the first both the unpaired occipital ganglion and the paired pharyngeal ganglia are feebly developed; in the second Strindberg failed to find either of these; in *Apis* the second stomodaeal invagination gives rise to the frontal ganglion, whereas from the third the pharyngeal ganglia originate.

Relatively few references to the development of the stomatogastric system in the Coleoptera are to be found. The frontal ganglion with its recurrent nerve, according to Heider (1889), originates from a furrow-like invagination of the stomodaeum, but Wheeler (1893) refers only to the frontal ganglion. Strindberg states that the frontal ganglion as well as the pharyngeal ganglia in *Chrysomela* arises in the usual manner. The occipital ganglia in this insect seem to be represented by two small cell masses located at the morphological anterior margin of the syncerebrum. In *Calandra oryzae* the stomatogastric system arises as three invaginations, according to Tiegs and Murray; Wray notes but one in *C. callosa*.

The Brain.—The composite suprastomodaeal nerve mass constitutes what is generally known as the "brain," or "archicerebrum." At the anterior end of the young arthropod embryo is a large cephalic lobe the neural elements of which may include an anterior median ganglionic rudiment and several pairs of lateral rudiments which soon unite to form the brain. In the cephalic lobe there is no external mark of segmentation. The definitive brain of the mandibulate arthropods consists of an anterior bilobed part, including the protocerebrum, the deutocerebrum, and the tritocerebrum. The first innervates the eyes; the second, the antennae; and the third, the second antennae when these are present. The protocerebrum and the deutocerebrum are always united above the stomodaeum, but the tritocerebral lobes, being derived from the postoral somites of the second antennae, are connected by a postoral commissure. In many cases the dorsal lobes are developed in the embryo from a single pair of generative centers in the ectoderm just as are the corresponding lobes of the brain in the Onychophora and in some of the Annelida; but since the annelid brain probably originated from a number of prostomial ganglionic centers corresponding to the sensory organs of the prostomium, one may reasonably expect the primitive arthropod brain to show a

similar origin. This is well demonstrated in the development of the brain of *Scolopendra*.

Among the higher arthropods, as Snodgrass (1938) has emphasized, the more primitive stages in the brain development are generally not shown in embryonic recapitulation, for the protodeutocerebral centers are usually proliferated from the ectoderm as a unified ganglionic cell mass, as in the Onychophora and in many of the Annelida. It is observed

FIG. 47.—Orthopteran. Cross section of head through protocerebrum. (am) Amnion. (ant) Primitive antennal coelom. (ect) Ectoderm. (eye) Eye plate. (gglc) Ganglion cells. (lob) First, second, and third brain lobes. (lr) Labrum. (mes) Mesoderm. (neur) Neuroblast. (opg) Optic ganglion. (stom) Stomodaeum.

by Baden (1936) and Roonwal (1937), however, that the brain of the grasshopper (*Melanoplus*, *Locusta*) is formed from five pairs of ganglionic centers, three of which give rise to the protocerebrum and the optic lobes, and the other two to the deutocerebrum and tritocerebrum, respectively. The brain develops in the cephalic lobes at about the same time that the ventral chain is formed. A thickening of the ectoderm is followed by the development of neuroblasts, thus establishing the neurogene and dermatogene layers. Three pairs of ectodermal thickenings can be distinguished, corresponding to the protocerebrum, deutocerebrum, and tritocerebrum. These are all connected with each other. The protocerebrum, by far the largest, is nearly as wide as the head lobes. Laterad and contiguous to it is an epidermal layer. Likewise on the median line undifferentiated ectodermal tissue is present (Fig. 48C). The deutocerebrum is represented by two thickenings, one on each side of the stomodaeum. Behind the mouth opening is the tritocerebrum in the form of two swellings separated by still undifferentiated ectoderm. As in the ventral nerve cord, the neuroblasts give rise to columns of daughter cells which develop into ganglion cells. The protocerebrum now becomes transversely

divided into three pairs of lobes (Fig. 47, *lob*), the most lateral being the optic lobes (*lob.1*). In the two median pairs of lobes the neuroblasts (*neur*) have the typical form of those found in the ventral nerve cords, the daughter cells (*gglc*) forming the usual ganglion cells whose interlacing fibers represent the neuropile. The neuroblasts degenerate after the formation of the daughter cells. Before the optic lobe is fully differ-

FIG. 48.—*Mantis religiosa*. Cross section of head through developing eye. A-C, successive stages. (*am*) Amnion. (*ect*) Ectoderm. (*ect. d*) Dermatogene cells. (*ect. ggl*) Gangliogene cells. (*eye*) Eye plate (disk). (*lob*) First, second, and third protocerebral lobes. (*mes*) Mesoderm. (From Viallanes.)

entiated and is still a part of the epidermis, the region may be distinguished by its rather large cells. Although it is generally conceded that no neuroblasts take part in the formation of optic lobes in insects, these larger cells in *Mantis* are termed "gangliogenes" (*i.e.*, neuroblasts) by Viallanes (1891). Heymons, in his account of the development of *Forficula*, states that they correspond to neuroblasts, not that they are neuroblasts.

The development of compound eyes in the paurometabolous insects is brought about by the formation of an eye disk (*eye*) in the ectodermal

layer lying next to the optic lobe (Fig. 48). Viallanes (1891) has shown that in *Mantis* the optic lobe (*lob 1*) frees itself entirely from the eye disk (Fig. 49), the postretinal fibers (*fb*) later growing out centrifugally from the lobe to join the disk. The same condition was found in *Xiphidium* by Wheeler (1893) and in *Locusta* by Roonwal (1937). On the other hand, that the optic lobe in some cases is only partially separated from the eye disk, a strand of nerve tissue which later forms the postretinal fibers remaining between them, has been demonstrated in *Forficula* by Heymons (1895a) and in *Eutermes* by Strindberg (1913). In *Locusta*

FIG. 49.—*Mantis religiosa*. Cross section of head through developing eye of an old embryo. (*deut*) Deutocerebral lobe. (*eye*) Eye plate (disk). (*fb*) Postretinal fibers. (*ggl. p*) External ganglionic plate. (*lob 3*) Third protocerebral lobe. (*stom*) Stomodaeum. (From Viallanes.)

the nuclei of the optic ganglion near its dorsal edge elongate and send out nerve fibers which go to the retinulae of the eye disk forming the post-retinal fibers. Roonwal found no evidence of fibers being sent out from the retinulae. In the Orthoptera, Dermaptera, and *Eutermes* the optic lobe is formed by delamination; in the Coleoptera and Hymenoptera, by invagination. In the latter class the optic disk, or plate, is formed from ectoderm lying outside and immediately surrounding that destined to form the optic lobes; *i.e.*, the optic lobe and the optic plate develop from separate areas of the ectoderm, whereas in the first class they are formed from the same area.

The origin of the fibers that constitute the commissures of the brain appears to differ among insects. Those in the commissures of the protocerebral lobes are said to arise from the lobes in *Locusta*, *Mantis*, *Xiphid-*

ium, *Eutermes*, and *Calandra* (oryzae) and from the epidermis between the lobes by the conversion of some of its cells into neurogene tissue in *Forficula*, *Pieris*, *Corynodes*, and *Apis*. The tritocerebral commissures are said to come from the lobes in *Locusta* and *Pieris* and from the epidermis between the lobes similar to the ventral cord in *Eutermes*, *Forficula*, *Calandra* (*callosa*), *Chalicodoma*, and *Apis*. In general, no commissure is formed between the lobes of the deutocerebrum, or at least it is not distinct from that of the protocerebrum. *Mantis*, according to Viallanes (1891), offers an exception. The neurilemma of the brain in *Mantis* develops from some surface ganglion cells. Certain points in which the development of the brain of the honeybee differs from the Orthoptera and Dermaptera are as follows: The cells of the second generation from the neuroblasts, instead of the first, form the definitive nerve cells; the three subdivisions of the protocerebrum are not at first plainly marked off from one another and are never separated by hypodermal ingrowths; finally, the optic lobes are formed by a deep invagination of the neurogenic ectoderm, as in the formation of the simple eyes in the beetles *Acilius* and *Hydrophilus* and in *Vespa*.

In its fundamental features the development of the nervous system in the collembolan genus *Isotoma*, including the formation of brain lobes, the development of the ganglion cells from neuroblasts, etc., is identical with that of pterygote insects. Although Philiptschenko (1912) failed to find it in *Isotoma*, Claypole (1898) notes the presence of an anlage of a sympathetic system in *Anurida*. Nor, in general, does the development of the nervous system in the chilopod *Scolopendra* differ greatly from that of the insects.

The Sense Organs.—Integumental sense organs distributed over various parts of the surface of the body, usually simple in structure consisting of but few cells, are modified epidermal cells functioning as tactile, gustatory, or olfactory structures. In their simpler form they consist of either single cells or a group of a few cells which distally develop a sensory style and inwardly are provided with a nerve. In late embryonic life certain ectodermal cells become conspicuous by reason of their greater size or other modifications, *e.g.*, the tactile bristles of caterpillars which develop in the embryo from trichogen cells. These cells (Fig. 311, *trich*) in some cases have become so enlarged as to extend far below the level of the adjacent epidermis. The olfactory and gustatory cells on the antennae and palpi more often develop in groups which may be found within pits. The auditory and static organs, located on the body or legs which are still more complex in structure, are likewise of ectodermal origin. But little is known of their embryonic development.

Most complicated are the visual organs. The compound eyes and the ocelli of paurometabolous and hemimetabolous insects and the simple eyes (adaptive ocelli) of the holometabolous insects are at least in part

formed during embryonic life. Among the few accounts we have of their embryonic development are those of Marshall (1935) and of Patten (1887, 1888).

Of the paurometabolous insects we have Marshall's account of the development of the eye in the female black scale (*Saissetia oleae*), an example of an extremely simple form.

The eye rudiment in this insect is a small disk-like area which is formed by a few epidermal cells, slightly larger than those adjacent, on each side of the head of the young embryo. This eye disk invaginates rapidly (Fig. 50A); the margin around the mouth of the invagination

FIG. 50.—*Saissetia oleae*. A, invagination of eye rudiment. B, eye vesicle after completed invagination, before development of lens. C, transverse section of eye. (ep) Epidermis. (l) Lens. (rt) Retina. (ves) Vesicle. (vit) Vitreous body. (From Marshall.)

comes close together until, its cells meeting, a vesicle is finally cut off from the rest of the epidermis in the form of a somewhat spheroidal body lying between the ectodermal surface and the lateral margin of the brain (Fig. 50B). The cuticular layer that covers the embryo external to the invaginated vesicle first becomes smooth and convex, loses its small folds, then forms a bulging disk. At first there are epidermal cells lying beneath the lens, but later they move away from the center toward the margins. The cells forming the vesicle consist of two groups: the outer smaller group of about four cells which form the corneagen cells and the vitreous body; and the inner larger group which gives rise to the retina. The vitreous body then secretes a lens which during embryonic life becomes biconvex (Fig. 50C). Pigment granules form in the retinal cells, which are yellow at first but finally become dark brown or black. It is doubtful if any rhabdoms occur in the ocelli of this insect. No change occurs in the structure of the ocellus during the first instar. At

the end of the first instar the cuticular lens first formed is shed with the body cuticula, the new one secreted by the vitreous body taking its place. Entad of the vitreous body, between it and the retina, a large irregularly shaped crystalline body is formed, possibly by the cells of the vitreous body. The definitive ocellus thus consists of four parts: the lens secreted by the vitreous body, the vitreous body, the crystalline body possibly also secreted by the vitreous body, and the retina. The retinal cells are at first nucleated, but the nuclei probably pass to the nerve fibers each one of which is connected to a retinal cell. Ocelli developed in the embryo remain unchanged throughout the insect's life.

Precursors of the compound eyes of the holometabolous insects are the simple eyes (stemmata, adaptive ocelli) of the larvae. Patten's

FIG. 51.—Adaptive ocellus of *Acilius* larva. (ep) Epidermis. (l) Rudiment of lens. (n) Nerve. (ret) Retina. (rod) Cuticular rods. (sl) Slit in retina. (vit) Vitreous body. (x) Retinal cells bordering slit. (From Patten.)

account of the development of these structures in the embryo of *Acilius*, one of the water beetles, has shown that the later developmental stages occur after hatching. In the larva of *Acilius* there are three pairs of stemmata on each side which differ more or less from one another in structure. The ventral stemma of the third pair, being somewhat typical, will be described here. The rudiment, which at an early stage reminds one of the cup-shaped eyes of some mollusks, consists of a simple pit-like depression in a thickened part of the epidermis (Fig. 51A). The deep cells which form the wall of the pit and which are continuous with the thinner adjacent body wall (ep) are arranged in a single layer. The distal end of the elongate cells have a cuticular margin (rod) and at their inner ends give off nerve fibers which unite to form the optic nerve (n). Before this stage is reached the larva has emerged from the egg. Subsequently, the eye pit closes toward the exterior (Fig. 51B), the epidermal marginal parts pushing toward the center of the pit until they meet. Thus an eye cup is formed which is two-layered, the central part of the outer layer (vit) becoming the lenticular layer or vitreous body, while the

peripheral parts become the pigmented iris. The cuticula covering the rudiment gradually thickens in a chitinous lens (*l*). The deeper cup-like layer forms the retina (*ret*) from the cuticular margins of which the optic rods are derived. A slit (*sl*) traversing the retina is bordered by the horizontally placed rods of the large retinal cells (*x*) which lie next to it. Not until later larval stages do the stemmata become fully developed. Whether the ocelli of insects originate by an invagination or by delamination of the epidermis has been the subject of some controversy. Both of the examples given above are of the first type. It is true also for *Hydrophilus* (Fig. 52) (Patten, 1887) as well as for *Periplaneta*, but in

FIG. 52.—*Hydrophilus*. Ocellus of newly hatched larva. (*ep*) Epidermis. (*l*) Lens. (*mid*) Middle layer of optic rudiment. (*ret*) Retinal layer. (*vit*) Vitreous body (lentigen layer). (From Patten.)

the latter case development of the ocelli is wholly postembryonic. The eye in *Julus* likewise develops postembryonically.

Imaginal Disks.—Although not usually thought of in connection with the embryonic development, it should not be overlooked that some imaginal histoblasts become obvious before the holometabolous insect hatches from the egg. Pratt (1900) has shown that three imaginal disks are already present in the head of *Melophagus ovinus* in the embryo in the form of simple ectodermic thickenings. One of these lies in front of the stomodaeum, and a pair behind it. In the embryo, likewise, three pairs of dorsal and three pairs of ventral imaginal disks appear. The latter give rise to the imaginal legs; of the former the first two pairs remain rudimentary; the last pair forms the imaginal halteres. Likewise also during embryonic life, but only shortly before the rupture of the egg envelopes, two pairs of disks appear in front of the anus for the formation of external genitalia. Imaginal disks for the formation of the abdominal hypodermis and of the internal imaginal organs first become recognizable as such during postembryonic life.

The ectodermal origin of the fore- and hind-gut has already been discussed in the preceding chapter in connection with the development of the alimentary canal.

References

Baden (1936, 1937), Butt (1934*b*), Carrière (1886), Cholodkowsky (1891), Escherich (1902), Graber (1891), Hottes (1928), Janet (1899), Marshall (1935), Nelsen (1931), Nelson (1914), Nusbaum (1883), Patten (1887, 1888), Pflugfelder (1937), Pratt (1897), Riley (1904), Rittershaus (1925), Schaefer (1938), Sen (1939), Sikes and Wigglesworth (1931), Snodgrass (1936), Stiles (1939), Tichomiroff (1879), Toth (1935*a*), Viallanes (1891), Wheeler (1891*a*, 1893*b*).

See also list of general works cited in Chap. II.

CHAPTER IX

MESODERMAL DERIVATIVES

COELOMIC SACS

The mesoderm at gastrulation in the Eutracheata, as has already been described, may develop in several ways: (1) by proliferation and immigration from the median longitudinal area of the ventral blastoderm (Fig. 41F)—this type is found among Apterygota, and Orthoptera (*Gryllotalpa*, *Blattella*, *Periplaneta*, *Gryllus*, etc.)—(2) by growth of the lateral ectodermal plates over the median plate as in *Gasteroidea*, *Pieris*, *Diacrisia*, *Sphinx*, *Apis* (Figs. 41D,E), etc.; (3) by invagination of a median strip of the ventral blastoderm which forms a tube, as in some Coleoptera, Diptera (Fig. 329A), *Chalicodoma*, etc. This tube flattens down, obliterating the lumen, and thus forms a solid multilayered mesodermal mass. Following gastrulation, segmentation takes place whereby the mesoderm is divided up into masses corresponding to the future body segments. The transverse segmentation is most distinct in the more primitive pterygotes, especially the Orthoptera. Later a cavity, or lacuna, appears in the right and left halves of most of the mesodermic segmental rudiments. The lacunae are the coelomic cavities; the mesodermic tissue surrounding them, the coelomic sacs (Figs. 151, *coel*).

In most instances the cavities of the coelom are formed secondarily by clefts that appear in the solid mesoderm. This is the case in *Gryllus*, *Gryllotalpa*, *Carausius*, *Hydrophilus*, *Callandra (oryzae)*, *Siphonaptera*, *Formica*, etc. In other insects the lateral margin of each mesodermic segmental rudiment is folded over, thus enclosing a cavity. This type is found in *Locusta*, *Blattella*, *Eutermes*, *Sialis*, *Gyropus*, *Diacrisia*, *Callandra (callosa)*, etc.

In the case where the mesoderm is formed as a flattened tube, the cleft, or schizocoele, does not necessarily develop in the place originally occupied by the lumen of the tube. However, Carrière (1890) found that in *Chalicodoma* the clefts arise precisely where the lumen of the mesoderm tube was located. Heider (1889) described a similar condition in *Hydrophilus*. If this type of development really occurs in these forms, we have examples, apparently rare among insects, where the coelomic cavities may develop directly into the definitive haemocoel. Here the cavities (enterocoele) of the primitive segments represent paired diverticula of the archenteron (Figs. 39, 40). The inner wall

of the sacs would form the splanchnic mesoderm; the outer wall, the somatic mesoderm; and the cavities themselves, the definitive body cavity. Escherich (1900) in his study of the muscoidean flies placed special emphasis on the similarity of development between that of the muscids and of the chaetognath *Sagitta* wherein an enterocoele is formed. Wiesmann (1926), however, points out that among the Orthoptera (as exemplified by *Carausius*), the Myriapoda, and the Onychophora, the coelomic cavities form as clefts in the mesoderm and not as diverticula of the archenteron. The fact that enterocoelic development does not occur among the more primitive insects should prevent one from laying too great a phylogenetic significance on its sporadic occurrence in the muscids and other highly specialized insects.

Coelomic cavities are lacking in the Diptera so far as known and also in the lepidopteran genus *Ephestia* (Sehl, 1931). They are also lacking in some head segments and in the last abdominal segment of other insects and related arthropods. The coelomic cavity appears to be lacking in the labrum of insects except in *Carausius* and *Locusta* among the Orthoptera. A pair of preantennal coelomic cavities is present in *Carausius* as well as in the chilopod *Scolopendra*, in both cases correlated with the presence of rudimentary preantennal appendages. Hirschler (1909) states that the beetle *Donacia* lacks antennal coelomic cavities, the only exception recorded among those insects where sacs normally occur, but Tiegs and Murray (1938) venture the opinion that the pre-mandibular sac (second antennal) which Hirschler claims to have found in this insect is in reality the antennal sac. Second antennal coelomic cavities, either lacking or rudimentary in most insects, are present in *Locusta* (Roonwal, 1937). They are also recorded for the chrysomelid beetle *Euryope* by Paterson (1932) and for *Calandra callosa* by Wray (1937). The mandibular and the first maxillary coelomic cavities are either absent or rudimentary in the beetles *Donacia crassipes*, *Calandra oryzae*, *Hydrophilus*, and some others. In insects generally, however, except the Diptera, coelomic cavities occur in the gnathal and thoracic as well as the abdominal segments except the last one or two.

Among the lower Eutracheata (chilopods, Orthoptera, etc.) coelomic sacs are very strongly developed, extending into the rudiments of the appendages (Fig. 152, *lb*) and in some cases appearing more or less triangular in cross section or even with large diverticula, as in *Scolopendra*, *Locusta*, and *Carausius*. According to Korotneff (1885) in *Gryllotalpa*, shortly before segmentation appears, the mesoderm divides along the median longitudinal line into two strips. A cleft then appears in each strip, thus forming two flattened tubes. Later when segmentation occurs, each tube is constricted at each intersegmental region, forming the coelomic sacs. Ayers (1884) reported a similar condition in *Oecanthus*.

Graber, Heider, Heymons, and other workers, on the other hand, maintain that only among some highly specialized insects as in the honeybee is a tubular coelom developed without first forming the metameric coelomic sacs. The coelomic sacs in the Orthoptera are closely correlated with the formation of the appendages, the first anlage of the sac being fully restricted to the cavity in the appendage. Formed in a similar manner are the sacs in *Sialis lutaria* and *Eutermes* (Strindberg, 1915*d*, 1913*b*) and in the Ephemeridae (Heymons, 1896*a*).

Among more highly specialized insects the coelomic cavity does not extend into the appendages. The cavity of the appendages is filled with a compact, irregularly disposed mesoderm in the Coleoptera, the coelomic cavities being restricted to the laterodorsal part of the germ band. Similarly in the Lepidoptera, Homoptera, Heteroptera, and Hymenoptera the coelomic cavities are restricted to the sides of the germ band. In *Pieris* according to Eastham (1930) they are circular in cross section but fusiform longitudinally, extending far into the intersegmental region, only just failing to be continuous from one segment to another. In the honeybee no coelomic sacs, as such, are distinguishable, the two flattened mesodermal tubes on each side being continuous longitudinally according to Nelson. Their splanchnic and somatic layers are well defined and thick. In *Chalicodoma*, the mason bee, the thin-walled portion of the mesoderm is distinctly divided into segmentally arranged sacs, which however are so flattened dorsoventrally that visceral and somatic layers are in contact with one another, except at their lateral margins. In the margins in a longitudinal direction the sacs run into each other, forming a tube.

Still more modified are the conditions among certain Homoptera (aphids) and Heteroptera (*Pyrrhocoris*) where Will (1889) and Seidel (1924) found that the sacs remain open toward the yolk. *Lepisma*, among the Apterygota, according to Heymons (1897*b*), has large sacs formed in a manner similar to those of the Orthoptera.

THE MUSCULATURE

The muscles of the body and appendages arise from the somatic layer of the mesoderm; those of the alimentary canal, from the splanchnic layer. In some forms of the eutracheates such as the Orthoptera in which the coelomic cavities are large, the muscles develop as tubular evaginations which constrict from the somatic layer and sooner or later lose their lumen. With the more highly specialized insects, on the other hand, in which the coelomic cavities are narrow and poorly developed or are wholly lacking, the muscles arise from isolated migrant cells from the coelomic wall as in *Forficula*, or they develop directly from the parts

of the mesenchyme-like mesodermal tissue in the Coleoptera, Diptera, Hymenoptera, etc. With the exception of the ventral longitudinals most body muscles arise from the lateral coelomic walls. The ventral longitudinal muscles arise where the somatic and splanchnic layers meet. These muscles are the first to develop, and in the Orthoptera according to Heymons (1895*b*) they develop from special coelomic diverticula. From this part the intersegmental transverse muscles also arise. Muscles of the appendages develop from the coelomic sacs which have entered the ectodermal evaginations in the Orthoptera and related forms, in the higher groups from the undifferentiated mesoderm.

The musculature of the stomodaeum and proctodaeum in general arises from mesoderm that has entered the primary head and anal segments independent of the coelomic sacs. The mid-gut muscles, as has already been stated, form from the splanchnic mesoderm—in *Forficula* by delamination, in *Blattella* by migration of cells.

The history of the derivatives of the coelomic sacs of the various segments has been studied in a number of insects, especially among the Orthoptera by Heymons (1895*b*) and more recently in *Carausius morosus* by Wiesmann (1926) and in *Locusta migratoria* by Roonwal (1937) as well as more briefly in other insects by several writers. From the labral sacs the labral musculature arises in *Locusta*. In *Carausius* the pre-antennal sac gives rise to the stomodaeal musculature. The relatively large antennal sacs in *Locusta* give rise not only to the anterior and posterior portions of the cephalic aorta but also to the investment of the pharyngeal ganglion and of the corpora allata, the fatty tissue, and the antennary muscles. A part of the mandibular sacs of *Locusta* and *Carausius* gives rise to mandibular muscles; an anterior pouch of these sacs forms the antennary muscles in *Carausius*. Maxillary muscles in the Orthoptera generally develop from the first maxillary sacs. In *Carausius* the median diverticulum of the second maxillary sac forms the longitudinal ventral muscle strand; the ventral diverticulum, the maxillary muscles; and the laterodorsal diverticulum, the longitudinal muscles, the tortion muscles of the head, splanchnic muscles, and some nonmuscle tissue.

The growth of all coelomic sacs from the second maxillary to the sac in the caudal extremity of the body ends in the breaking down of the partition walls that separate the coelomic cavities, with the result that a continuous mesodermic tube is formed on each side of the body in the chilopods (Heymons, 1901), Orthoptera (Heymons, 1895*a*, *et al.*), Coleoptera (Lécaillon, 1898), Hymenoptera, and other forms. The diversity among the different orders of the Eutracheata of muscle development in thorax and abdomen is so great that generalizations will not be attempted here. Abstracts of the detailed accounts of the development

in *Scolopendra* by Heymons (1901), of *Carausius* by Wiesmann (1926), of *Locusta* by Roonwal (1937) and others are given in Part II.

DEFINITIVE BODY CAVITY

After the degeneration of the walls that separate the longitudinal row of coelomic sacs, converting them into a coelomic tube, one on each side of the median line, some investigators state that an open communication is established between the coelomic lumen and the epineural sinus. This is said to occur in *Hydrophilus*, *Blatta*, *Forficula*, and some chrysomelids, among them *Donacia*, according to Heider (1889), Cholodkowsky (1891), Heymons (1895*b*), Lécaillon (1898), and Hirschler (1909), respectively. In *Carausius* Wiesmann (1926) found that an actual opening between the coelomic cavities and the epineural sinus did not arise but that, instead, thinning of the inner coelomic wall occurred which would permit diffusion of the haemolymph. The coelomic cavities are little by little obliterated by the conversion of the walls of the sacs into a fat body and muscle anlagen excepting only that the ampullae of the ducts of the reproductive organs are retained. Indirectly, then the coelomic sacs contribute to the formation of the body cavity of *Carausius* as in other insects. The definitive body cavity, therefore, may be considered a mixocoel. Paterson (1932) likewise states that in the chrysomelid beetle, *Euryope*, there is no direct communication between the coelomic cavities and the epineural sinus, which is in agreement with McBride's (1914) observation that an opening between coelomic cavity and epineural sinus is contrary to what is known of the later development of the coelom in other animals. All authors, however, agree that the first anlage of the definitive body cavity is formed independently of the coelomic cavities. Some writers state that the epineural sinus is formed by the retraction of the yolk from the inner surface of the germ band. This occurs in *Carausius* after the formation of the first anlage of the mid-gut epithelium, and Wiesmann (1926) is inclined to the opinion that this is what takes place in other animals also. On the other hand, Roonwal (1937) says that in all insects except the Acrididae it is at first not delimited dorsally, *i.e.*, on the side of the yolk, by a membrane. In the Acrididae this sinus at the time of its first appearance is bound dorsally by a membrane as in *Stenobothrus* and *Locusta*. It should be mentioned that a similar membrane has recently been described by Schölzel (1937) as occurring in the head louse and by Miller (1939) in the stone fly.

During the growth of the embryo of *Locusta* the epineural sinus becomes enlarged and forms the definitive body cavity which is then the haemocoel. With the conversion of the walls of the dorsal coelomic pouches into fat, etc., the coelomic cavities also merge into the epineural

sinus. Philpitschenko (1912) failed to find an epineural sinus in the collembolan *Isotoma*, but it may have been overlooked.

CIRCULATORY SYSTEM

The development of the dorsal blood vessel, or heart, and of the dorsal diaphragm, except for minor differences, is similar for all the Eutracheata. The origin of these structures was first observed by Korotneff (1883, 1885) in the mole cricket (*Gryllotalpa vulgaris*), and since then the further investigations of Grassi (1884), Heider (1889), Wheeler (1889), Heymons (1895a), and others working with various insects have fully confirmed his findings. The cells that are to form the walls of the heart, known as "cardioblasts," are differentiated at the dorsal junction of the somatic and splanchnic mesoderm layers. As these layers grow dorsad, the cardioblasts, which first are recognizable by reason of their larger size, become, in certain orders at least, more or less crescent-shaped, their convex sides directed toward the ectoderm, the concave sides of the two rows facing each other (Fig. 21). When the horns of the crescents finally meet, a longitudinal, middorsal tube is formed, constituting the heart. The closure of the heart tube, in general, first takes place at the posterior end of the embryo, later in the neck region where the heart connects with the aorta. In *Donacia* Hirschler (1909) noted that the fusion of the cardioblasts first occurred on the ventral side at the posterior extremity of the embryo. At the anterior end in the region of the stomadaeum, on the other hand, the dorsal wall of the heart is completed first. In the genera *Donacia*, *Chrysomela*, and *Formica*, the cardioblasts are rounded and not crescentic at first. With some insects, before the two rows of cardioblasts meet, between the cardioblasts and the yolk there is a blood space filled with fluid. This space, especially large in the crickets and some acridids, is less well developed in *Forficula*, in Coleoptera, and in the roaches. In some cases pulsation has been observed in these blood sinuses. In *Locusta migratoria* Roonwal (1937) records the formation of a primary pair of lateral blood sinuses which are bounded dorsally by the provisional dorsal closure and ventrally by the somatic mesoderm and sometimes also by the ectoderm forming the lateral edges of the germ band. During blastokinesis, the provisional dorsal closure (ental membrane) breaks away from the edges of the germ band and curls upward to bound the yolk for some time. The amnion, which now forms the dorsal closure of the embryo, becomes joined to the provisional dorsal closure middorsally. Thus a second pair of lateral sinuses arises in place of the first one. They are bounded dorsally by the amnion, ventrally by the provisional dorsal closure (afterward by the splanchnic mesoderm), and laterally by the somatic mesoderm. The two lateral sinuses later fuse to form the common dorsal blood sinus, and

finally from the latter the definitive heart cavity arises by the fusion of the cardioblasts of either side.

The dorsolateral wall of the somatic mesoderm, reduced to a thin sheet as it grows dorsad, forms the dorsal diaphragm (pericardial septum). Shortly before emergence, fan-shaped bundles of muscle fibers appear in this septum attached at one end to the body wall and at the other to the ventral wall of the heart. In *Carausius* the diaphragm is originally laid down as a two-layered sheet.

The dorsal aorta is formed from the median walls of the antennal coelomic sacs and not from cardioblasts. Hirschler contends that in *Donacia* the aorta develops from the intercalary coelomic sacs. Paterson (1932) reports a similar condition in the chrysomelid *Euryope*. In *Silpha*, one of the carrion beetles, however, Smreczyński states that the aorta arises from the median walls of the antennal sacs, the suspensory ligaments being formed from the remaining parts of the sacs. Likewise in *Apis*, *Pieris*, *Forficula*, *Eutermes*, *Carausius*, and other Orthoptera the aorta originates from the antennal sacs, this appearing to be the normal method of formation. For an account of the development of the heart of the locust the reader is referred to Chap. XV.

BLOOD CELLS

Earlier writers have not been in agreement as to the mode of origin of the blood cells which have been variously described as arising from the yolk cells, from the cells of the serosa, from the walls of the heart, from undifferentiated mesoderm cells, from the subesophageal body, from the entoderm, and even from the ectoderm.

Hirschler (1909) states that the blood cells arise from the middle strand that lies between the two rows of coelomic sacs. In his opinion, however, the middle strand, whose cells in many insects aid in the formation of the mid-gut epithelium, is entodermic, and therefore so also are the blood cells. In *Isotoma* Philpitschenko (1912) likewise derives both blood cells and mid-gut epithelium from the middle strand. Leuzinger and Wiesmann (1926) state that the blood cells of *Carausius* come from a secondarily reconstructed middle strand which like the first middle strand also gives rise to mid-gut epithelial cells. They, however, regard the blood cells (haemocytes) as mesodermal or possibly intermediate between mesoderm and entoderm. In *Apis* the blood corpuscles are described by Nelson (1915) as large round cells approaching in size the oenocytes. Both nucleus and cytoplasm are pale, the latter being much vacuolated and frequently enclosing deeply stained granules. These cells, regarded as mesodermal, arise in the immediate vicinity of the midventral line and are to be found in the epineural sinus. With the disintegration of the subesophageal body in the silkworm embryo the

cells that are set free Toyama (1902) interprets as blood cells. Will (1888), Schwangart (1904), and Nusbaum and Fulinski (1906) as well as Hirschler regard the blood cells as entodermal. Recent workers, though, are generally agreed that the blood cells are mesodermal and for the most part arise from the midventral strand.

PERICARDIAL CELLS

The pericardial cells were first described by Wielowiejski (1883). They are associated with the fat body and, as the name indicates, found near the heart. They are readily distinguishable from the fat cells in the pericardial chamber. Heymons (1895a) found that in the Blattidae and Gryllidae they originate from the somatic layer of mesoderm. In *Forficula* they do not attain their characteristic appearance until post-embryonic life. In *Locusta*, according to Roonwal (1937), they first make their appearance in the embryo about a day after blastokinesis, arising from the somatic mesoderm abutting on the ventrolateral aspect of the heart. Wiesmann (1926) states that in the walking stick *Carausius* these cells migrate out as free cells from the pericardial septum, or diaphragm.

THE PARACARDIAL CELL STRAND

The term "paracardial cellular cord," or "cell strand," was proposed by Heymons (1895a) for a paired structure that he found in *Forficula* at the sides of the dorsal blood vessel in metameric arrangement between the wing muscles of the heart in the pericardial septum. The cells of this strand are conspicuous by reason of their size and pale color even before revolution. They arise in the center of the individual body segments from the dorsal parts of the coelomic sacs and retain their peculiar character throughout their entire embryonic development. Heymons points out the resemblance of this cell strand to the "guirland cell strand" described by Weismann (1864) which he discovered in the larvae of muscoidean flies. Kowalewsky (1886) called attention to the physiological equivalence between the guirland cell strand and the pericardial cells. Just as with the guirland strand so is the paracardial strand especially well developed in embryonic and larval life of *Forficula*; in adult life it has become less conspicuous. Histologically the cells of the paracardial strand and the pericardial cells in *Forficula* appear to be identical, and for this reason Heymons feels justified in considering the paracardial and the guirland cell strands as similar.

The paracardial cell strand is lacking in both the Blattidae and Gryllidae but present in *Chalicodoma* (Carrière and Bürger) and in the ants (Strindberg, 1913b). In the dorsal diaphragm (pericardial septum) of *Apis*, Nelson (1915) found pale lenticular cells whose size approximates

that of the fat cells. Since the cells in *Apis* have the same origin as the cells of the paracardial strand of *Forficula* and *Chalicodoma*, Nelson expresses the opinion that their homology can scarcely be open to question although they are not connected in a strand.

THE FAT BODY

In the body cavity of insects, cell masses, in some cases loosely held together, containing both fatty oil and proteid material constitute the fat body. It is derived from the mesoderm and found in the embryo occupying the haemocoel in greater or lesser amount. In *Locusta* (Roonwal, 1937) the bulk of the median and lateral walls of the dorsal section of the coelomic sacs from the second maxillary to the tenth abdominal segments, as well as the lateral wall of the dorsoanal pouch of the antennary coelom, forms fat; but the labral, mandibular, and first maxillary mesoderm sacs do not seem to share in this process. In *Carausius*, likewise, fat is not formed by the first two gnathal sacs. In *Calandra* the fat body, according to Tiegs (1938), occurs in two distinct parts: (1) a bulky visceral portion occupying most of the haemocoel and in later larvae almost obliterating it; (2) a comparatively inconspicuous parietal zone of smaller less vacuolated cells, lying just under the epidermis and external to the muscles. The main portion of the fat body is derived from the inferior wall of the coelomic sacs from the labial to the ninth abdominal segment. The parietal fat body arises independently of the visceral and seems to be derived from cells originating in the external walls of the coelomic sac.

Nelson (1915) states that in the honeybee, with the exception of those in the pericardial chamber, the fat cells are formed from that part of the visceral mesodermal layer which is not used up in the production of the enteric muscles. This peculiarity is also shared by the mason bee (*Chalicodoma*), so possibly it may be a condition prevailing among the aculeate Hymenoptera, although Strindberg (1913*b*) in his account of the development of several species of ants belonging to the genera *Formica* and *Camponotus* as well as of the termite, *Eutermes rotundiceps*, and the beetle, *Chrysomela hyperici*, makes the general statement that the fat body in these insects is derived from the somatic mesoderm, as Heymons has found to be the case among the Orthoptera. The fat body both in the haemocoel and in the pericardial chamber, then, seems to be derived, with few exceptions, from the somatic mesoderm in insects generally, including the apterygotes, as well as in the chilopods.

THE PHOTOGENIC ORGANS

There were, in general, two views as to the origin of the photogenic, or light-producing, organs of the fireflies, or Lampyridae. According to

one view they developed from the ectoderm; according to the other, they are related to the fat body and therefore mesodermal. The results of the work of Williams (1916) on both *Photuris pennsylvanicus* and *Photinus consanguineus* and of Hess (1922) on *Photuris pennsylvanicus* have demonstrated their origin from the mesoderm. Hess states that in the embryo of *Photuris* the first indication of the formation of the light organs is noticeable just as the embryo revolves from its backward-turned position and starts to coil up. At this time groups of fat cells migrate ventrally in the eighth segment and come to lie in the region of the future light organs. Soon after these cells become localized, they separate from the other fat cells and appear to have fewer and smaller fat globules. Three or four days later there is a differentiation into photogenic and reflector areas, the cells of the former being denser, less vacuolate, and with denser granulation than the latter. Light is produced before emergence of the larva. Williams' account deals mainly with the development of the organs of the adult.

THE SUBESOPHAGEAL BODY

The structure that Wheeler (1893a) designated as the "subesophageal body" (Fig. 310, *suboesb*) consists of a complex of unusually large cells which in the embryo is found in the tritocerebral segment. Although primarily an embryonic organ, it occurs in the nymphs of *Gryllus* and the Blattidae and in the adults of termites. The structure is now generally regarded as a derivative of the tritocerebral (premandibular) mesoderm, although Nusbaum and Fulinski (1906, 1909), Hirschler (1907), Schwangert (1904), and Wray (1937) considered it as developing from the anterior entodermal mass. It occurs in the embryos of the Orthoptera, Plecoptera (Miller, 1939), Isoptera (Strindberg, 1913b), Mallophaga (Strindberg, 1916a), Coleoptera (Wray, 1937; Tiegs and Murray, 1938), and Lepidoptera. In *Stenobothrus* (Graber, 1891) and *Locusta* (Roonwal, 1937) it arises from the mandibular segment. In *Calandra oryzae* according to Tiegs and Murray it is derived from the mesoderm but becomes secondarily part of the mid-gut wall and has the appearance of developing from the latter. This may account for the reports of an entodermal origin. The cells of the organ are characterized by their large size and their larger, paler nuclei. In most insects the organ degenerates before emergence of the larva. In the more generalized Orthoptera and Plecoptera it originates as a paired structure, but in the Lepidoptera it is either single or vaguely bilobed as in *Diacrisia*.

HEAD GLANDS IN THE APTERYGOTA

Head glands in the Apterygota as in the Pterygota are for the most part of ectodermic origin; only the paired tubular glands of *Campodea*,

Japyx, *Machilis*, *Lepisma*, and related genera and also of the Diplopoda offer an exception. They are derived from the mesoderm and in structure resemble nephridia. The first anlage of these mesodermic glands appears early in the second maxillary segment at the level of the ganglion as a vesicle with distinct epithelial walls. The efferent duct alone is of ectodermal origin. The tubular mesodermic glands are wanting in both the Chilopoda and the Pterygota.

The manner in which the anlage of the tubular head glands (Fig. 98, *hg*) develop and especially their derivation from the mesoderm substantiates the view of Philpitschenko (1912) that they are retained labial nephridia. They are therefore fully comparable to similarly retained nephridia of other arthropods and of *Peripatus*. They develop exclusively from mesoderm except for a portion of the duct which is ectodermal.

THE REPRODUCTIVE ORGANS

It is noteworthy that the anlagen of the internal parts of the reproductive organs in many instances are spread over a number of abdominal segments in insects and to a still greater extent in the chilopods. In the dorsal part of the splanchnic layer of the segments a genital ridge is developed laterally (Figs. 17, 18, *gr*) for the reception of the germ cells that have been differentiated at the caudal end of the egg and migrate forward as has previously been described. At first this ridge is formed in several segments—in some cases, as in *Pyrrhocoris*, in segments one to eight. So long as the primitive somites are still intact, the germ cells adhere to the genital ridges. While the germ cells continue to develop, the genital ridges of the somites of each side unite into a single longitudinal band of cells, one on each side. The development of the genital ridge into a gonad occurs when the germ cells that are distributed through a number of segments migrate forward and become enveloped by the cells of the mesodermal genital ridge of that region. The manner in which this consolidation of the germ cells and the development of the gonad around them is accomplished differs with the group to which the insect belongs. In any case the germ cells are fully covered by the mesodermal cells, the former giving rise to spermatozoa, or eggs, and nurse cells, the latter to the epithelial envelope. The account of Lautenslager (1932) of the development of the female gonads of *Solenobia triquetrella* (Psychidae) is in essential agreement with the observations of earlier writers on Orthoptera. The paired segmental groups of germ cells, lying in the fourth, fifth, and sixth abdominal segments, condense and unite on each side into a single group having the position of the definitive gonad in the fifth segment. Here each composite group of germ cells becomes enclosed in a layer of small mesodermal cells. The latter form a thin sheath

about the germ cells dorsally and laterally, but ventrally they form three thick cellular masses, which later give rise to the ovarian pedicles and the lateral ducts of the ovaries. According to Lautenschlager the follicle cells of the definitive egg tubes of *Solenobia* also take their origin from the cells of the mesodermal sheaths of the gonads.

In *Pyrhocoris apterus* Seidel (1924) found that the segmental groups of germ cells, formed at an early embryonic stage, become surrounded individually by mesoderm epithelium and remain thus, up to a relatively late period of development, as a series of distinctly separated gonadial rudiments segmentally distributed on each side of the body in somites two to eight of the abdomen. Later they all assemble in segments two and three, where those of each lateral group develop directly into the seven genital tubes of the adult organ. The lower tubular parts of the primary elements unite to form the lateral duct.

In the honeybee the genital ridges of the female at first extend along the splanchnic walls of the mesodermal tubes from the second to the seventh abdominal segments, inclusive. Later they become shorter and thicker and finally reach only from near the anterior end of the fourth abdominal segment into the anterior end of the seventh.

Beyond the region of the germ cells the genital ridges are continued posteriorly, but here they are much reduced in size and consist of simple cellular strands. These parts of the ridges will form the mesodermal parts of the lateral genital ducts. In many insects the primitive ducts of the female in embryonic and larval stages turn downward posteriorly and are attached to the ectoderm at the posterior end of the ventral wall of the seventh abdominal segment or at the intersternal membrane. The male ducts of the Orthoptera, as described by Wheeler and Heymons, extend into the tenth segment and are here similarly attached to the ectoderm.

The primary paired gonads of insects are segmentally arranged, and the continuous genital ridges later formed are secondary structures resulting from the fusion of the series of primary gonads on each side of the body. It seems scarcely probable, therefore, that the subsequent division of the genital ridges into a series of ovarian or testicular tubes can represent a primitive segmental structure of the reproductive organs, though in a few adult apterygote insects and in the embryo of *Pyrhocoris apterus* the tubes do coincide with the abdominal segments.

The early segregation of the germ cells in *Blattella* into groups within the dorsal parts of the intercoelomic septa, says Snodgrass, is highly suggestive of a similar arrangement of the germ cells in many adult Annelida in which the gonads are simple swellings of the dissepiments, retaining the germ cells beneath a thin mesodermal epithelium. In the annelids, however, the gonads may occur on almost any part of the

coelomic walls; but wherever they are formed, the germ cells are not long retained within them but are soon thrown out into the body cavity, where they mature.

FIG. 53.—Section through a coelomic sac of *Leptinotarsa*. (cbl) Cardioblasts. (coel) Coelom. (ect) Ectoderm. (g) Germarium of the gonad. (nc) Nerve cord. (sp) Spiracle. (splm) Splanchnopleure. (sus) Suspensorium. (x) ventral strand. (From Wheeler.)

dorsal plate and the ventral strand containing the germ cells is the germarium, or the region of the primitive ovary from which are formed the egg tubes of the definitive organ.

The development of the reproductive organs is, in general, the same in both male and female of insects having compound gonads. By a multiplication of the cells along the bases of the genital ridges each gonad in the female comes to be suspended from the splanchnopleure by a cellular sheet (Fig. 53, *sus*), which will develop into the terminal filaments of the ovarioles (Fig. 55). A thickening of the fold along the lower border of the ridge forms a ventral strand of the gonad which gives rise to the ovariole peduncles and the calyx of the oviduct; posteriorly it is continuous with the free part of the lateral duct. The middle part of the gonad (*g*) between the suspensorial

FIG. 54.—Female gonad of *Blattella*. (gc) Germ cells. (sus) Dorsal suspensorium, differentiated into terminal filaments (tf). (x) Ventral strand continuous with duct (d). (Adapted from Snodgrass.)

The germ cells at this stage, as described by Heymons in *Blattella*, are evenly distributed throughout the length of the median part of the gonad, and the organ increases in thickness owing to their multiplication.

The dorsal plate now separates from the walls of the body cavity, and its flat, elongate cells become arranged in about 20 vertical rows (Fig. 54, *tf*). These columns of cells form the terminal filaments of the definitive ovarioles. The first appearance of the egg tubes is indicated by a series of dorsal swellings of the middle region corresponding to the columns of filament cells. Then the swellings are converted into definitive ovarian lobes by a deepening of the grooves between them, until finally the gonad is cut vertically into separate compartments as far as the ventral strand. The compartments are the ovarian tubes, each of which is covered by an epithelial layer of mesodermal cells and contains a number of egg cells (*gc*). In the opinion of Snodgrass (1933) this probably represents the primitive condition of the female reproductive organ formation.

FIG. 55.—Later stage of ovary of *Blattella* with gonad divided into ovarioles. (*d*) Duct. (*ovt*) Ovariole. (*tf*) Terminal filament. (*x*) Calyx. (Adapted from Snodgrass.)

The exit apparatus of the egg tubes is formed from the ventral strand of the gonad, which becomes cleft between the attachments of the tubes upon it and thus divided into the rudiments of the ovariole pedicles (Fig. 55). The undivided part of the ventral strand and its posterior continuation become the lateral oviduct (*d*), the anterior end of which supporting the pedicles is widened to form the calyx (*x*). By a shortening of the calyx, the egg tubes of the roach become horizontal, and the ovary assumes its definitive form and position. In many insects, however, as in Ephemera, Dermaptera, Plecoptera, Phasmidae, and Acrididae, the ovarioles preserve their more primitive serial arrangement on the elongate calyx, as in an immature stage of the cockroach (Fig. 55).

The development of the testes does not differ materially from that of the ovaries. The sperm tubes usually lack terminal filaments, and the division of each testis into compartments is not always apparent externally and is sometimes incomplete. In *Pieris* the lumen of the testis is undivided until about the time of hatching, when the formation of the septa begins which will divide the organ into four tubular sections. The septa are infoldings of the testicular wall, which grow inward toward the posterior ventral part of the organ where the duct arises.

The later history of the genital rudiment consists of a differentiation of the inner cellular elements; the formation of the definitive sperm tubes, or the so-called testicular "follicles"; the establishment of the sperm tube ducts (vasa efferentia); and the formation of the gonadial part of the vas deferens. The following is a summary of testis development in *Melanoplus differentialis* given by Nelsen (1931).

At the beginning of the postrevolution period in the development of the embryo, the genital rudiments have somewhat shortened, reaching now only to the end of the seventh abdominal segment. By the middle of this period, the indifferent mesodermal cells of each gonad begin to differentiate into connective-tissue elements which form the intratesticular partitions among the germ cells, thus segregating the latter into groups of one or more cells each. The partition-forming cells are probably generated from cells at the junction of the gonad proper with the ventral cell strand. The actively proliferating area here located is termed by Nelsen the "germinal center." Each cell group, or cell nest, thus secondarily isolated, marks the nucleus of a definitive sperm tube, or "follicle."

By the time of hatching, the gonads have the form of two cords lying immediately below the heart, extending from the rear half of the third abdominal segment into the anterior half of the sixth. The germ cells have multiplied until there are about four or five cells in each group. Now, the "indifferent mesoderm cell," Nelsen states, leaves the periphery of the gonad and pushes into the center of each germ-cell group where it sends out cytoplasmic processes that fill the spaces between the germ cells. This interpolated cell becomes the apical cell of the group; the entire nest of cells is surrounded by a capsule of connective-tissue cells. The whole formation, which will be retained in the apex of each sperm tube, Nelsen calls the "apical complex." The growth of the apical complexes causes a series of lobes to appear on the dorsal surface of the gonad, which are the beginnings of the definitive sperm tubes. Undifferentiated cells now grow upward from the germinal center against the lower end of each apical complex, while at the same time the outer epithelial sheath grows inward between the dorsal lobes of the gonad until it invades the germinal center. In this manner the young sperm tube is formed, consisting of a germarium, which is the apical complex, and of a duct (vas efferens) derived from the germinal center, the whole structure invested in a fold of the outer epithelial sheath. The further activity of the gonad, which takes place during postembryonic life, is the formation of the sperm cysts and the further differentiation of internal cellular elements.

The primitive mesodermal exit ducts of the gonads become the lateral oviducts in the female and the vasa deferentia in the male, except in so far as they may be partially replaced by branches of the ectodermal median ducts. Since the mesodermal ducts are derived from the coe-

lomic walls, they probably originate as channels between epithelial folds continuous with the epithelial covering of the germ cells, which eventually close to form tubes.

The idea that the reproductive ducts of the arthropods are modified nephridial tubes is purely theoretical, and there is nothing to suggest that they are not canals of the mesoderm formed specifically for the conduction of the germ cells to the outside of the body such as exist among some of the Annelida (Snodgrass, 1933).

The primary mesodermal oviducts of insects undoubtedly opened to the exterior on the seventh abdominal segment, since in the embryos and larvae of many modern insects they are attached to the ectoderm at the posterior end of the venter of the seventh segment. The termination of the mesodermal oviducts in the seventh segment is now known to occur in all the larger orders and in some of the smaller ones including the Thysanura. The mesodermal oviducts retain in the adult stage the primitive position of their openings on the seventh venter or between the seventh and eighth sterna only in the Ephemera. The paired female gonopores of the Ephemera are in some species widely separated; in others they are approximated and open into a slight median depression. In the Dermaptera, however, the lateral oviducts open into a short median ectodermal pouch between the seventh and eighth sterna. Many insects in their embryonic and postembryonic development recapitulate the primitive condition found in Dermaptera, in that the first rudiment of the common oviduct appears as a median ingrowth on the posterior part of the seventh venter with which the approximated lateral ducts become united.

The first rudiment of the median duct is formed in the late embryonic or an early nymphal stage as an ectodermal invagination on the posterior part of the venter of the seventh abdominal segment. In Acrididae and *Philaenus* the primitive gonopore here located runs out in a median groove on the eighth venter. Later the edges of this groove, beginning anteriorly, grow together and convert the channel into a cuticle-lined tube. In this way the primary opening on the seventh segment is lost, as the median duct is extended through the eighth segment and acquires its definitive opening behind the sternal plate of this segment.

A second invagination is formed in most insects at the posterior end of the eighth abdominal segment which gives rise to the sperm receptacle. Hence, with the posterior extension of the oviduct, the gonopore and the spermathecal opening come to lie close together. In the majority of insects these two openings are carried inward by the formation of a copulatory pouch, or bursa copulatrix, invaginated above the eighth sternum. The pouch finally may take the form of an elongate sac or

slender tube continuous with the oviduct. On the venter of the ninth segment there is commonly formed a third median invagination, which gives rise to the accessory glands, the openings of which may be included in the copulatory pouch.

That the embryonic vasa deferentia of the male Orthoptera end posteriorly with hollow terminal enlargements, or ampullae, inserted into the appendage rudiments of the tenth abdominal somite has long been known. The cavities are present in the ampullae long before the lumina appear in the other parts of the ducts. The ampullar cavities are ventral remnants of the coelomic sacs of the tenth abdominal somite, and similar though transient ampullae of coelomic origin may occur in the preceding abdominal somites. To the ampullae of the tenth segment of the male, however, are attached the posterior ends of the genital strands that become the vasa deferentia. The ampullae persist first as terminal parts of the lateral ducts but later united as an anterior part of the definitive median ejaculatory duct, the posterior part of this duct, however, being of ectodermal origin.

According to Wheeler's (1893) account of the development of the genital ducts in *Conocephalus*, the embryonic female ducts, which likewise terminate with ampullae, end in the appendage rudiments of the seventh abdominal segment, but there is also a pair of ampullae in the tenth-segment appendages, which appear to be homologues of the male ampullae. The account of Heymons (1890, 1895) of the ducts in Dermaptera, Blattidae, and Gryllidae is essentially in agreement with that of Wheeler for *Conocephalus* in so far as the male ducts are described as terminating in mesodermal ampullae in the tenth segment and the female ducts in ampullae of the seventh segment. According to Heymons, however, there is evidence of a primary branching of the ducts in *each* sex to both the seventh and the tenth segments. Wheeler, on the other hand, believed that male insects never have ampullae or branches of the genital ducts in the seventh segment. Heymons' illustration of *Forficula* gives a convincing example of the branching of a genital duct to the two segments, but his identification of the posterior branch as the definitive oviduct is evidently wrong, since the definitive female ducts in Dermaptera open on the seventh segment.

In the Apterygota the gonads likewise form from the splanchnic mesoderm. The duct from the gonad which passes through the fourth segment is also formed from the splanchnic layer. Since the gonad is ventral in position in *Isotoma*, differing in this regard from the pterygotes, a terminal filament is lacking.

A more detailed summary of the development of the reproductive organs, especially with reference to the morphological implications, is given by Snodgrass (1933, 1937).

References

Ayers (1884), deBeer (1932), Biegel (1922), Brandt (1878), Carrière (1890), Faussek (1911), Graber (1891), Grassi (1884), Hasper (1910, 1911), Henschen (1929), Herold (1839), Hertwig (1881), Heymons (1891, 1892), Jackson (1939), Janet (1899), Jaworsky (1880), Korotneff (1883), Lautenschlager (1932), Lécaillon (1898*a*), Nelsen (1931), Okada (1935), Newport (1841), Nusbaum (1884*b*), Patten (1884), Petrun-kewitsch (1898), Saling (1907), Schwangart (1907), Seidell (1924), Snodgrass (1933, 1936, 1937), Tichomiroff (1879), Tichomirowa (1892), Wheeler (1892*a*), Wiesmann (1935), Will (1888*b*), Wong and Li (1934).

See also the list of general works in Chap. II.

CHAPTER X

POLYEMBRYONY AND PARTHENOGENESIS

POLYEMBRYONY

The term "polyembryony" is applied by zoologists to cases in which two or more embryos develop from a single egg, although its use in cases of twinning is not strictly correct. The phenomenon occurs sporadically among many animals, both vertebrates and invertebrates, and habitually among certain bryozoans, annelids, parasitic Hymenoptera, and the mammals (armadillos).

Polyembryony in insects was discovered by Marchal in 1898, but not until 1904 did he publish a full account. It is known to occur in the groups Chalcidoidea, Serphoidea (Proctotrupidae), and Braconidae of the parasitic Hymenoptera. Recently Noskiewicz and Poluszynski (1935) have recorded its occurrence also in the Strepsiptera, a group of parasitic insects related to the beetles. Nearly a decade before Marchal's work, Bugion (1891) in a paper on *Ageniaspis fuscicollis* called attention to the novel fact that embryos were placed in a flexuous tube which floated in the haemolymph of the host caterpillar (*Hyponomeuta*) at the side of the intestine, but he did not suspect that all the embryos originated from a single egg. The principal conclusion of Marchal's researches were that the egg of *A. fuscicollis* is laid in the egg of its host but continues its development into the larva and that from the single egg of the parasite many individual parasites develop. Some points in the development left untouched by Marchal were treated subsequently by Silvestri (1906) in his study of *Litomastix truncatellus* wherein he described the formation of the polar bodies, fertilization, cleavage, and the development of asexual larvae. In a series of later papers he dealt with the embryology of several species of parasitic Hymenoptera, both monembryonic and polyembryonic. Martin (1914) was the next investigator dealing with this subject, placing especial emphasis on the development of the oöcyte in the ovarium of *A. fuscicollis*. In 1915 Patterson published an account of the late stages of development of *Copidosoma gelechiae* and since then a series of papers covering the development of *Paracopidosomopsis floridana*. The latter species, which is a common parasite of the cabbage looper (*Autographa brassicae*), is apparently identical with the insect known under the name of *Litomastix* or *C. truncatellum*. Following Patterson's account of *C. gelechiae* was a more extended one by Leiby (1922) on the same species. This was followed by papers by Leiby and Hill on *Platygaster hiemalis* and

P. vernalis. More recently Parker (1931) discovered that the braconid *Macrocentrus gifuensis* also undergoes polyembryonic development with the production of about 10 individuals from a single egg. *M. abdominalis* may belong in the same category.

Since the polyembryonic development of several species is discussed in some detail in the chapter on Hymenoptera in Part II, it suffices here to give a brief review.

Polyembryonic species are all parasitic upon either Hymenoptera or Diptera. They oviposit in the eggs of their hosts and emerge as adults nearly always from the fully grown host larva. From one to eight eggs are deposited by the female parasite at a time within the host egg. Some species rarely deposit more than one egg in a host egg; others deposit two as a rule; and still others deposit from four to eight eggs. Both fertilized and unfertilized eggs develop, the former giving rise to females, and the latter to males. At times, according to Leiby, one fertilized female may deposit both fertilized and unfertilized eggs in a host egg at one insertion of the ovipositor, and the brood developed therefrom will consist of both male and female individuals.

Whether the egg is fertilized or not, maturation takes place in which the polar bodies are not thrown off. Instead they are retained to form, together with a differentiated part of the egg, a thickened membrane known as the "trophamnion" (Figs. 263, 272) which invests the embryonic portion of the egg during early development and later functions as an envelope capable of extracting from the host such elements as are necessary to bring about the development of the parasites from the fertilized or unfertilized egg nucleus to the primary larval stage. Henceforth the growth of the parasite is by direct feeding of the larval stages within the host larva which has meanwhile hatched from the egg and is growing to reach the pupal stage. The posterior region of the parasite egg containing the fertilized or unfertilized nucleus becomes enlarged by the division and subdivision of the oöcyte nucleus. If it is limited to a single division, only two embryos are formed, but in most of the species thus far studied division and subdivision of the embryonic and daughter embryonic nuclei continue to a point where from 1,600 to 1,800 daughter nuclei are formed, which result in the development of as many embryos.

Embryonic development having been completed to the primary larval stage, by means of host elements fed through the trophamnion, the larvae then feed directly upon the internal tissues of the host. Their feeding upon the host kills it just as it is about to transform to the pupal stage, the parasite larvae having meanwhile matured. They then transform to pupae within the carcass of the host larva and later emerge simultaneously as adults from their individual cells in which they have passed the pupal stage.

It seems evident that twinning is just one step in advance of a very highly specialized embryological metamorphosis exhibited by some of the parasitic Hymenoptera that develop in the egg stage of their hosts. This is demonstrated by the origin, presence, and similar function of the trophamnion in both the monembryonic and the polyembryonic species. The close relationship between monembryonic and polyembryonic insects with regard to the origin of polyembryony is exhibited in three species of *Platygaster*: *herricki*, *hiemalis*, and *vernalis*. All are parasites of the Hessian wheat fly and oviposit in the egg of the host. All species occur in the same locality. *P. herricki* develops only by monembryony; *P. hiemalis* develops both monembryonically and by the twinning process, the female depositing from four to eight eggs in the host egg which give rise to about the maximum number that the host larva can tolerate. *P. vernalis* develops only by polyembryony in its generalized form, depositing one egg that gives rise to 15 to 20 adults, the maximum number that the host larva can accommodate.

A number of references to the presence of a cellular envelope about the embryo of monembryonic entomophagous parasites have been published. Some authors, in speaking of the embryology of the parasitic Hymenoptera, term this envelope the "amnion"; others speak of it as the "serosa"; still others consider that both amniotic and serosal layers are present; and finally the terms "pseudoserosa" or "trophic membrane" or "trophamnion," in part derived from the terminology used in polyembryony, are applied. In this group of insects the cells constituting the envelope apparently serve a nutritive function. Jackson (1928) and, recently and more briefly, Vance (1931) have reviewed this subject.

PARTHENOGENESIS

The natural development of an egg without having been fertilized by a male gamete is the phenomenon known as "parthenogenesis." It occurs naturally in several groups of animals, among them rotifers, crustaceans, and insects, and may artificially be produced in echinoderms, mollusks, and amphibians. Since parthenogenesis is of interest to the embryologist chiefly because of its cytological features in connection with maturation, only a brief survey of its general aspects need be given here.

The various types of parthenogenesis may be classified (A) in accordance with the sex of the parthenogenetically developing individual or (B) according to the regularity of the occurrence of the phenomenon or (C) with respect to the chromosome behavior of the individual.

A. In accordance with the sex:

1. Arrhenotoky, when unfertilized eggs give rise to males, fertilized eggs to females.

2. Thelytoky, when unfertilized eggs give rise exclusively or nearly exclusively to females.
 3. Amphiterotoky, when both sexes may arise from unfertilized eggs.
- B. In accordance with the regularity of its occurrence:
1. Exceptional parthenogenesis. Unfertilized eggs, that normally degenerate, occasionally develop, as with the silkworm.
 2. Normal parthenogenesis. Unfertilized eggs that normally develop. Two groups may be recognized:
 - a. Facultative parthenogenesis, wherein the eggs may be either fertilized or not, as in the case of the honeybee, the unfertilized egg giving rise to drones, the fertilized egg either to queens or to workers.
 - b. Obligative parthenogenesis, wherein all eggs, at least with individual generations, remain unfertilized. In this group parthenogenesis may be constant, a male seldom or never appearing, as with some phasmids, Thysanoptera, psocids, coccids, pschids, Rhynchophora, chalcids, etc., or it may be cyclic as with the aphids.
- C. With respect to chromosome behavior. Two primary groups may be recognized under this division: (1) haploid and (2) diploid parthenogenesis.
1. Haploid parthenogenesis. Familiar examples are certain aculeate Hymenoptera, among them the honeybee. Here the males are exclusively haploid, the females diploid, reduction not taking place in spermatogenesis but occurring in oögenesis. It follows that fertilized eggs produce females which are diploid; unfertilized eggs, males, which are haploid.
 2. Diploid or somatic parthenogenesis. This occurs when the individuals retain the normal diploid chromosome number. Several types have been recorded under this group. In the gallfly (*Neuroterus lenticularis*) Doncaster has shown that there are two classes of parthenogenetic females. The egg of the first class gives off no polar bodies, retains the diploid number (20) of chromosomes, and develops parthenogenetically into a sexual female. The egg of the second class gives off two polar bodies, retains the reduced number (10) of chromosomes, and develops parthenogenetically into a male. In the Aphididae and a number of other insects, among them *Brachyrhinus ligustici*, whose development is described in Part II, there is but one maturation division, this without reduction. In the phasmids *Carausius morosus* and *Bacillus rossii* there are two maturation divisions but neither with reduction. In several forms, among them a race of *Lecanium hesperidum*, the reduced polar body

unites with the egg nucleus, acting as a sperm, thereby restoring the diploid number of chromosomes.

Parthenogenesis has been recorded for a number of orders of insects, among them Thysanura, Orthoptera, Thysanoptera, Corrodentia, Homoptera, Lepidoptera, Coleoptera, Strepsiptera, Diptera, Hymenoptera. Some of these records still rest upon insufficient evidence. Winkler (1920) states that it is still a question whether or not parthenogenesis occurs among the Strepsiptera, and Hughes-Schrader (1924) writes that fertilization is essential for reproduction in the stylopid *Acroschismus wheeleri*, although several workers have suggested the possibility of parthenogenetic development in this species. Hughes-Schrader (1925-1930) has demonstrated that all the so-called "females" of *Icerya purchasi* in reality are hermaphrodites capable of self-fertilization of their own eggs by their own sperm and therefore not parthenogenetic.

Slifer and King (1932) and King and Slifer (1934) report that in unfertilized eggs of the grasshopper *Melanoplus* the maturation divisions are completed at nearly the same rate as in fertilized eggs. The embryos developing from these eggs frequently contain both haploid and diploid cells. This, as well as genetic evidence from parthenogenesis in the grouse locusts (King and Slifer 1933), indicates that the maturation divisions are normal and that there is no fusion of a polar-body nucleus with the true egg nucleus but that during cleavage there is a doubling of chromosomes without separation into two nuclei. The animals reared to maturity were all females. This, coupled with the fact that from thousands of unfertilized eggs several hundreds hatched but only about 20 lived to maturity, seemingly indicates that only those individuals which successfully attain a diploid condition live to maturity. Since the second generation gave results similar to the first, the high mortality must be ascribed to the haploid condition itself, not to uncovered lethal genes.

Bugini (1931) states that natural parthenogenesis is more prevalent in some races of silkworms than in others. The parthenogenetic tendency is transmitted and accentuated by heredity. It may also be produced artificially by centrifuging the eggs according to Clement (1917, 1921), and Bataillon and Su (1931a) report that it can be induced by chloroform or weak acids and that it frequently results in an activation superior to that of fertilization. Harrison (1933) and others have reported that it is sometimes induced by attempted hybridization. A peculiar case is reported by Shull (1930) for aphids. Here the mode of reproduction of an individual is determined before birth by external factors (light and temperature). It is the determination of the mode of

reproduction of an individual by the action of factors upon its mother rather than upon the generation affected.

Paedogenesis.—This is a form of parthenogenesis in which the eggs develop precociously within the larva or the pupa. Uichanco (1924) has redefined the term "paedogenesis" as "that method of reproduction whereby during the immature stages of the mother the ovum reaches a condition which enables it to begin a new germ-cell cycle." It has been recorded in the cecidomyiid genera *Miastor* and *Oligarces*, in the chironomid genus *Tanytarsus*, in the beetle genus *Micromalthus*, in the heteropterous genus *Hesperoctenes*, and, according to Parker (1922), possibly in the blowfly *Calliphora erythrocephala*.

This method of reproduction was first discovered by Wagner in 1861 and confirmed by Leuckart (1865) and others. The species concerned was the cecidomyiid *Miastor metraloas* which was subsequently studied in detail by Kahle (1908). In *M. americana*, Hegner (1914) found that each of the two ovaries contains 32 oöcytes, each oöcyte accompanied by a group of nurse cells. As the oöcytes increase in size, the nurse cells become smaller. Finally the oöcytes with the nurse cells become separated from the ovary and are forced by the movements of the larval mother into some other part of the body. Only a portion of the oöcytes produce young; the others degenerate. A polar body is given off at maturation without reduction, the body then dividing mitotically. The development of the eggs resembles that of other nemocerous Diptera but carried on within the body of the mother larva. When the eggs hatch, the young feed for a time on the tissues of the mother in the manner of parasites. When the larvae are well developed, they break through the body wall to become free-living.

The paedogenetic development of another cecidomyiid, *Oligarces* sp., has been recorded by Harris (1924). The manner of production of its offspring resembles that of *Miastor*. Males as well as females arise from mass cultures of larvae that have been produced paedogenetically, but males and females do not arise from the same individual larva under normal conditions, evidence indicating there is a genetic distinction. Ulrich (1936) found that the European *O. paradoxus* in nature developed generations of males and females during the summer, whereas during the remainder of the year reproduction occurred paedogenetically. He concluded that alternation of generations is due to nutritional changes.

In 1870 Grimm described the development of a species of *Chironomus*, the pupa of which, through paired openings at the caudal end of the abdomen, deposited strings of eggs from which the flies hatched. According to the observations of both Schneider (1885) and Zavrel (1926), Grimm's statement regarding the presence of paired openings seems to be an error. The genus concerned is what is now known as *Tanytarsus*,

a member of the family Chironomidae. A species of the same genus, *T. dissimilis*, may also reproduce parthenogenetically, eggs being laid by the female immediately upon leaving the exuviae. Should the nearly mature pupa fail to transform, the eggs nevertheless develop, and thus reproduction is also paedogenetic. The eggs are laid in a gelatinous string, the string from each ovary containing about 60 obliquely placed eggs (Johannsen, 1910, 1937). Embryonic development takes place as in *Chironomus*.

A complicated case of paedogenesis is presented by the coleopteran *Micromalthus debilis* in which there are five mature reproductive forms. These are an adult female, a thelytokous paedogenetic female, an arrhenotokous paedogenetic female, an amphiterotokous paedogenetic female, and an adult male. The adult is probably sterile; the thelytokous paedogenetic female is the essential reproductive type, giving rise by parthenogenesis and viviparity to a sizable brood of indeterminate larvae. The arrhenotokous paedogenetic female matures a number of eggs of the potential male type, only one of which is shed. The haploid male arises from no other source. The amphiterotokous paedogenetic female has proved to be essentially a male producer in which the development of the male is arrested and female-producing eggs develop secondarily. The development of this insect was first described by Barber (1913) and later in more detail by Scott (1938). Another striking example of paedogenetic development has been described by Hagan (1931) for the heteropterous bat parasite *Hesperoctenes fumarius* which is also a viviparous form. An outline of its development is given in Part II.

Although a large number of parthenogenetic species of insects are also viviparous, there are many viviparous forms that undergo normal reproduction. Hagan (1931) has recently given a summary which with but slight change is reproduced here.

1. *Ovoviviparity*.—Viviparity with no nutritional structures, the egg containing sufficient yolk to nourish the young until hatching, *e.g.*, Coccidae, Coleoptera, Sarcophagidae, Chironomidae (*Tanytarsus*), Cecidomyiidae (*Miastor*), etc.

2. *Intussuctio-viviparity*.—Viviparity with nutritional structure for larva only, the egg having sufficient yolk to nourish the embryo until hatching. The larva is retained in the maternal uterus and nourished by means of specialized organs, *e.g.*, Hippoboscidae, Muscidae (*Glossina*, *Hylemyia*).

3. *Exgenito-viviparity*.—Viviparity following haemocoelous development and fat-body absorption, the embryo obtaining nourishment directly from tissues by means of a trophamnion, trophserosa, or trophchorion, *e.g.*, Strepsiptera, Chalcidae (in polyembryony), etc.

4. *Pseudoplacento-viviparity*.—Viviparity following the development of pseudoplacental organs, *e.g.*, *Hemimerus* (Diploglossata), *Hesperoctenes* (Heteroptera).

References

Polyembryony: Bugnion (1891), Daniel (1932), Ferrière (1926), Gatenby (1918), Hill (1922–1937), Howard (1906, 1917, 1925), Leiby (1922, 1926, 1929), Leiby and Hill (1923–1926), Marchal (1897–1906), Martin (1914), Noskiewicz and Poluszynski (1935), Parker (1931), Patterson (1915–1927), Riley (1907), Silvestri (1906–1937), Waterston (1920). Reviews on this subject are given by Gatenby, Leiby (1929), Patterson (1927), and Silvestri (1937).

Parthenogenesis: Barber (1913), Blochmann (1889), Bugnion (1931, 1932), Butt (1936), Cappe de Baillon *et al.* (1939), Gabritschewsky (1928, 1930), Gilmore and Whiting (1931), Goldschmidt (1917, 1931), Grandori (1924, 1930), Grimm (1870), Hagan (1931), Harrison (1933), Hegner (1914), Harris (1924, 1925), Hertwig (1920), Hewitt (1906), Hughes-Schrader (1924, 1930), Johannsen (1910, 1911, 1937), Jucci (1926), Kahle (1908), King and Slifer (1932, 1933), Lemoine (1887), Leuckart (1858*b*, 1865), Meinert (1864), Metschnikoff (1865), Niceti (1930), Pagenstecker (1864), Parker (1922), Parker (1931), Phillips (1903), Schneider (1885*b*), Scott (1938), Shull (1930), Siebold (1856, 1864), Silvestri (1908*a*), Smith (1938), Strindberg (1919*a*), Uichanco (1924), Ulrich (1936), Vance (1931), Wagner (1865), Winkler (1920), Zavrel (1926). Reviews on this subject are given by Hewitt, Phillips, and Winkler.

CHAPTER XI

MICROORGANISMS IN THE EGG

Blochmann (1888) appears to be the first to have recognized the normal presence of intracellular organisms in the eggs and body tissues of insects, although years earlier Leydig, Huxley, Metschnikoff, and others had already noted the presence in the embryos of aphids of what is now known as the "mycetom" in which microorganisms are harbored. These bacteroid bodies, which Blochmann first noted in ants and roaches, were designated by Wheeler (1889) as "Blochmann's bodies." Heymons (1895a) found them in the yolk of *Blattella germanica* and *Ectobia livida*, where they form a spherical mass. After revolution, the mass, which also includes yolk cells, is found in the mid-gut. Later the organisms, leaving the yolk cells behind, pass through the wall of the intestine and become lodged in the fat body.

Microorganisms have been recorded in the embryos of Orthoptera, Homoptera, Heteroptera, Anoplura, Mallophaga, Coleoptera, Diptera, Hymenoptera, and other forms. Opinions as to their character and their significance to the hosts differ greatly. Glaser (1920) states that in the blattids the organisms are motile bacteria, but in some aphids they are undoubtedly yeasts. Glasgow (1914) concluded that the organisms that appeared in the cultures from the eggs of *Anasa tristis* and that were certainly the same as those isolated from the caeca of the alimentary canal of the adult were bacteria. Recently Hinman (1932) recorded the presence of bacteria in the eggs of mosquitoes. Mansour (1930) likewise referred to the microorganisms found in the egg of *Calandra oryzae* as bacteria. He stated (1934), however, that they are not symbiotic in the strict sense of the term but are more properly referred to as "commensals." In the case of *C. granaria* as compared with that of *C. oryzae* he points out the nonimportance of these organisms in the life of their hosts. Brues and Glaser (1921), on the other hand, believe that in *Pulvinaria* the production of diastase, protease, and lipase by the organisms may serve to benefit the coccids and that therefore the possibility of real symbiosis cannot be excluded. Buchner (1930) and his followers take a similar stand.

For convenience Glaser (1920) uses the term "symbionts" for these organisms, although he is not convinced that there is true symbiosis. For a similar reason "symbiont" will be used in the following account.

SYMBIONTS IN THE EMBRYO

Coccidae.—Among the earliest references to the association of symbiotic microorganisms with insects is material relating to the Coccidae. Not until 1910, however, with the appearance of the works of Šulc and Pierantoni, was the true nature of these organisms recognized. Šulc demonstrated that the structure, to which Huxley many years before applied the name "pseudovitellus," was the seat of symbiotic microorganisms. To the structure he applied the name "mycetom," and to the cells containing the symbionts he gave the name "mycetocytes." Since then a number of works have appeared which were summarized by Buchner (1930) on the symbiosis between animals and plants in general and by Walczuch (1932) on the relation to coccids.

The transmission of symbionts to the offspring in the coccids, according to Walczuch (1932), always occurs within the body of the mother through infection of the ovarian eggs. This type of transmission occurs with other Homoptera as well as with Blattidae, Mallophaga, Siphunculata, Cimicidae, etc. With the Coccidae there are two ways in which infection may occur. In the first type the symbionts enter the egg at the base of the nurse cell by passage through or between the cells of the follicular epithelium. This type of infection occurs with most Coccidae and with the Cimicidae. The second type occurs with the coccid subfamilies Margarodinae, Orthezinae, Monophlebinae (except *Marchalina*), and Lakshadinae in which infection takes place through the posterior pole of the egg as with the Cicadellidae and other insects that bear symbionts.

The method by which the symbionts reach the egg differs with the different genera of coccids. The direct entrance of the mycetocytes into the egg follicle, as in the Aleurodidae, does not occur with the coccids, where in the majority of cases individual symbionts wander into the egg after being set free from the mycetocytes. The actual entrance of the symbionts into the plasma of the egg occurs at different periods depending on the subfamily of the insect. With the Lecaniinae, Diaspinae, Pseudococcinae, and Phaenococcinae maturation of the egg nucleus has scarcely begun before symbionts begin to glide down the plasmic strand from the nurse chamber; in the case of the Asterolecaniinae the symbionts enter the egg after the second cleavage stage. The entrance of the symbionts into the eggs of *Tachardina* and *Cryptococcus* takes place as with the winter eggs of the Aphidae, as described below.

Diverse also in the coccids is the origin of the mycetocytes and mycetom. The mycetocytes of *Tachardiella* in large part are derived from cleavage nuclei; those of *Tachardina*, from the yolk nuclei; the mycetocytes of *Orthezia* are mesoderm derivatives.

Aphididae.—Unlike Hirschler (1912), Toth (1933) found in all the genera and species of aphids studied by him symbionts in summer eggs only after the cleavage of the nuclei. At a time after completion of the blastoderm when the mycetom anlage fills the orifice between blastoderm and the follicular cells, symbionts pass into the blastocoele. With the inward growth of the mycetom anlage the yolk cells are pushed against the anterior wall of the blastoderm, become flattened, and finally form a mycetolemma, or envelope, of the mycetom. Simultaneously with the invagination of the germ band the invasion of the symbionts into the mycetom anlage takes place. The symbionts that infest the embryo are those which normally are present in the mycetom of the mother aphid. Toth (1933), confirming Klevenhusen, distinguished three principal types of symbionts: a rounded form, another distinctly smaller coccus-like form, and a bacillus-like form. Some species of aphids are infected with but one kind of symbiont; others with either two or all three forms. The first condition is most common. All three kinds are localized in different mycetocysts which collectively form the mycetom. The large rounded microorganisms are apparently the most primitive and occur without exception in all aphids. They normally measure 2 to 4 microns. The second form of symbiont is less than 1 micron in diameter but somewhat variable both in size and shape. This form Toth (1933) found only in species of the genus *Stomaphis*. The third form of symbiont is rod-like, usually less than 1 micron in diameter and varying in length from 4 to 20 microns depending on the host species.

Since the symbionts from a single full-grown aphid must infect a numerous progeny, rapid multiplication of these microorganisms is necessary. Division of the cells is strikingly synchronous not only in a single mycetocyte but often in the entire mycetom complex. With the division of a symbiont there is a reduction in size, sometimes accompanied by a loss of some of the gelatinous coat, followed by a gradual hypertrophy of the daughter cells, restoring them to the normal size.

A well-developed mycetom is always present in those aphids which actively feed. The rudimentary, short-lived males of *Stomaphis* and of *Pemphigus filaginus*, which do not feed, lack mycetom and symbionts. In the rudimentary short-lived females of *P. filaginus*, which likewise do not feed, the mycetom is reduced to a few mycetocytes; her symbionts are completely utilized for infection of the young. These observations of Toth (1933) seem to indicate that the symbionts have a nutritive value, bearing out the experimental work of Koch on *Sitodrepa* and of Aschner and Ries on Pediculidae. The relation of the mycetom to the developing embryo is described in Part II in the section dealing with the Aphididae.

Curculionidae.—The discovery of the symbiotic relations between certain bacteria and snout beetles is of recent date. Pierantoni (1927) refers to a symbiotic organ in *Calandra* the same year that Mansour (1927) described for the same species the "accessory cell mass," later (1930) recognized by Mansour as a mycetom, demonstrating the presence of the symbionts (or commensals) in the female sex organs of older embryos and in young larvae. Meanwhile Buchner (1927) had found microorganisms in the genus *Hylobius*. A comparative study undertaken by Scheinert (1933) revealed the presence of symbiotic bacteria in eggs and larvae of a number of genera and species of snout beetles, among them *Hylobius abietis* and *Liparus germanus*. The conditions in these two species are in most respects similar. In the larva of *Hylobius* an annular mycetom is found on the alimentary canal between stomodaeum and mid-gut. A dissolution of the structure takes place during pupal life. In older adults mycetocytes are no longer to be found. The organisms contained in them are probably discharged into the lumen of the mid-gut. In recently deposited eggs the organisms may be seen distributed in the yolk, abundant toward the anterior pole and in a thin concave-convex lenticular mass near the posterior pole. In the outward migration of cleavage nuclei those passing through the lenticular mass become laden with the organisms, while numerous vitellophags remain behind in the yolk. Cell walls soon form around the cytoplasmic zones that surround the nuclei, the cells at the posterior end, the primordial germ cells, forming a clump. In the manner just described the germ cells, both male and female, become infected. Scheinert saw no evidence of a germ-track plasm. Differentiation of the germ band and later of the inner layer takes place. Under the blastoderm (future serosa) of the region not covered by the germ band is a thin zone of organisms in which there are a number of yolk cells spaced at approximately equal distances. Accompanying segmentation is a shifting and a shortening of the germ band until the head lies near the anterior, the cauda near the posterior pole of the egg. This change in position results in a displacement of the anterior zone of symbionts into the anterior part of the yolk and where they are irregularly distributed around the displaced yolk cells. At this time the inner layer forms a continuous sheet; the germ cells lie irregularly massed at the posterior end of the inner layer near the proctodaeal invagination; and the stomodaeum is well advanced. The mid-gut epithelium, too, begins to form as outgrowths from the blind ends of stomodaeal and proctodaeal invaginations and hence are regarded as of ectodermal origin by Scheinert in agreement with Mansour.

When the stomodaeum has completed its growth, the blind end grows out into a pointed process which apically unites with a plasmic sac-like

reticulum of the yolk. This plasmic sac has the form of an *ellipsoid of revolution* or in longitudinal section that of an ellipse (Fig. 56, *net*). The organisms gathered from various parts are caught in the meshes of the plasmic net-like structure that is everywhere connected with the plasmic reticulum of the yolk. After a time symbionts are no longer to be found except on the net near which yolk cells also are to be seen. From the apex of the stomodaeum ectodermal cells wander down the apical plasma strand toward the yolk to form a cap-like structure over the anterior end of the net-like bacteria-bearing sac (Fig. 56). The net

FIG. 56.—*Hylobius abietis*. Stomodaeal (ectodermal) cells (*c*) migrating over the anterior end of the plasmic net (*net*). (*stom*) Stomodaeum. (From Scheinert.)

FIG. 57.—*Hylobius abietis*. Mycetom (*myct*) covering the limiting membrane (*lim. m*) of the stomodaeum (*stom*). (*ect*) Ectoderm. (*ent*) Entoderm. (From Scheinert.)

gradually contracts, causing a diminution in the size of the meshes and a concentration of the symbionts, drawing them toward the migrant stomodaeal cells (*c*) which now constitute the mycetocytes. With further contraction of the net the symbionts are forced into the mycetocytes which thereupon form a compact cellular body (mycetom) attached to the tip of the stomodaeum (Fig. 57, *myct*). The centrifugal gliding migration of the mycetocytes on the closing stomodaeal membrane (*lim.m*) and their pushing peripherally between the ectodermal and entodermal cells finally form an annular mycetom *outside* the alimentary canal at the junction of stomodaeum and mid-gut (Fig. 58, *myct*), thus completing the larval mycetom. After this the union between stomodaeum and mid-gut is restored.

As has been stated above, the germ, or sex cells in *Hylobius*, *Sibinia*, and *Calandra* become infected with symbionts (bacteria) at the time of blastoderm formation. This applies to all sex cells, both male and female. The symbionts degenerate in the immature testes. In the ovaries the larger mass of microorganisms become lodged in the proximal lying nurse cells of the ovarian tube, although there are symbionts in the oöcytes as well. The early infection of the primordial germ cells seems to be typical for all snout beetles except the Cleoninae.

In many Apionidae the mycetom is represented by a clavate tubule adjacent to the four Malpighian tubes. In *Protapion* two of the six

FIG. 58.—*Hylobius abietis*. Passage of the mycetom (*myct*) between entoderm (*ent*) and ectoderm (*ect*) nearly completed forming a ring around apex of stomodaeum (*stom*). (From Scheinert.)

Malpighian tubes become infected. *Ceutorhynchus* and *Cionus* possess infected cells which are derived from infected embryonic tissue and later in part unite to form an organ-like structure. In a species of *Lixus* the larva emerging from the egg feeds upon the infected eggshell and thereby becomes infected.

Other Orders.—References to the symbionts occurring in the embryos of other insects will be found in Part II under Mallophaga and Anoplura.

References

- Blochmann (1888, 1892), Brues and Glaser (1921), Buchner (1930), Emeis (1915), Fraenkel (1921), Glaser (1920), Glasgow (1914), Hecht (1924), Heymons (1895a), Hinman (1932), Hirschler (1912), Hovasse (1930), Klevenhusen (1927), Koch (1931), Mansour (1927, 1930, 1934b), Mercier (1906), Pierantoni (1927), Richter (1928), Ries (1931), Scheinert (1933), Schölzel (1937), Schrader (1923), Shinji (1919), Speyer (1929), Šulc (1910), Tarsia (1933), Tiegs and Murray (1938), Toth (1933), Uichanco (1924), Walczuch (1932).

Buchner's text has an extensive bibliography.

CHAPTER XII

EXPERIMENTAL EMBRYOLOGY

DETERMINATION

Development from egg to adult is physiologically a continuous process regardless of the form changes involved. Nevertheless it is convenient to treat the subject under two arbitrary subheads, the present chapter being concerned primarily with development within the egg. The second division would include the development after emergence from the egg.

Although experimental insect embryology is still in a very early stage in comparison with experimental vertebrate embryology, it has reached a point where the literature is sufficiently extensive and the results sufficiently definite to make a résumé in English seem desirable.

Most of the important data on the embryonic stages are of recent date. Historically the first experiments were those of Wheeler (1889) and Megušar (1906) on gravitational effect by the inversion of eggs. The first important experiments were those of Hegner on beetle eggs. In 1908 he studied the effects of puncturing the egg and allowing part of the contents to flow out, in 1909 the effects of centrifugal force, and in 1911 the effects of killing regions of the egg with a hot needle. A lapse of about fifteen years followed, during which the little experimental data came from genetical and cytological investigations. Then, with the work of Reith (1925), Seidel (1926), and Pauli (1927) began the series of experiments that form the basis of experimental embryology of insects of today. To Seidel and his colleagues we owe most of our knowledge of the vital processes occurring in the insect egg.

The following review in large part is taken from a paper by Richards and Miller (1937).

For our purposes we shall regard "*determination*" as the process of primary chemo-differentiation that "sets the course" along which a given region of the egg is to develop, *i.e.*, determines its fate. Determination lays the invisible foundation for morphological differentiation. It may, and probably always does, vary in degree, becoming increasingly more strict as development proceeds, and so may also be expressed as "a limitation of potencies." *Differentiation* has been aptly defined by Schnetter (1934a) as "visible distinctive configuration." It is the realization, as visible development, of the capacities of a region acquired by earlier or simultaneous chemo-differentiation.

The degree of determination existing in the egg at a given stage of development is reflected in the ability of the egg to readjust itself toward the production of a normal embryo after a defect is imposed upon it. The more fixed the determination the less the power of regulation. Insect eggs may accordingly be grouped into (1) *indeterminate*, (2) *incompletely determinate*, and (3) *determinate* types. An indeterminate type of egg is one in which the parts of the embryo are not predetermined at the time of fertilization, and hence an egg with great regulative powers under experimental conditions. A determinate type of egg is one in which the parts are wholly predetermined before or during fertilization, and hence an egg with little or no regulative power and given to mosaic formation under experimental conditions. An incompletely determinate type of egg is intermediate between these two. A graded series is found from the highly indeterminate eggs in certain of the lower insect orders through incompletely determinate eggs to the completely determinate eggs of the higher Diptera. This indeterminate-determinate series will be discussed in detail later.

EXPERIMENTAL MATERIALS AND METHODS

The forms experimented upon include Orthoptera, Odonata, Coleoptera, Diptera, and Hymenoptera. Both aquatic and terrestrial types have been used; study of the development of the latter is frequently facilitated by immersion in water. Observations on living eggs are possible when they are naturally transparent or translucent and in some cases after removal of the chorion. In experimental studies normal eggs are always used as controls, and in some problems "experimental controls" are also used (*e.g.*, partially versus completely constricted eggs). The experimental techniques that have been used may be summarized as follows:

1. Cauterization.—(*a*) Killing a small region or several regions with a hot needle either to produce a minute scar or to eliminate certain areas. (*b*) Light cauterization to produce localized contractions of the yolk system. (*c*) Unilateral heating with a microcauterizer to produce minute splits by unequal expansion of the egg materials.

2. Irradiation with ultraviolet light to (*a*) kill selected nuclei, (*b*) kill certain areas of the egg, (*c*) cause temporary changes in the cytoplasm, (*d*) produce a minute scar, or (*e*) observe the effect of *in toto* irradiation of oriented eggs.

3. Puncturing the egg with a cold needle, either to allow part of the egg contents to flow out or to injure, divide, or alter the germ band.

4. Producing yolk fissures by bending the egg.

5. Constricting the egg (completely or incompletely) at various points with a fine hair.

6. **Centrifuging** the egg in various positions.

7. **Modification of environmental factors.**

8. **Genetic analysis** of "normal" mosaics, intersexes, and gynandromorphs in studies on fertilization, cell lineage, sex determination, and to a lesser extent organ formation.

In regard to techniques that have been used upon other invertebrates and upon vertebrates it is of interest to note that (1) separation of early blastomeres is of course impossible owing to the superficial cleavage, but this aspect is covered by the foregoing techniques 2, 5, and 8; (2) vital staining for marking egg regions has been tried unsuccessfully by Seidel, and No. 2 above had to be used instead; and (3) tissue culture methods, parabiotic twinning, and operative technique in the sense of transplantations have not been successfully accomplished with insect eggs. The tough chorion together with the turgidity and fluidity of the egg contents hinders manipulation.

NUCLEAR MOVEMENTS IN CLEAVAGE AND BLASTODERM FORMATION

Analysis of the motivating factor or factors in nuclear movements is difficult because of the inability to separate cause from effect in observational data. The movement is not impeded by repeated mitoses during migration; in fact, Huettner (1935) says movement may in certain cases be accelerated during mitosis in *Drosophila*. The movement of the centrioles during mitosis shows that they cannot be the causative factors even though they constantly lie toward the egg periphery in undividing nuclei (Huettner, 1933; Strasburger, 1934). The repulsion tendency cannot possibly function to cause centrifugal movement of the nuclear sphere.

Three possibilities remain: (1) active nuclear movement which pushes the cytoplasm in front of it and draws that behind, (2) plasma streaming which carries the nuclei along passively, and (3) some unknown attractive influence from the surface region. The only observation that can be considered in favor of the first hypothesis is Strasburger's report that plasma streaming does not occur in nonnucleated but seemingly uninjured parts of the egg of *Calliphora*. But this is by no means conclusive evidence even for this species, since he does not consider such questions as the possible failure of local activation, altered viscosity, or other possible invisible physicochemical changes in these cauterized eggs. He attempts to circumvent the difficulty of ascribing active nuclear movements to the nucleus by suggesting that the movement is due to the protoplasmic island in whole or part, but this is unsupported and also conflicts with his own data on the formation of the inner cortical layer and with Seiler's data to be discussed below. Another possibility that

has not been suggested by any previous author is that the qualitative differences between the various nuclei, as expressed by the nonmigration of vitellophags, might conceivably result in surface-tension phenomena around each nucleus. Such differences, arising from differences in the nuclei themselves, might possibly inaugurate the general plasma streaming and also cause the differences between the movements of various nuclear types, perhaps largely by causing the vitellophags not to participate in the general outward movement or actually to move against it. In favor of the second hypothesis—plasma streaming—there are two positive observations: (a) Strasburger's report that when some of the nuclei anterior to the point of cauterization are delayed from entering the cortical layer in eggs of *Calliphora*, the inner cortical layer is formed in those regions before the nuclei reach it; (b) Seiler's report (1924) that the eggs of *Phragmatobia* (moth) hybrids occasionally undergo "cleavage" of the cortical layer to form a pseudoblastoderm even though no cleavage nuclei are present in the egg. His illustrations show clearly that those areas which undergo this "cleavage" process have a considerably thickened cortical layer. Both these cases certainly represent a plasma streaming without nuclei, from which it is reasonable to assume that the plasma streaming is the primary factor in these movements. But plasma streaming alone leaves unexplained those cases where vitellophags are left behind in the yolk (unless the plasma streaming is local and caused by the nuclei—its general appearance being due to a summation of local effects around each nucleus). The third hypothesis is indefinite. It is included here partly as a possible answer to the occasional nonmigration of vitellophags, partly as a possible source of origin of the plasma streaming.

The factor or factors causing the centrifugal migration of the nuclei must be the same that bring an end to the random orientation of the mitotic figures and arrange the nuclei in the form of a hollow sphere. It would seem that only a centrifugal plasma streaming could accomplish this. But from what could such a plasma streaming originate? Certainly not directly from randomly oriented nuclei. Perhaps it is unwise to attempt delimitation to any single factor or part, but it seems possible that the stimulus might arise from the distant influence of the cortical layer. The original shape, later movements, and change of shape of the nuclear sphere are not too well correlated with the original thicknesses of the various regions of the cortical layer so it can scarcely be a truly quantitative relationship. Nevertheless Schnetter (1934a, p. 161) points out that there are certain quantitative correlations in the honeybee egg. He describes the outward movement of the nuclei as occurring in waves passing anteriorly and posteriorly from the region of the differentiation center (*q.v.*), the nuclei first reaching the surface

anteriorly and ventrally near the locus of polar-body formation, and suggests that a motivating impulse is transmitted from the differentiation center following the release of the qualitatively distinct "Richtungs-plasma" into the periplasm. There are, then, two possible origins of this centrifugal movement, both hypothetical: (a) a more or less general effect from the cortical layer or (b) qualitative differences not necessarily included in the developmental centers although sometimes correlated with the differentiation center. Either is substantiated but not proved by Strasburger's observation that light cauterization of the egg of *Calliphora* frequently results in a displacement anteriorly of the nuclear sphere. If either of these suggestions is true, then the origin of the plasma streaming is one of the first indications of the activation of the *general* dynamic egg system.

With respect to stimulation to blastoderm formation there are four noteworthy points: (1) Seidel's and Reith's observations that delay in (*Platynemís*) or failure of (*Camponotus*) cell-wall formation occurs after elimination of the activation center; (2) Eastham's observation of the formation of cell boundaries from the cytoplasm of the *original* cortical layer; (3) Seiler's observation of "cell" formation without nuclei but with a thickening of the cortical layer; and (4) Strasburger's demonstration of the formation of cell walls at a definite time after entrance of the nuclei into the cortical layer. The first suggests that cell formation is aided or determined by the activation center; the second might be interpreted as suggesting that there is a predetermination of the cortical layer to form cells; the third must be interpreted as either a partial activation causing both localized streaming and cell formation or a partial activation causing streaming which in turn causes cell formation; and the fourth suggests that cell formation is wholly a function of the nuclei. The natural assumption is that all these factors are involved but that they have different potencies in different insects.

THE INDETERMINATE-DETERMINATE SERIES

By differences in the time of appearance of the visible morphological characteristics of development, especially the germ cells, Seidel (1924) showed that it is possible to establish a series ranging from indeterminate through incompletely determinate to determinate types. In indeterminate eggs the visible separation of regions of different prospective significance occurs after blastoderm formation, and organ segregation follows after differentiation of the germ layers and segmentation. In determinate eggs this visible differentiation occurs before or during blastoderm formation.

Following this lead experiments were devised by Seidel and his associates to determine if this series is also illustrative of the potencies of the

egg parts as determined by the regulative power or, conversely, the degree of predetermination of the egg parts. These studies have shown that Seidel's series is fundamentally accurate both for visible differentiation and for the degree of predetermination of the various egg parts. From both viewpoints it is a matter of time (time or stage of visible differentiation and time of determination), indeterminate eggs becoming more and more determinate as development proceeds, determinate eggs being fully determined by the time of fertilization. Schnetter gives the following revised scheme:

Whether or not Schnetter is justified in listing the foregoing sequence seems open to question. In the first place no experimental data are available for either the Hemiptera or the Lepidoptera, and these two orders are placed in the series wholly on a basis of the time of visible differentiation of the various parts. A more serious criticism lies in the implication of homogeneity within single orders. Experimentally very few species have been studied, these being representative of the orders Odonata, Orthoptera, Hymenoptera, Neuroptera, Coleoptera, and Diptera. There is good reason to expect considerable variation within the order Hymenoptera, polyembryonic forms seeming to be highly "indeterminate." Perhaps similar variation will be found within other orders.

Indeterminate eggs have a certain amount of determination at the time of fertilization. Bilaterally symmetrical ones have the polarity and dorsal and ventral sides irrevocably determined. In the absence of experimental data it is not possible to evaluate the variation in position of the embryo of the radially symmetrical egg of the bug *Pyrhocoris*; though the embryonic axis varies through 90 degrees, it is not possible to say whether its position is determined before, during, or after fertilization. Except for the fundamental axes, indeterminate eggs possess great regulative powers, as shown by dwarf embryos and duplications. Experimentally produced twins and duplicated parts show that there is in the early blastoderm a specific disposition of materials for the formation of the germ band but that when these materials are separated, each part tends to form a whole structure rather than only an isolated part. This power becomes more limited as development proceeds, but studies on regeneration show that the power of regulation is not entirely lost until the adult stage.

In *Platynemis* Seidel (1928, 1929a) reports that shortening the longitudinal axis by constricting the egg results in dwarf but otherwise

normal embryos. Duplications that result from splits induced by cautery also show that the prospective potency of the egg parts is greater than the prospective significance at the time the various anlagen are set apart; each duplicated part is larger than one-half the size of the same organ in a normal embryo, so that the sum of the two duplicated parts is greater than the size of a single normal organ. This power of duplication is possessed by all organs, external and internal. It occurs never in the longitudinal axis, seldom in the dorsoventral axis, but commonly in the transverse axis. The interpretation given is that determination occurs in these three axes in this same order. In *Tachycinetes* Krause (1934) reports a correlation between the type of mechanical injury to the germ band and the effect. Frontal fissures give duplications in the dorsoventral axis; median and oblique fissures of various extents and positions give symmetrical or asymmetrical, transverse anterior or posterior duplications or parallel twins (division of differentiation center?); and fine splits give duplications of single organs. Effects produced by operating at different stages show that determination of the main axes is followed by determination of segments in the longitudinal axis, then of the lateral halves within these segments, and finally of individual organs. Oka (1934) reports preliminary experiments showing only that the egg of the cricket is of the regulative type.

Incompletely determinate eggs are intermediate between the two extreme types. They are capable of considerable regulation following experimental interference in early stages, but the power is lost much sooner than in indeterminate eggs. Dwarf formation has been observed, but not duplication of parts. The absence of duplications indicates that strict determination of the presumptive anlagen occurs early.

In the Hymenoptera Schnetter (1934*b*) reports that constricting the honeybee egg at the stage of the "uniform blastoderm" (12-hour embryo) can result in a normal dwarf embryo. Later blastoderm stages (24-hour embryo) are less labile and more inclined to mosaic formation with a shift in the regions of different prospective significance (Fig. 60). In the ant *Camponotus*, Reith (1931*b*, 1932*b*) shows by cauterization and constriction that the egg possesses considerable regulative power until the completion of the visible zonation by differential thickening of the cortical layer (presumably under influence of the activation center). After that it is determinate though not so highly so as dipterous eggs. By centrifuging he shows that stratification of the egg parts prior to the cortical zonation blocks development but that later centrifuging does not prevent formation of a fairly normal germ band. These two sets of data show that within this order there is a difference in the time of determination, that of the ant occurring noticeably earlier than that of the honeybee. DuBois (1938) has found that *Sialis lutaria*, a member

of the order Neuroptera, a form not previously studied, is nearer the determinate than the indeterminate type.

In the beetle *Bruchus*, Brauer and Taylor (1934) show by constriction and cauterization that determination occurs quite early, the egg becoming a true mosaic during blastoderm formation. In *Sitona*, Reith (1935) reports that the determination process occurs slightly later than in the ant and seemingly at about the same time as in the honeybee.

Determinate eggs have been found only in the Diptera; but at least as far as the germ cells are concerned, Hegner's results indicate that the chrysomelid beetles might also be placed here as well as the other insects in which the presumptive germ cells are segregated as "pole cells" during blastoderm formation. Determinate eggs always give mosaic formations under experimental conditions, the few slight exceptions showing an extremely small amount of regulative power. Accordingly, the parts of the embryo must be looked on as entirely self-differentiating after fertilization or, at least, incapable of development beyond their prospective significance.

Reith (1925), Pauli (1927), and Howland and Robertson (1934) report that cauterization of dipterous eggs invariably gives mosaic development. Slight regulative power is shown by Reith's report that the mid-gut anlagen of either end may form an entire mid-gut and also, by Strasburger's (1934) report, that slight cauterizations at the beginning of cleavage may delay the migration of the cleavage nuclei to the posterior part of the egg without preventing formation of a normal embryo—the posterior parts developing slightly later than the anterior parts.

Cytoplasmic Determination.—It is evident that the distinction between "regulative" and "mosaic" eggs in insects, as in other groups, is not sharp and that the designations mean little unless the period of development is specified. The earlier an egg assumes a mosaic nature the "more determinate" it is, but even the most "indeterminate" of insect eggs eventually becomes "determinate." The primary seat of the chemo-differentiation (predetermination) is the cytoplasm as a whole, and the formation of cells plays only a secondary or indirect part. The fact that development is less disturbed by late than by early centrifuging (Hegner, 1909; Pauli, 1927; Reith, 1932*b*) suggests that fixation of determination is accompanied by increased cytoplasmic rigidity (viscosity) either before or after cell formation.

DEVELOPMENTAL CENTERS

The Activation Center.—Seidel (1929*b*) has used the term "Bildungszentrum" to designate a region situated near the posterior pole of the egg and necessary for development. This center is responsible for

the activation of the egg system, and so it is here designed "the activation center," following Huxley and deBeer (1934). The literal translation "formative center" is ambiguous and may carry unwarranted implications. It is not a visibly distinct part of the egg but can be more or less closely delimited by experiments. It functions by the production of some substance that diffuses forward through the interior of the egg and initiates development. In its absence no true differentiation of the embryo occurs.

FIG. 59.—Graphic diagram of the development of the egg of the damselfly *Platynemesis*. (a) 4-nuclei stage with bracket indicating the position of the activation center. (b) 256-nuclei stage with curved line indicating the diffusion anteriorly of the product of the activation center. (c) Beginning of cell-aggregation with bracket indicating the position of the differentiation center. (d-e) Formation and completion of the embryo anlage. One egg division equals 24μ . (Modified from Seidel, 1934.)

The activation center has been most elaborately analyzed in the damselfly (*Platynemesis*) by Seidel (1926-1934). In this species (Fig. 59) the anterior border of the activation center coincides approximately with the presumptive posterior end of the embryo (about one-ninth the length of the egg from the posterior pole), but its posterior extent is undetermined. The point at which the germ band later invaginates into the yolk marks its locus. Here the functioning of the activation center depends upon an interaction between the cleavage nuclei and the region of this center. When the cleavage nuclei are late in reaching this region because of abnormal distribution, killing of one of the first two cleavage nuclei with ultraviolet light, or constricting the egg and later removing the constriction, the functioning of this center is delayed. Careful com-

parison with normals shows that none of these delays causes any effect on later development other than delaying the onset. If, however, the cleavage nuclei are prevented from entering this region by a constriction of the egg, no development ensues, although the anterior parts continue to live, undergo "yolk cleavage," and eventually form an extraembryonic blastoderm. Partial constrictions show clearly that it is the nuclei that must reach this area, not some chemical that can diffuse through the yolk system. The reaction is not limited to the surface of the egg (which lacks a distinct cortical layer), since peripheral parts in the region of the center may be killed by ultraviolet light without preventing normal development. Finally, the removal of constrictions and constricting after the nuclei enter this region both show by the production of embryos that the injury to the egg does not block development. Therefore we must conclude (1) that the egg contains two quantitatively or qualitatively different regions (compare animal and vegetal poles of other eggs) and (2) that neither the cleavage nuclei and their cytoplasm nor the activation center is capable of producing a normal or even partial embryo alone but that they react together to furnish a product that allows normal development to proceed along axial and symmetrical lines that have already been laid down.

Seidel further shows that after the nuclei have entered this region, more and more can be constricted off from the posterior end of the egg without blocking development. The action of the center spreads slowly over a considerable area, so that well before the assembling of cells to form the germ band its effect has been felt over the entire presumptive germ band (see curved line in Fig. 59). The interaction product must diffuse forward through the yolk system, since a partial constriction after the nuclei reach the activation center does not prevent an embryo from being formed anterior to the constriction. In some eggs there is a visible change in the structure of the yolk proceeding apace with the diffusion of factors from the posterior pole anteriorly. Furthermore, this product activates the differentiation center which will be discussed below.

In the ant *Camponotus*, Reith (1931, 1932) shows by constriction and cauterization that an activation center is present near the posterior pole, but he has not delimited it closely. In this species it differs from *Platynemis* in that the cleavage nuclei are not responsible or even necessary for its functioning. Its activation must be induced by some product concerned in fertilization, presumably produced not later than the time of fusion of the egg and sperm nucleus, since the visible effect of the functioning of the activation center is seen in very early cleavage stages. This product must diffuse through the yolk system just as the product of the activation center does, since neither is impeded by partial

constrictions, yet obviously they cannot be the same substance. Another interesting difference from *Platynemís* is that the activation center in this species induces a visible zonation (differential thickening) of the cortical layer prior to the migration of the cleavage nuclei. This visible differentiation begins at the posterior pole and passes slowly to the anterior end of the egg, as does also the "activating power." Attempting to localize the activation center to a visibly distinct part of the posterior region of the egg, he noted that the disintegration of the "pole disk" is correlated with the action of this center. The pole disk, however, cannot be the essence of the center, since it is lacking in the ant *Lasius* which gives similar experimental results. Nor can the effect be traced to the bacterial symbionts, since their injury is not correlated with that of the embryo. As in *Platynemís*, the activation center must be ascribed to an invisible difference in the egg regions.

In the beetles *Bruchus* and *Sitona* Brauer and Taylor (1934) and Reith (1935) report the presence of an activation center in the posterior region of the egg. In both these beetles the functioning of this center begins during cleavage and is finished when the nuclei enter the cortical layer (*i.e.*, later than in ants). In *Bruchus*, Brauer and Taylor state that when the constriction is made sufficiently early to exclude nuclei from the posterior end of the egg, the anterior portion forms "only a poorly developed blastoderm," yet "a protoplasmic isthmus . . . however narrow it may be, serves to conduct the organizing principle anteriorly." Hence it would seem that the nuclei are necessary for the functioning of the activation center in *Bruchus* as in *Platynemís*.

The Differentiation Center.—The visible differentiation of the insect embryo begins in the presumptive prothorax and from this region proceeds anteriorly and posteriorly. Descriptive embryology shows that the spread of differentiation from the thoracic region is a general principle of insect development and, as Schnetter (1934*a*) points out, may be considered as typical of insects as is superficial cleavage, though there may be exceptions in regard to both (in other arthropods and annelids differentiation begins in the head). The term "differentiation center" is here restricted to a physiological concept and is not applied to the visible starting point of differentiation, even though physiological and morphological phenomena normally occurring at a common locus may at times appear to be experimentally separable.

In *Platynemís* the region where the two rows of assembled nuclei first come together to form the germ band marks the place from which all later differentiation proceeds anteriorly and posteriorly; it lies in the presumptive thoracic region, about one-third the length of the egg from the posterior pole (Seidel, 1926, 1929*b*, 1934). In the honeybee (Schnetter, 1934*a*) the visible embryonic differentiation begins near the anterior end

of the egg (presumptive cervical region) at the site of polar-body formation, where the cortical layer is thickest, reticular cytoplasm is most concentrated, cleavage nuclei become most numerous and first reach the surface, vitellophags first appear, heterochronous mitoses first set in, and cell partitions are first formed. A qualitative distinction of this region during cleavage is indicated by differential staining with thionine but not with haematoxylin. This region also has precedence in all later differentiation (formation and closure of mesodermal furrows, segmentation, appearance of appendages, etc.). Spread of morphological differentiation from a definite region is not so evident in the eggs of higher Diptera.

Experimental methods have demonstrated, as one might expect, that this region of initial morphological differentiation is of fundamental physiological significance, incorporating the so-called "differentiation center." The results of constricting *Platynemís* eggs (Seidel, 1934) show that this center normally coincides with the starting point of morphological differentiation, though seemingly this morphological manifestation can be experimentally separated from the primary physiological center. The differentiation center extends from the second gnathal (maxillary) segment to the second thoracic segment with its mid-point in the anterior half of the presumptive prothorax (Figs. 59c, 62a).

Seidel (1929b, 1931, 1934) further shows that no differentiation can occur in an isolated region of the egg of *Platynemís* unless the differentiation center is present in whole or in part. The center can function only after the product of the activation center has reached it by diffusion. It does not affect blastoderm formation but does directly influence the assembling of blastoderm nuclei and heterochronous divisions in germ-band formation, although heterochronous divisions alone occur when almost the entire center is tied off. Unlike the activation center, the differentiation center cannot function normally with even a relatively slight constriction of this region of the egg. A very loose ligature outside the boundaries of this center will allow the formation of the germ band on both sides of the ligature; but if it is only slightly tighter, even though the blastoderm and yolk remain unsevered, the germ band forms on one side only. Since no continuity is destroyed in any part of the egg by such a constriction, the center's action cannot depend solely upon the spread of a substance but must involve an energy transfer, *i.e.*, must be a dynamic phenomenon. Cell aggregation to form the germ band is not prevented by killing a complete girdle of blastoderm cells over the entire region of the center (by ultraviolet irradiation). Initiation of this process must therefore originate in the "yolk system," *viz.*, the yolk with its included cytoplasmic reticulum and vitellophags. Localized contractions of the surface of the yolk system, produced by cautery or

point irradiation before or during the time of cell aggregation, result in changes in the length, shape, and position of the embryonic rudiment. The spaces between the yolk and chorion thus formed, or resulting when a ligature is loosened, serve as foci for cell aggregation which can thus be artificially and prematurely produced outside the normal region. These data indicate that the direct action of the differentiation center is due to a wave of contraction in the yolk system spreading anteriorly and posteriorly from the center, the yolk system retracting from the chorion in such a way that the evenly distributed blastoderm cells are forced to fill the resulting space. In this manner cells first aggregate in the region of the differentiation center, and the size and shape of the germ band are molded by the space between yolk and chorion. This makes it clear how the differentiation center can be the center of a field of activity without necessarily involving the actual transport of any material substance, the result of constrictions being due to interference with yolk movements. Additional proof of the dynamic nature of the differentiation processes in *Platynemís* is furnished by the fact that killing a girdle of cells by ultraviolet irradiation either in front of or behind this region where visible differentiation normally begins causes a corresponding shift (backward or forward, respectively) of the position of the initial differentiation. The yolk system is, in effect, temporarily reduced in size, and the visible differentiation begins in the same relative position within the new system that it held in the larger system. If, then, the differentiation center is a definite region within the egg (as it seems to be), it must remain at one end of the reduced system while its action originates in a new location.

In the camel cricket (*Tachycines*) (Krause, 1934) the order of decreasing regulation ability (lost earliest by the thorax), the relative frequency of organ duplications (least often in prothorax), and certain asymmetrical duplications show that differentiation along both longitudinal and transverse axes proceeds anteriorly and posteriorly from the first thoracic segment. He suggests that the presence of a differentiation center may account for the nonoccurrence of doubling along the longitudinal axis.

The results of constricting eggs at successive points along their length enabled Schnetter (1934b) to mark off "potency regions" in the 12-hour blastoderm of the honeybee egg. Each of these regions when present in whole or in part guarantees the *complete formation* of the corresponding embryonic systems (cf. "harmonic equipotential regions," e.g., limb field in Amphibia). Thus regulation in the honeybee egg is, in general, "stepwise," a given region developing as a whole or not at all. In Fig. 60a it can be seen that all the potency regions lie within or extend into the region of the differentiation center. Accordingly it may be regarded as a "concentration center" for potencies enabling whole formation of the various organ regions. Figure 60b shows that there is a shift

of these potency regions during the time between the 12- and 24-hour blastoderm. This, with a few preliminary experiments on an intermediate stage, indicates that there is a gradual shifting of these boundaries out of the differentiation center and into their definitive position. These facts suggest that the differentiation center bears a causal relation to the development of the embryonic regions. The fact that a fixed (morphological) region of the bee egg may have a prospective potency in an early stage that is entirely different from (not merely more extensive

FIG. 60.—Schematic Anlagen plan of the honeybee egg. (a) Posterior boundaries of the potency regions (" . . . those regions of which a small part must remain in the egg to enable the formation of the entire corresponding organ region") in the 12-hour blastoderm. (b) Expansion of the same regions along the longitudinal axis in the 24-hour blastoderm. (Modified from Schnetter, 1934b.)

than) its prospective significance as shown in a later stage indicates that chemo-differentiation is not only progressively increasing as development proceeds but that there is also occurring a *redistribution* of the chemo-differentiated materials. Furthermore, a shift in the region of first visible differentiation in developing dwarfs following constrictions in the 12-hour stage (as evidenced by the more posterior position of the beginning of the mesodermal furrows) indicates that this point assumes about the same relative position in the decreased whole as in a normal egg. So presumably dynamic factors are of fundamental importance in the egg of the honeybee as well as *Platynemis*.

In the higher Diptera the data from cauterization, constriction, and centrifugation (Reith, 1925; Pauli, 1927; Rostand, 1927; Strasburger, 1934) show that in all cases mosaic or partial embryos are produced by elimination of any egg part irrespective of the age of the embryo. A physiological differentiation center affecting larval organization is not demonstrable, although Henshaw's data (1934) indicate that there is some physiological regulator of early embryonic differentiation in *Drosophila*, since only weak doses of X rays were required to block development before gastrulation but much stronger doses were required later.

Interaction of Centers and Other Regions of the Egg.—Seidel (1934) has shown that in *Platynemís* an interaction between the cleavage nuclei and the region called the "activation center" results in a product that diffuses forward in the egg (see Fig. 59a,b). As this product passes anteriorly, there is a visible change in the structure of the yolk. However, this product does not directly affect differentiation; it functions by the activation of the differentiation center. The latter, in turn, appears to induce the onset of heterochronous cell divisions and the contraction of the yolk system which brings about the aggregation of cells to form the germ band and the later shift in the position of the same.

Comparison of the reactions of the activation center and differentiation center of *Platynemís* under similar restrictions indicates that they differ in mode of action. A loose or temporary constriction in the region of the activation center results in no abnormality but only delay. But a loose or temporary constriction in the region of the differentiation center (after functioning of the activation center) invariably results in an abnormal embryo. This is elucidated by proof that the first functions by the production and diffusion of a specific material substance, the second by dynamic movement processes which must have some as yet unknown physicochemical basis.

The realization of the importance of dynamic phenomena in development has enabled further analysis of the processes underlying determination and regulation and of the significance of the "centers." Such an analysis, based primarily on his findings in *Platynemís*, has been begun by Seidel (1934). The predominant notes in his discussion are the importance of the entire egg as a substrate for dynamic processes in determination, the subordination of the so-called "centers" to the system as a whole, and the alternation of dynamic processes and "material reactions" during development. The latter is quite evident in the sequence of events in *Platynemís*, viz., the migration of cleavage nuclei, the reaction between nuclear and cytoplasmic factors in the activation center, the diffusion of the reaction products cephalad from the activation center, reaction with the yolk system, and the contraction of the yolk system originating in the region of the differentiation center. The determina-

tion process is carried out by this alternating series of dynamic processes and material reactions, the former involving the egg system as a whole and enabling the reactions of more or less delimited substances and structures, the centers, to take place. In this light, regulation is not dependent upon the powers of definite centers but upon dynamic processes or structures made possible through such processes. It follows that regulative ability is limited by the degree of rigidity of the arrangement of all the substances and structures necessary for development. Regulation can occur only in that part of the egg in which normal dynamic processes can happen, and the degree of regulation depends upon the extent to which they can proceed unhampered. As Seidel says, the entire egg must be regarded as a system in which not only the embryonic tissues and included factors but also the extraembryonic parts must be held responsible for the determination of the organ regions.

In no other group is there a set of data for any one species sufficiently extensive to permit such a complete analysis of factor interaction. Reith (1931, 1932, 1935) shows an activation center at the posterior end of the egg of the ant and the weevil. The action of its product is similar to that in the damsel fly, but the onset of its action is not dependent on the entrance of cleavage nuclei into the region but is initiated presumably by some part or product of fertilization. However, in the beetle *Bruchus* Brauer and Taylor (1934) give a brief report indicating that the cleavage nuclei are necessary for the action of the activation center. Schnetter (1934b) was unable to demonstrate an activation center in the honeybee egg, but he has shown the presence of a differentiation center which seems to bear a causal relation to the development of the embryonic rudiment. These data, although differing in certain details from the damsel fly, indicate that dynamic factors are responsible for the arrangement of the structural elements, since regulation involves a shift in the site of initial differentiation along with that of the potency regions. The more rigid the system the less the regulative power—a principle that may involve the viscosity of the cytoplasm as suggested by the results of centrifuging the eggs of other insects. In these insects, also, determination is probably brought about by a harmonious series of interacting processes.

In the determinate type of egg (Reith, 1925; Pauli, 1927; Sturtevant, 1929) we must assume that the determination attained by such series of events is in large measure completed by the time of fertilization so that the various egg regions are "self-differentiating."

THE ANLAGEN PLAN OF THE EMBRYO

The only satisfactory worked-out anlagen plan of any indeterminate or incompletely determinate type of insect egg is that given by Seidel

FIG. 61.—Plan of the presumptive organ anlagen for the blastoderm stage. (a) dorsal side of egg, (b) left side, (c) ventral side. (ant) Antenna anlage. (eye) Eye anlage. (l) Labrum anlage. (mand) Mandible anlage. (max 1-2) Maxillae anlagen. (th 1-3) Thoracic segment anlagen. (s. oes. g) Supra-esophageal ganglion anlage. (Modified from Seidel, 1935.)

FIG. 62.—Graphic representation of the shifting of the anlage regions of the left side of the egg in reference to the movement of cell nuclei. (a) Blastoderm stage through (b), cell aggregation to form the germ band, to (c) the completed embryo anlage. Abscissa: time in hours after the two-nuclei stage. Ordinate: number of divisions from the posterior pole of the egg (one division equals 24 μ). (Modified from Seidel, 1935.)

(1935) for *Platynemís*. This is well shown in Fig. 61, which gives the blastoderm plan from all three views, and in Fig. 62, which shows the changes undergone during the formation of the embryo. The first phase of shortening of the embryo occurs simultaneously with the onset of action of the differentiation center (Fig. 62*a,b*). During this time the presumptive head and abdominal regions contract while the thoracic region increases in length as a result of two movement tendencies, one drawing the materials toward the region of the differentiation center (between the gnathal and thoracic anlagen), the other drawing the entire presumptive embryo toward the posterior end of the egg. The two tendencies coincide in front of the differentiation center but are opposed posterior to it. In the second phase of shortening (Fig. 62*b,c*) the head and gnathal anlagen expand while the thorax and abdomen shorten. During this phase the action of the differentiation center is no longer apparent. The entire embryo continues to move posteriorly and soon invaginates into the yolk. During and immediately following invagination the parts of the embryo elongate and assume larval proportions.

From Seidel's detailed discussion of irradiation defects as marks in making these maps we note the following: (1) The study is hindered by regulation processes. (2) Raising the temperature accelerates the differentiation process more than the healing process and so aids the formation of defects. (3) For certain organs the experiments show a "defect correlation" rather than a "developmental correlation." For instance there is a high correlation of eye and thoracic defects which Seidel suggests may be due to a primary defect changing yolk contraction and thereby altering the molding of the embryonic anlage. (4) Defect experiments do not show the true morphological course of development owing to the indirectness of physiological investigation; more truly they indicate a plan of the various factor regions.

Schnetter (1934*b*) gives a partial segmental map of the 12- and 24-hour blastoderm of the honeybee egg (Fig. 60) showing a shift in the prospective significance of the parts of the blastoderm between these two stages. Incidentally he says that after the formation of the germ band, the differentiation center no longer belongs to the structure of the whole egg but only to the embryo. With the shift of the presumptive embryonic parts the middle of the differentiation center shifts from division 24 of the egg to division 28.

For the determinate (mosaic) egg of the Diptera, Reith (1925) and Pauli (1927) show that the parts of the embryo originate as presumptive anlagen at the same points where they later make their appearance and that little or no regulation occurs. Sonnenblick (1934) and Howland and Child (1935) report that normal larvae and adults may develop from punctured *Drosophila* eggs from which a portion of the contents has been extruded. Owing to doubt as to the exact nature of this

extruded material it is not possible to evaluate these results. However, Sturtevant (1929) shows by genetic analysis of *Drosophila* gynandromorphs that the presumptive imaginal disks must occupy the same relative positions in the blastoderm as the points where they later make their appearance in the larva. As healing processes are not involved in this case, it seems that a shift in prospective significances such as Schnetter describes for the honeybee does not occur in *Drosophila*.

ORGAN FORMATION

Endoderm.—There are no really pertinent experimental data concerning the endoderm. The mid-gut is clearly not the primitive archenteron. It is formed, practically regenerated, later in development from rudiments. Eastham (1927) and Snodgrass (1935) review the subject from a comparative-morphological standpoint. The principal difficulty arises from the fact that in some insects the lining of the mid-gut arises from mesenteron rudiments carried in on the tips of the stomodaeal and proctodaeal invaginations, whereas in other insects this lining is produced by proliferation from the tips of *unilaminar* stomodaeal and proctodaeal invaginations. Eastman (1927) and Richards (1932) have suggested that this is only a difference in the time of determination of the functional endoderm. Using maps of prospective significance, Richards illustrates the difficulty encountered if we consider the functional endoderm as determined before its growth into the definitive mid-gut in forms in which it arises by proliferation from the unilaminar tips of the stomodaeal and proctodaeal invaginations. He suggests that in such forms it is not determined before this time and that its determination must be a function of the position of the cells concerned.

Reith (1925) reports that the mid-gut anlagen are practically the only part of the housefly egg capable of development beyond their prospective significance. In this species more than half the mid-gut is formed from one end when either the stomodaeal or the proctodaeal invagination is absent.

Germ Cells.—In certain insects (honeybees, moths, etc.) the gonads and apparently also the germ cells originate in the genital ridge of the splanchnic mesoderm. This type has not been studied experimentally during embryonic stages. In certain other insects the germ cells are segregated at the posterior pole of the egg during cleavage (called "pole cells"). Their further development is more or less independent of the rest of the embryo.

Hegner (1908, 1911) showed that the elimination of the posterior pole from the eggs of chrysomelid beetles, either by pricking and allowing part of the egg contents to flow out or by killing with a hot needle, results in an embryo lacking germ cells and possessing certain structural defects.

Reith (1925) obtained similar results with the housefly. Geigy (1931a) reports that killing the posterior pole of *Drosophila* eggs by ultraviolet irradiation during cleavage results in adults whose gonads are composed of only mesodermal elements (*i.e.*, contain no germ cells). Shorter irradiation frequently resulted in unilateral castration. The single gonad might be small, of normal size, or larger than normal. To explain these large single gonads he accepts Ruppert's suggestion that in addition to killing some of the cells the ultraviolet rays cause an adhesiveness of the germ cells so that they stick together during migration into the embryo instead of separating into two gonadal groups. More exacting data on *Drosophila* are given by Howland and Robertson (1934). They dechorionated eggs and killed part or all of the pole cells by carefully localized point cauterization. The sole effect was partial or total sterility. Therefore the pole cells are not only destined to form the definitive germ cells but incapable of being regenerated by an otherwise normal embryo.

Order of Embryonic Determination.—In addition to the determination process passing anteriorly and posteriorly from the thoracic differentiation center there is sometimes a later, secondary determination for specific organ characteristics. The data are from intermediates.

To explain intersexes of the gypsy moth, Goldschmidt (1927, 1931) postulates that the individuals begin development as one sex, that a physiological change constituting a turning point occurs, and that subsequent development is characteristic of the other sex. All structures finally determined before the time of this change will be of the former sex; all determined later will be of the opposite sex. An intersex is then a "time mosaic" of male and female parts due to differences in the time of determination of specific organ types (Shull, 1930b). In application it is assumed that in the induced change from one sex to the other the order of determination is the reverse of the order of modification in specimens successively more like the opposite sex. Applying this, Goldschmidt finds that the sex of the gonads and abdomen is determined before that of the wings and antennae. One of the most interesting points is that the onset of histological differentiation of the sexual characters does not necessarily signify that the sex of those organs is finally determined. This is clearly shown by the gonads. These may develop to the point of containing almost mature eggs or sperm and then following sex reversal have the differentiated germ cells degenerate and be replaced by the differentiation of germ cells of the opposite sex. All this occurs because of the genetic constitution of the cells themselves and presumably is not influenced by hormones.

Shull (1930b, 1931) reports that when the offspring of winged females of the aphid *Macrosiphum* are gradually changed from gamic to partheno-

genetic type, the differential features of successive offspring change at different times and rates. The first to change are the color of the antennae and the color and size of the tibial sensoria, then the body color and reproductive system. Within the reproductive system the colleterial glands and seminal receptacles change sooner than the ovarioles. However, when the mother is induced to revert to the production of gamic instead of parthenogenetic offspring, this series of changes instead of occurring in the same order occurs in the reverse order contrary to expectations based upon the time of determination hypothesis. This phenomenon remains unexplained.

HALLEZ'S LAW OF ORIENTATION

This "law" formulated by Hallez (1886) is based on the observation that the mature egg within the ovary lies in such a position that all three axes of the presumptive embryo are oriented coincidentally with those of the mother. From this it follows that the embryonic axes are determined in the egg before laying. Although this is certainly a general rule, it is not universal. In the radially symmetrical egg of the bug *Pyrrhochoris*, Seidel (1924) reports that the longitudinal embryonic axis may vary from being coincident with the longitudinal axis of the egg to being transverse to it. Also there are certain insects (e.g., *Melanoplus*, Slifer, 1932a) in which it is reported that the embryo begins to develop in the reverse position with the head toward the micropylar opening at the posterior end of the egg but that the "normal" position is attained by a later reversal of the embryo during blastokinesis. *Pteronarcys proteus*, likewise, according to Miller (1939), does not conform to the law, the prospective position of the embryo being at right angles to the longitudinal axis of the ovariole. Neither does blastokinesis alter this relation, even though the frontal (horizontal) plane of the embryo changes from a position parallel to the venter of the egg to one parallel with its lateral walls.

Seidel (1929a) reports that frontal doubling, induced by the production of splits in the egg at the beginning of cleavage and resulting in the formation of mirror-image symmetrical twins within the egg, indicates the determination of a dorsoventral axis (as well as other axes) at this early stage in the development of *Platycnemis*. Mirror images result from the inversion of one of the three axes in the formation of one partner; this presupposes the existence of polarity at least in the inverting plane. Frontal and lateral doubling have also been induced by splits in the germ band of *Tachycines* (Krause, 1934).

References

Extended bibliographies are given in two reviews on experimental embryology: one by Seidell (1936), the other by Richards and Miller (1937).

PART II
CHAPTER XIII
OLIGOENTOMATA AND APTILOTA

COLLEMBOLA

THE SPRINGTAIL (*Isotoma cinerea* Nic.)

Isotoma cinerea is a grayish species, not exceeding 1.5 mm. in length, generally distributed in northern Asia, Europe, and the United States. It occurs in colonies under recently loosened bark of trees and logs. The eggs are spherical, measuring 0.15 mm. in diameter. The nucleus lies near the center of the egg (Fig. 63) surrounded by yolk which contains yolk globules of varying sizes.

Segmentation of the eggs, as described by Philpitschenko (1912), is total and at first equal (Figs. 64, 65), the cells dividing mitotically. Each blastomere contains a nucleus, imbedded in a plasma mass which in turn is covered by the yolk. At the 16-cell stage the regularity of the divisions is lost, some of the blastomeres sinking below the surface and thus producing a morula. By the time the 64-cell stage is reached, the plasma mass with the enclosed nucleus no longer occupies the center of the blastomere but has moved to its surface. The nucleate plasma masses of the peripheral blastomeres move to the outer surface of the egg (Fig. 65), forming thus a blastoderm in subsequent cleavage stages (Fig. 66). The blastoderm is completed by additional cells migrating to the surface and possibly also by the mitotic division of cells that have already reached the periphery. Cells that have remained behind after completion of the blastoderm (Fig. 67) are the yolk cells, or vitellophags (*yc*), and also a small mass of contiguous cells, the germ cells (*gc*), which at this stage are not yet morphologically distinguishable from the yolk cells. The segregation of the germ cells occurs possibly as early as the 16-cell stage. It is possible also that some yolk cells may have migrated back into the yolk from the periphery.

FIG. 63.—*Isotoma*. Egg.

The inner layer is formed by a division of the cells of the blastoderm, giving rise finally to a complete second layer of cells below the first (Fig. 68). Within are the yolk cells (*yc*), differing from the peripheral

FIG. 64.—*Isotoma*. Egg in eight-cell stage.

FIG. 65.—*Isotoma*. 64-cell stage.

cells in being vacuolate, and the cluster of germ cells (*gc*) now well differentiated.

The embryo has now become oval with a somewhat accentuated pole where the dorsal organ will develop. The cells of this organ (*dc*), developed from the outer layer and increasing in depth, soon are sharply

FIG. 66.—*Isotoma*. Peripheral migration of cleavage cells.

differentiated from the adjacent cells, beneath which the inner layer of cells degenerate (Fig. 69). The cells of the dorsal organ later become elongate and strongly vacuolate. While this organ is developing, the outer layer of cells of the embryo begins to secrete a cuticula. After

FIG. 67.—*Isotoma*. Blastoderm stage. (*bld*) Blastoderm. (*gc*) Germ cells. (*yc*) Yolk cells.

FIG. 68.—*Isotoma*. Two-layered stage. (*gc*) Germ cells. (*il*) Inner layer. (*yc*) Yolk cells.

FIG. 69.—*Isotoma*. Anlage of dorsal organ (*dc*). (*ect*) Ectoderm.

the cuticula has formed, a deep meridian furrow (*fr*) develops around the embryo, passing behind the dorsal organ (Fig. 70). In addition to the meridian furrow, shallow wrinkles appear on the surface of the embryo.

FIG. 70.—*Isotoma*. Longitudinal section. Development of meridian furrow (*fr*). (*do*) Dorsal organ. (*ect*) Ectoderm. (*gc*) Germ cells. (*il*) Inner layer. (*yc*) Yolk cell.

As the meridian furrow deepens, the dorsal organ is swung out of position (Fig. 71, *do*). The cuticula (*cut*), designated by Claypole (1898) as the first crenated membrane, now loosens and lies free between embryo and

FIG. 71.—*Isotoma*. Longitudinal section. Formation of first crenated membrane (*cut*). (*do*) Dorsal organ. (*fr*) Furrow. (*yc*) Yolk cell.

chorion, and a new cuticula is formed. The chorion then ruptures, and the embryo expands, causing the meridian furrow and all wrinkles to smooth out, the chorion (*ch*) adhering cap-like in two sections to the

surface of the embryo (Fig. 72). At the time the chorion ruptures, the second cuticle (*cut 2*) of the embryo also loosens to form the second crenated membrane of Claypole (1898).

After the chorion has ruptured, it is apparent that the embryonic rudiment (germ band) forms a belt around the yolk, the head and tail ends nearly meeting at the dorsal organ (Fig. 72). The cells of the germ band are columnar and two-layered, the outer forming the ectoderm; the inner, the inner layer. The cells of the original blastula which lie on the sides of the egg have become flattened and thinner and have lost

FIG. 72.—*Isotoma*. Rupture of chorion (*ch*). (*cut 1, cut 2*) First and second crenated membranes. (*gc*) Germ cells. (*hl*) Head lobes.

the inner-layer cells which have migrated into the inner layer of the germ band (Figs. 73, 74). According to Uzel, the germ band of *Campodea* is formed in a similar manner. Since the flattened cells on the sides together with the germ band form an envelope covering the yolk, and since they are a part of the original blastula, these flattened cells may be called the "amnioserosa." The germ band now shows distinct head lobes (Fig. 76, *hl*), a broad tail lobe, and four body segments. After the rupture of the chorion, which takes place about five days after egg deposition, the dorsal organ takes on another character. The cells themselves retain their previous appearance, with vacuolate inner and a fibrillar outer part, but are more expanded with the outer fibrillar part projecting

FIG. 73.—*Isotoma*. Cross section of head. (*cut 1, cut 2*) First and second crenated membranes. (*ect*) Ectoderm. (*il*) Inner layer.

FIG. 74.—*Isotoma*. Cross section of posterior end. (*am. ser*) Amnioserosa. (*cut*) Crenated membranes. (*do*) Dorsal organ. (*ect*) Ectoderm. (*gc*) Germ cells. (*il*) Inner layer.

beyond the cellular layer and spread out mushroom-like. The outer end in most cases shows a connection with the second crenated membrane (Figs. 72, 74) but in some cases is still connected with the first crenated membrane (Fig. 75). The dorsal organ appears to be glandular and may

FIG. 75.—*Isotoma*. Dorsal organ. (*am. ser*) Amnioserosa. (*cut*) Crenated membrane.

possibly be concerned with the molting of the crenated membranes. Buds of head and thoracic appendages are now evident as well as the anterior abdominal segments (Figs. 76, 77). A section through the region of an appendage now reveals that the inner layer consists of two layers laterally and of one layer in the middle which indicates developing coelomic sacs ("somites") without a cavity (Fig. 78). In this species

FIG. 76.—*Isotoma*. Embryo before blastokinesis. (*ant*) Antenna. (*do*) Dorsal organ. (*gc*) Germ cells. (*hl*) Head lobe. (*lb*) Labium. (*md*) Mandible. (*mx*) Maxilla. (*th*) Thoracic appendages.

Philipstchenko (1912) found no evidence of an intercalary segment between antennae and mandibles. With the increase in size of the antennae their position becomes more lateral although at this stage still postoral.

Meanwhile the neuroblasts have become evident and distinctly differentiated from the adjacent cells which lie between the buds of the appendages (Fig. 78, *neur*). A neural furrow, however, has not been observed. As development progresses, a peculiar form of blastokinesis occurs which is neither a rotation nor a revolution. The ventral surface of the embryo

FIG. 77.—*Isotoma*. Sagittal section of early embryo. (*do*) Dorsal organ. (*ect*) Ectoderm. (*gc*) Germ cells. (*il*) Inner layer. (*lb*) Labium. (*md*) Mandible. (*th*) Thoracic rudiments. (*yc*) Yolk cell.

between the first maxillary segment and the first abdominal segments becomes somewhat flattened and then begins to push into the yolk (Fig. 79). By this time antennae and thoracic legs have increased in length, and segmentation has begun. The mouth parts have increased in size, and there appear between them the paired parts of the hypopharynx, the

FIG. 78.—*Isotoma*. Cross section. (*coel*) Coelome. (*ect*) Ectoderm. (*mds*) Middle strand of inner layer. (*neur*) Neuroblasts.

superlinguae (paraglossae of Philpitschenko), which, however, are not provided with a corresponding ganglion. On the first abdominal segment there develops a pair of buds which later are modified into the *tubus ventralis*. As in the other appendages, the mesoderm here fills the evagination. The posterior part of the abdomen now also becomes seg-

mented, three divisions posterior to the *tubus ventralis* usually being visible, while at the posterior end the beginning of the proctodaeum is

FIG. 79.—*Isotoma*. Longitudinal section. (abd) Abdominal rudiments. (do) Dorsal organ. (hl) Head lobe. (md) Mandible. (mx) Maxillae.

evident. The stomodaeum, which made its appearance a short time before, has lengthened, the apex of the invagination reaching the yolk (Fig. 80), the inner layer being absent at this point. Both in front of and behind the stomodaeum is a cell mass which will give rise to the anterior

FIG. 80.—*Isotoma*. Sagittal section of anterior end. (am.ser) Amnioserosa. (hl) Head lobe. (lr) Labrum. (nc) Nerve tissue. (stom) Stomodaeum.

FIG. 81.—*Isotoma*. Cross section of mandibular segment. (coel) Coelome. (ect) Ectoderm. (md) Mandible. (mds) Middle strand of inner layer. (n) Nerve tissue. (sl) Superlingua.

end of the future digestive epithelium of the ventriculus. Meanwhile, the cells of the nervous system (Figs. 81, 82) become more sharply marked,

distinctly separated into right and left halves and covered dorsally by a single layer of cells.

FIG. 82.—*Isotoma*. Cross section of thorax. (*coel*) Coelome. (*ect*) Ectoderm. (*mds*) Middle strand of inner layer. (*nc*) Nerve cord. (*th*) Thoracic appendage.

The invagination of the embryo into the yolk by buckling of the thoracic section now has reached its maximum (Figs. 83, 84). The dorsal organ (*do*) now lies in the neck region of the embryo covered laterally by the body wall and in part by the serosa. The yolk is still completely

FIG. 83.—*Isotoma*. Embryo after blastokinesis. (*abd*) Abdominal appendage. (*ant*) Antenna. (*do*) Dorsal organ. (*md*) Mandible.

enclosed by embryo and amnioserosa. In this stage the anterior and posterior parts of the body are nearly parallel, the appendages directed toward each other, only the antennae and the anlagen of the appendage

of the fourth abdominal segment (the furca), as well as abdominal segments five and six, being directed outwardly. The embryo retains this position until emergence. It is obvious that frontal sections made of the head of the embryo at this time, if carried on through the body, would

FIG. 84.—*Isotoma*. Late embryo. (ant) Antenna. (do) Dorsal organ. (fk) Furca.

furnish frontal sections of the abdomen but cross sections of the thorax. The proctodaeal invagination is located in the sixth segment; the telson is fused with it and represented by a small supra-anal and two subanal lobes.

As development progresses, the edges of the ectoderm of the body wall, by proliferation, gradually replace the amnioserosa which forms the temporary lateral and dorsal wall of the embryo. Meanwhile, the lower layer has become segmented to form the somites or coelomic mesodermic masses. In the gnathal region of the head, the inner-layer bridge above the neural ridge, which connects the right and left sides, has disappeared (Fig. 85) but is still present in thorax (Fig. 82) and abdomen. The lateral mesodermic somites are apparently

FIG. 85.—*Isotoma*. Cross section of maxillary segment. (am. ser) Amnioserosa. (coel) Coelome. (mx) Maxilla. (n) Nerve cord. (palp) Maxillary palpus. (prot) Protocerebrum.

lacking in the sixth abdominal segment, but the posterior inner-layer cell mass covering the tip of the proctodaeal invagination is present (Fig. 86), which, like the anterior cell mass, takes no part in the formation of the 13 pairs of somites.

At this time, *i.e.*, about 10 days after egg deposition, there are 13 pairs of nerve ganglia, those of the abdomen as yet less pronounced, none being

FIG. 86.—*Isotoma*. Sagittal section of posterior end. (*abd*) Abdominal appendages. (*gc*) Germ cells. (*il*) Inner layer. (*proct*) Proctodaeum.

found in the sixth segment, and indicated only by the apparent presence of ephemeral neuroblasts in the fifth segment. The head (Figs. 85, 87, *n.ggl*) and thoracic ganglia are well developed; of the three brain segments the tritocerebrum is smallest and postoral in position. The germ cells,

FIG. 87.—*Isotoma*. Half of cross section through labial segment. (*ggl*) Ganglion. (*hg*) Tubular head gland. (*lb*) Labium. (*palp*) Labial palp.

FIG. 88.—*Isotoma*. Oblique section through mandibles. (*am. ser*) Amnioserosa. (*br*) Brain. (*md*) Mandible. (*sl*) Paraglossa. (*stom*) Stomodaeum.

though increased in number at this stage, are still in the yolk near the posterior part of the embryo (Fig. 86).

From the time the chorion ruptures until after completed blastokinesis, 5 days have elapsed, or 10 days since the deposition of the eggs. The remaining steps in the development, the completion of body parts and organs until hatching, require on an average 10 more days, or a total of 20 days of incubation. During this final period of 10 days the number of simple eyes on each side increase to eight, and the appendages acquire the definitive number of segments: four for the antennae, five for the legs, and three for the fork. Mandibles and maxillae also increase in size (Fig. 88). The dorsal closure of the body is accomplished by the growth of the ectoderm to replace the degenerating cells of the amnioserosa. The dorsal organ is taken into the alimentary canal at the time of the closure of the dorsal wall and digested with the remains of the yolk (Fig. 89). Shortly before emergence of the insect the dorsal organ as well as

FIG. 89.—*Isotoma*. Oblique, almost frontal section of thorax of late embryo. (ac) Alimentary canal. (do) Dorsal organ. (f) Fatty tissue.

the remains of the yolk have entirely disappeared from the alimentary canal.

The first evidence of digestive epithelium development is seen about 10 hours after egg deposition. This cellular layer originates from an anterior, a posterior, and a diffuse median anlage (Figs. 90, 91). Above the stomodaeum is a mass of cells which will give rise to the esophageal muscle (Fig. 90, *mus*). The apex of the stomodaeum is free from inner-layer cells. Below the stomodaeum (Fig. 90, *mge*) is another mass which will give rise to the anterior pair of rudiments of the mid-gut epithelium as well as muscles of the lower wall of the esophagus. A mass of inner-layer cells surrounds the tip of the proctodaeum (Fig. 91, *mge*) which will give rise to the posterior end of the mid-gut epithelium. As has already been described, dorsad of the developing nerve cord there is a sheet of inner-layer cells connecting the right and left coelomic masses (Figs. 81, 82, *mds*). This is the middle strand. With the development of the nerve cord and the growth of the neural ridge the cells of the middle strand are liberated, some of them migrating to the yolk surface where

they later unite with the cells of the anterior and posterior mid-gut epithelial ribbons. The middle strand gives rise to the blood cells. As development goes on, stomodaeum and proctodaeum become longer, the

FIG. 90.—*Isotoma*. Sagittal section through head. (am. ser) Amnioserosa. (br) Brain. (lr) Labrum. (mge) Mid-gut epithelium. (mus) Muscle. (n) Nerve tissue. (stom) Stomodaeum. (yc) Yolk cell.

FIG. 91.—*Isotoma*. Sagittal section of posterior end of body. (am. ser) Amnioserosa. (mge) Mid-gut epithelium. (mus) Muscle. (n) Nerve tissue. (proct) Proctodaeum.

former somewhat geniculate (Fig. 92), the latter widening at the tip and freed from inner-layer cells. Malpighian tubules do not develop.

The cells of the anterior and posterior cell masses (mid-gut epithelium rudiments) now enlarge; from each lateral edge a cell strand arises, the two arising from the stomodaeum growing backward, those from the

FIG. 92.—*Isotoma*. Sagittal section of anterior end. (br) Brain. (do) Dorsal organ. (lr) Labrum. (mus) Muscle. (n. ggl) Nerve ganglion. (stom) Stomodaeum.

proctodaeum growing forward (Fig. 93) until these strands (ribbons) meet. The widening of the ribbons soon causes them to unite below, thus forming the lower wall of the ventriculus and later, by the increasing width of the ribbons, closes the alimentary canal on the dorsal side also.

The part played by cells from the middle strand has already been mentioned. The muscle layer of the ventriculus, as in other insects, arises from the splanchnic wall of the mesoderm.

FIG. 93.—*Isotoma*. Frontal section through posterior end of body. (g) Gonad and duct. (lim.m) Limiting membrane. (mge) Mid-gut epithelium. (mus) Muscle. (proct) Proctodaeum.

FIG. 94.—*Isotoma*. Sagittal section of late embryo. (ant) Antenna. (br) Brain. (ggl) Ganglion. (gut.1) Esophagus. (gut.2) Mid-gut. (gut.3) Hind-gut. (suboesg) Subesophageal ganglion. (tv) Tubus ventralis.

Before the yolk in the ventriculus has wholly disappeared, the thin wall (Fig. 93, *lim.m*) that separates the proctodaeum from the ventriculus is absorbed, thus establishing continuity. The membrane that separates

stomodaeum from the ventriculus, however, is not broken down until the yolk is wholly absorbed. It may be observed that late in the developmental period a blue pigment forms in the ectoderm, a characteristic common to the adult also. This pigment is also present in both stomodaeum and proctodaeum but absent in the cells of the ventriculus, an indication, perhaps, that the mid-section and the end sections of the alimentary canal have a different origin. There is no indication in *Isotoma* that the yolk cells play any part in the formation of the digestive epithelium.

After 10 days' incubation the neuropile is first in evidence in the dorsal part of each ganglion with nerve cells surrounding it. The three-seg-

FIG. 95.—*Isotoma*. Cross section through first abdominal segment. (*am. ser*) Amnioserosa. (*ggl*) Ganglion. (*mge*) Mid-gut epithelium. (*neurp*) Neuropile.

FIG. 96.—*Isotoma*. Cross section of third abdominal segment. (*am. ser*) Amnioserosa. (*gc*) Germ cells. (*ggl*) Ganglion. (*mge*) Mid-gut epithelium. (*neurp*) Neuropile. (*ret*) Retinaculum.

mented brain is fully formed during the latter half of the developmental period, when also the ganglia of three gnathal segments fuse into the definitive subesophageal ganglia. Later also the cephalization and fusion of the abdominal ganglia take place (Fig. 94, *ggl*). In general, the development of the nervous system appears to follow the course of pterygote insects.

The differentiation of the mesodermic somites in each segment begins about 10 days after egg deposition. Whether the absence of an epineural sinus is characteristic (Figs. 95, 96) or due to an artifact is not apparent. The laterodorsal muscles are derived from the somatic walls of the somites; mesad of this is the fat body (*f*); and still nearer the median line, the ventral longitudinal muscles, both derived from the median somatic walls of the somites. The splanchnic wall of the somites furnishes the muscles of the ventriculus and later also takes part in the formation of the

gonads. On the dorsal edge of the developing somite (Fig. 97, *cbl*) are the minute cardioblasts.

Of special interest are labial glandular structures, not found in pterygote insects unless they correspond to the embryonic esophageal gland. In *Isotoma* some time before the differentiation of the mesodermic somites, in the labial segment at the level of the nerve ganglion, a little glandular vesicle (Fig. 87, *hg*) is in evidence. Later during the course of development the vesicle becomes flask-shaped with a slender duct leading toward but not communicating with the exterior (Fig. 98, *hg*). This

FIG. 97.—*Isotoma*. Cross section of thorax. (*am. ser*) Amnioserosa. (*cbl*) Cardioblasts. (*do*) Dorsal organ. (*ggl*) Ganglion. (*mge*) Mid-gut epithelium. (*mus*) Muscle. (*neurp*) Neuropile. (*yc*) Yolk cell.

FIG. 98.—*Isotoma*. Parasagittal section through head. (*br*) Brain. (*oc*) Ocelli. (*ggl*) Ganglion. (*hg*) Head gland.

structure is therefore not of ectodermic origin, though later an ectodermic connection with the exterior is established. According to the evidence presented by Philpitschenko (1912) these glandular structures appear to be homologous with nephrideal head glands found in certain other Arthropoda.

As has already been stated, the germ cells of *Isotoma* were segregated in the 16- or 32-cell stage. By the time the proctodaeum is well formed, the germ cells have divided into two groups and pass from the yolk into the tissue of the visceral wall of the mesodermic somites (Fig. 99, *gc*) of the third and fourth abdominal segments. Later the germ cells migrate forward into the first to the third segments where the gonads form ventrad of the alimentary canal. The gonads and their ducts develop from the visceral mesoderm, the latter in the fourth abdominal segment. By reason of their ventral position, the gonads do not develop a terminal filament.

The embryonic development of the collembolan *Anurida maritima* as figured and described by Claypole (1898) agrees in most particulars with

that of *Isotoma cinerea* as outlined above. Philpitschenko (1912) points out a few discrepancies which he ascribes to differences in interpretation.

It is conceivable that the "diffuse" middle strand here described together with the cell masses that surround the stomodaeal and proctodaeal rudiment constitutes the preprimordium of the entoderm and that cells immediately adjacent represent mesoderm.

FIG. 99.—*Isotoma*. Oblique frontal section of posterior end of body. (*abd*) Abdominal appendages. (*gc*) Germ cells. (*mus*) Muscle. (*proct*) Proctodaeum. (*yc*) Yolk cells.

The species occurs in Europe, but members of the genus occur also in the United States. The eggs, according to Uzel (1898), are laid during the warmer months in clumps of four or five or, less commonly, either fewer or

DIPLURA

Campodea staphylinus Westw.

Campodea staphylinus is a slender insect about 6 mm. long living in damp places under stones or in rotten wood and leaves.

FIG. 100.—*Campodea*. Section of egg with germ disk. (*bld*) Blastoderm.

FIG. 101.—*Campodea*. Section of egg with germ disk.

more. One egg of the clump is stalked to form a support for the entire cluster. The egg, which is spherical, measures about 0.4 mm. in diameter.

The periplasm is exceedingly thin. By the time there are 64 cleavage nuclei, each in an island of cytoplasm, they reach the surface where the nuclei continue to divide to form the blastoderm. At this stage no nuclei remain behind in the yolk. At one side of the egg a small circular area is formed where the blastoderm is thicker and provided with two

FIG. 102.—*Campodea*. Section of egg with entoderm cells (*ent*).

irregular layers of nuclei (Fig. 100). From all parts of the surface, nuclei migrate toward the margin of the thicker area, with the result that the upper two-thirds of the blastoderm loses most of its nuclei and the lower third gains them (Fig. 101). Nuclei then leave the center of the thickened area and pile up on the sides, leaving but a single layer in the center (Fig. 102). Occasional cells come to lie above on the inner side of the

FIG. 103.—*Campodea*. Section of egg with mesoderm cells (*mes*). (*ent*) Entoderm.

FIG. 104.—*Campodea*. Section of egg. (*am. ser*) Amnioserosa. (*ect*) Ectoderm. (*ent*) Entoderm. (*mes*) Mesoderm.

thickened ring of cells. These are the future entoderm cells (Fig. 102, *ent*). Another migration of nuclei then takes place, reducing the thickness of the ring wall and restoring nuclei to the upper part of the egg as well as to the center of the ring (Fig. 103). The cells that increase in number in the center of the ring later give rise to the mesoderm (*mes*).

Numerous scattered entoderm cells (*ent*) that are derived from the entoderm cells of the ring wall (Fig. 102, *ent*) and that were pushed toward the yolk may now be observed on the inside of the thin blastoderm wall (Fig. 103, *ent*). As development proceeds, the upper, nonembryonic part of the blastoderm becomes thin, while in the lower or embryonic part the outer layer of ectodermal cells becomes columnar and those of the inner layer flat (Fig. 104). The germ band is broadest at the head end where the head lobes are prominent, narrower in the middle section, and again somewhat wider at the posterior end (Fig. 105). At this stage the thin lateral parts of the original blastoderm may be designated as the "amnio-

Fig. 105.—*Campodea*. Germ band.

Fig. 106.—*Campodea*. Embryo with dorsal organ (*do*).

serosa." Meanwhile, the inner-layer mesoderm in the abdomen has divided longitudinally. Segmentation of head and thorax occurs with the appendages (labrum, antennae, mouth parts, and legs) becoming evident. With the segmentation of the anterior part of the abdomen the proctodeal invagination appears. When segmentation of the abdomen is completed, the appendages of the intercalary (premandibular) segment become distinct, and later rudimentary appendages form on the intermediate abdominal segments. The last (tenth) abdominal segment later will be provided with cerci.

The entoderm cells (Fig. 104, *ent*), which at an early stage are found rather uniformly dispersed on the inner surface, later migrate into the yolk where they become distributed. Of their further history Uzel (1898) has given no information.

Before the segmentation of the abdomen has been completed, a dorsal migration of some cells from the amnioserosa gives rise to a primary dorsal organ (Fig. 106, *do*). Meanwhile an extremely thin cuticula has been shed from the surface of the embryo and envelopes and lies close

to the inner surface of the chorion. At this time also the labrum gradually elongates to overhang the stomodaeal invagination.

Blastokinesis occurs in the same manner as in *Isotoma*, a buckling in of the thoracic region (Fig. 107) until the embryo lies with its dorsal side turned outwardly (Fig. 108), the amnioserosa shrinking and thereby crowding the yolk into the embryo. During this process the dorsal organ diminishes in size but maintains its position near the posterior margin of the head lobes. A further lengthening of the embryo causes the caudal end to push past the left side or, less commonly, the right side of the head. The embryo thereby acquires a somewhat spiral position in the egg. The

FIG. 107.—*Campodea*. Blastokinesis of the embryo.

FIG. 108.—*Campodea*. Embryo after completion of blastokinesis. (am. ser) Amnioserosa. (do) Dorsal organ.

mid-gut epithelium, according to Uzel, is not completed until after emergence of the insect from the egg which takes place 14 days after egg deposition.

THYSANURA

THE SILVERFISH (*Lepisma saccharina* L.)

The egg of *Lepisma saccharina* is elongate, oval, and about 1 mm. long, with the micropyle at the anterior end of a firm, tough chorion. The cleavage nuclei migrate to the periphery except for some yolk cells which remain behind. The minute germ disk, as described by Heymons (1897), develops in the ventroposterior part of the blastoderm. Posterior to the middle of the germ disk on the yolk side, a small area of inner-layer cells appears probably by migration from the germ disk. The cells of the blastoderm are large and flat; those of the germ disk small and closely packed. The former, since they take no part in the formation of the embryo but form an envelope, constitute the serosa. The germ disk now sinks into the yolk (Fig. 109), the membranous part surrounding the disk constituting the amnion. The amniotic cavity, unlike that of most insects, is relatively large and remains open to the exterior at the amniotic

pore or point of invagination, except for a chitin plug which forms when a thin chitin membrane is secreted from the outer surface of the serosa. Meanwhile segmentation of the body and development of the appendages and internal organs go on. The mesoderm develops as a single layer of cells interrupted on the median longitudinal line except at the cephalic end. When the dorsal ectoderm wall closes, the coelomic sacs, which had remained open on the dorsal side until this time, also close. Coelomic sacs are found in the antennal, gnathal, thoracic, and 10 (possibly 11) abdominal segments. The sacs (Fig. 109) in structure strikingly resemble those of the Blattidae. The development of muscles, fat, heart, blood

FIG. 109.—*Lepisma*. Longitudinal section. (am. cav.) Amniotic cavity. (mes) Mesoderm. (proc.) Protocephalon. (ser) Serosa. (y) Yolk.

cells, and nervous system resembles those of the Orthoptera. The ganglion cells of the central nervous system, however, do not cover the dorsal surface of the neuropile of the ganglia. The tracheal system develops rather late, the invaginations appearing about the time of the eversion of the embryo from the yolk. Two pairs of thoracic and 9 (or possibly 10) pairs of abdominal spiracles develop. Oenocytes seem to be lacking.

When the segmentation of the embryo is completed the serosa contracts anterodorsally, and the amnion everts, the embryo thereby being drawn toward the periphery (Fig. 110). Following this the amniotic pore expands, the embryo everts, and the amnion stretches over the surface (Fig. 111, *am*) as the serosa (*ser*) still further contracts. The two membranes together with the embryo thus form an envelope around the yolk. The embryo now lies on the surface except for the ventrally flexed part of the abdomen. The shrinkage of the serosa involves a crowding together

of its cells. As development continues, the serosa is drawn into the yolk which in turn is gradually absorbed, so that at the time of the dorsal closure only that remains which lies in the mid-gut.

The germ cells are recognizable very early at about the time the germ band begins to sink into the yolk. They form a mass of cells at the caudal end of the germ disk, distinctly separated from the ectodermal cells.

FIG. 110.—*Lepisma*. Longitudinal section. (am) Amnion. (br) Brain. (c. fil) Caudal filament. (fg) Frontal ganglion. (ggl) Abdominal ganglion. (hyp) Hypopharynx. (lb) Labium. (lim. m) Limiting membrane. (lr) Labrum. (proct) Proctodaeum. (th. ggl) Thoracic ganglion. (visc. ggl) Visceral ganglion.

They are also readily distinguished from the mesoderm cells by their somewhat larger nuclei. Later the germ cells migrate, in a manner similar to those of the Orthoptera, to the segmentally arranged genital ridges, five pairs of which develop in the female and three double pairs in the male. Terminal filaments are developed neither in the ovaries nor in the testes.

The development of stomodaeum and proctodaeum offers nothing unusual. From the latter two pairs of small evaginations arise which form the Malpighian tubules. The origin of the mid-gut, however,

differs from that of most insects. When the serosa is completed, the yolk will be seen to have divided into numerous, not very sharply defined yolk spherules, or compartments, within each of which is a yolk nucleus (Fig. 109). The yolk nuclei, derived from yolk cells, differ but little from those of the germ disk. After the young larva leaves the egg, the yolk spherules separate from each other, retracting toward the mesodermal wall of the mid-gut, thus leaving a lumen which is filled with a fluid,

FIG. 111.—*Lepisma*. (am) Amnion. (lr) Labrum. (md) Mandible. (mx) Maxilla (proct) Proctodaeum. (ser) Serosa.

probably in part derived from dissolved albuminous and fatty substances. After the rupture of the stomodaeal membrane, the lumen extends into the fore-gut. Some of the yolk nuclei, each of which is now surrounded by a plasma layer and therefore properly called a "yolk cell," migrate out of the yolk spherules. Perhaps instead of a migration it may rather be a dissolving and absorption of the yolk substance. However that may be, the yolk cells attach themselves to the mid-gut mesoderm wall, where they undergo active mitotic division, thus forming here small clusters of five or six cells each (Fig. 112, *crypt*). Heymons (1897) did not follow the

development of the larvae further than this point, but in some captured specimens only a little larger than the reared ones the mid-gut epithelium had already assumed its definitive form, and he therefore assumed that further proliferation of the clusters of yolk cells gave rise to the mid-gut lining. The definitive lining (digestive epithelium) consists of rather large cylindrical cells between which at intervals are clusters (*nidi*) of smaller, closely crowded replacement, or regenerative, cells. As no proliferations of cells at the tips of either stomodaeal or proctodaeal

FIG. 112.—*Lepisma*. Cross section of seventh abdominal segment. (f) Fat. (ggl) Seventh abdominal ganglion. (h) Heart. (mus) Muscle. (st) Stigmata. (y.nu) Yolk nucleus.

invaginations take place, Heymons (1897) concludes that in *Lepisma* the mid-gut epithelium is of entodermal origin.

OBSERVATIONS ON THE DEVELOPMENT OF APTERYGOTA IN GENERAL

Cleavage in *Campodea* and *Lepisma* is superficial; in *Isotoma*, *Anurida*, *Achorutes*, and *Macrotoma*, as in many arachnids and crustaceans, it is at first total but later becomes superficial.

The entoderm in *Campodea*, according to Uzel, arises from a thick ring of cells at the ventral pole of the egg, the cells later migrating to the inner wall of the blastoderm and thence into the yolk. The yolk cells are the source of the mid-gut epithelium in *Lepisma* according to Heymons (1897). In *Macrotoma* and *Achorutes* cleavage cells migrating back from the

periphery before and after the formation of the blastoderm and gathering in a ball of cells in the center of the egg are said by Uzel (1898) to be entodermal. The mid-gut epithelium arises from bipolar rudiments, augmented by cells from the middle strand, in *Isotoma* (Philipschenko, 1912).

The germ band in *Lepisma* and *Campodea* is formed by a migration of cells to the ventral side where the band develops. In *Isotoma* the entire blastoderm first acquires an inner layer. Later the inner layer breaks down on the sides, leaving a broad strip of inner-layer cells in the dorso-ventral circumference interrupted only between the future head and tail where the primary dorsal organ is formed. With *Macrotoma* the first anlage of the germ band appears in the form of four blastoderm thickenings which will develop into the head lobes and the mandibular segment. The germ band in *Isotoma*, *Anurida*, and *Campodea* is very long, extending nearly around the egg periphery. At blastokinesis the embryo reverses its position, bringing the dorsal side to the surface by a buckling process (Figs. 79, 84, 107), as in *Geophilus*. This type of reversal occurs also in *Macrotoma*. In *Lepisma* and *Machilis* the very short germ band sinks into the yolk with formation of a sort of amnion and serosa.

The abdomen of *Campodea* in the embryo as well as in the adult is composed of 10 distinct segments, in addition to the anal plates. In the young embryo of *Lepisma* there are 11 abdominal segments in addition to the anal plates. In older embryos of *Macrotoma* but 6 abdominal segments may be counted in addition to the minute anal plates. Rudiments of appendages develop on the intercalary (premandibular) segment in *Campodea*. At first postoral in position, as are also the antennae, they later migrate forward.

References

- COLLEMBOLA: *Achorutes armatus*; Uzel (1898). *Anurida maritima*; Claypole (1898, 1899), Folsom (1900), Ryder (1886b). *Anurophorus laticis*; Lemoine (1883). *Entomobrya (Degeeria) spp.*; Uljanin (1875). *Hypogastrura purpurascens*; Strebel (1932). *Isotoma sp.*; Packard (1872). *I. cinerea*; Philipschenko (1912). *I. grisea*; Prowazek (1900). *I. walkerii*; Packard (1871b). *Neanura muscorum (Achorutes tuberculatus)*; Uljanin (1875). *Orychiurus (Anurophorus) sp.*; Uljanin (1875). *Podura sp.*; Barrois (1897), Uljanin (1875), Weismann (1882). *Sminthurides aquaticus*; Falkenhan (1932). *Sminthurinus aquaticus*; Strebel (1932). *S. niger*; Strebel (1932). *Sminthurus sp.*; Wagner (1900). *S. fuscus*; Lemoine (1883). *Tetradontophora gigas*; Heymons (1896b). *Tomocerus plumbeus*; Hoffmann (1911). *T. vulgaris*; Uzel (1898).
- APTILOTA: *Thysanura*; Bekker (1927), Brandt (1878), Uzel (1897a, 1898). *Campodea sp.*; Grassi (1886). *C. staphylinus*; Uzel (1897b, 1898). *Japyx solifugus*; Grassi (1886). *Lepisma saccharina*; Heymons (1896b, 1897b, 1905). *Machilis alternata*; Heymons (1905).

CHAPTER XIV

EPHEMERIDA, ODONATA, PLECOPTERA, EMBIARIA, DERMAPTERA, HEMIMERINA

EPHEMERIDA

THE MAY FLY (*Ephemera vulgata* L.)

The eggs of *Ephemera vulgata* are ovoid, about 0.3 mm. in diameter, and covered with a gelatinous substance which swells when deposited in the water. The developmental period, at a temperature of 20 to 25°C., is about 10 or 11 days. The germ band arises at the posterior end of the egg. As development progresses, the posterior end of the germ band is pushed into the yolk until it reaches the anterior end of the egg and then with a further increase in length becomes S-shaped in the yolk. The embryo is thus of the immersed type, resembling that of the damsel flies. The movement in blastokinesis likewise takes place as with the damsel fly, whereby the embryo assumes a position on the ventral surface of the egg.

Segmentation of the embryo, according to Heymons (1896c), occurs while it is still immersed in the yolk. On the abdomen appear 11 pairs of small, flat appendages the last of which will develop into the pair of caudal filaments (cerci). The median filament is the elongate tergite of the eleventh abdominal segment.

The tracheal system, which arises as in terrestrial insects from lateral ectodermal invaginations, does not contain air at the time of hatching and is not fully developed until later. The mid-gut in the newly hatched nymph is still filled with yolk; the stomodaeum and proctodaeum, on the other hand, are well developed, the latter with two Malpighian tubule evaginations. Gonads are feebly differentiated during embryonic life.

According to Heymons (1896a), the serosa in the Ephemeridae consists of large pavement cells; the amnion, however, is made up of small cells similar to those of the germ-band from which it is clearly derived.

Murphy (1922) makes the observation that in the embryo of *Baetis posticus* the early appearance of the inner lobe of the mandible and the fact that it is articulated but has no musculature suggest the possibility of a primitive structure. It occupies the same relative position on the mandible as the lacinia mobilis of certain crustacea (*Mysis*, *Arolana*). Embryological evidence indicates that the movable inner lobe of the May-fly mandible is a lacinia. A mandibular palp is present at no stage of embryonic development. *Ephemera vulgata* used by Heymons for his

embryological study is a burrowing May fly. The mandibular tusk, which he calls the "morphological equivalent of a mandibular palp," is a secondary modification appearing at the time of differentiation of the canines and molar region. It is lateral in origin but arises from the outer apical region.

ODONATA

DRAGONFLIES AND DAMSEL FLIES

The eggs of *Libellula pulchella*, *Erythemis simplicicollis*, and *Plathemis lydia*, the three species of Odonata studied by the junior author, vary

FIG. 113.—*Libellula*. A–C, longitudinal section, successive stages. (cc) Cleavage cells. (nu) Nucleus.

slightly in shape and size, but their development is similar in all respects. They are laid in the same localities, and the actions of the female during oviposition are similar. The females of all three species lay the eggs as they fly in circles over the water and dip their abdomens momentarily to wash off the egg mass being extruded from the oviduct. The eggs of the mass sink to the bottom singly, and each soon produces a viscid substance which causes the egg to stick to anything it touches. Sometimes the eggs drift into a clump and become deeply imbedded in a mass of jelly. The eggs of *Plathemis lydia* are ovoid in form but are pointed at both ends. There is no difference between dorsal and ventral sides. The eggs of *Libellula pulchella* and *Erythemis simplicicollis* are approximately the same size but are smaller than those of *Plathemis* and are not so pointed.

The shell of all three is tough and creamy white; the yolk is very dense; and the globules often appear cuboidal or hexagonal in cross section. The peripheral cytoplasm, which is very thin, adheres so closely to the chorion that a thin vitelline membrane reported in other species was not seen. Maturation and fertilization were not observed. In the egg of *Libellula*, three hours old, a nucleus is present at the center of the yolk,

indicating that maturation and fertilization occur previous to that time (Fig. 113A). A short time later, cleavage nuclei are on their way to the

FIG. 114.—*Libellula*. (am) Amnion. (bld) Blastoderm. (gb) Germ band. (hl) Head lobe. (y) Yolk.

periphery (Fig. 113B). In an egg six hours old two nuclei and three cytoplasmic masses appear, indicating this to be probably the eight-cell stage.

The nuclei, as they migrate from the center of the egg toward the periphery, are surrounded by small amounts of cytoplasm. The yolk mass seems to be closely packed so that each nucleus is tightly wedged in by blocks of yolk with cytoplasm streaming out in the interstices between blocks. When the nuclei reach the surface and enter the cortical layer, they are spaced far apart (Figs. 113C, 114A), and the cytoplasm between them appears thread-like in cross section (Fig. 116, *pr*). Figure 115 shows a section of the blastoderm after the cleavage nuclei have multiplied for some time and the yolk in the vicinity has been liquefied.

After the blastoderm is completed, a strip on the ventral side of the egg thickens, forming the germ band, the remainder of the blastoderm becoming very thin. A depression then appears near the posterior end of the

FIG. 115.—*Libellula*. Section of blastoderm (bld). (ch) Chorion. (y) Liquefied yolk.

germ band. As this depression deepens, the germ band moves toward the posterior pole of the egg and withdraws into the yolk through the depression until about half its length is immersed, the rest, including

FIG. 116.—*Libellula*. Posterior end of egg. (cc) Cleavage cell. (ch) Chorion. (pr) Periplasm.

the head lobes, remaining at the surface (Figs. 114*B, C*). Therefore the germ band of these species is only partially immersed, differing from some other members of the order in this respect.

FIG. 117.—*Calopteryx*. Longitudinal sections. A–C, successive stages. (am) Amnion. (am. cav) Amniotic cavity. (ant) Antenna. (gb) Germ band. (hl) Head lobe. (ser) Serosa. (From Brandt.)

According to Brandt (1869), in *Calopteryx* the invagination continues until the head shifts its position so that its vertex is directed toward the posterior pole (Fig. 117). This is the immersed type of germ band. The

invagination of the embryo in this species (Fig. 117) produces a pit in the yolk mass, one wall of which is the embryo itself (*gb*); the other wall on the dorsal side of the egg, the amnion (*am*). Before the head of *Calopteryx* withdraws completely, segmentation begins, and appendages appear (Fig. 118A). As the embryo lengthens, the caudal end doubles on itself, forming a hook (Fig. 117C). The tail folds under the abdomen (Fig. 118A) and maintains this position even after the embryo withdraws from the yolk. When the axis of the head is finally shifted, the opening behind it is closed by the serosa (Fig. 118B). The amnion in the head region now forms a large sac, part of which lies in contact with the serosa. Just

FIG. 118.—*Calopteryx*. Longitudinal sections. A–C, successive stages. (*am*) Amnion. (*am. cav*) Amniotic cavity. (*am. ser*) Fusion area of amnion and serosa. (*emb*) Embryo. (*hl*) Head. (*ser*) Serosa. (From Brandt.)

before rotation of the embryo, the amnion and serosa fuse where they are in contact, a split appears here, and the envelopes immediately begin to contract. The opening enlarges, but the amnion and serosa remain fused around the edges. The head is forced through the opening as the envelopes contract, turns sharply, and moves along the ventral side toward the cephalic end (Fig. 118C). The embryo continues to grow and takes up most of the ventral side of the egg, while the shrinking envelopes cover the yolk on the dorsal side. The serosa forms the thickened dorsal organ; the amnion, the provisional dorsal closure.

In *Plathemis* the gastrula furrow appears on the ventral side while the posterior half of the embryo is immersed. Cells along the midventral side push inward to form the gastrula ridge (Fig. 119A) which later flattens

out as the inner layer. The area of fusion between the amnion and serosa in *Platthemis* extends along the anterior part of the embryo. When the split appears, the head does not push through; but the envelopes, as they contract, pull back from the ventral side to expose the embryo. As

FIG. 119.—*Platthemis*. Cross sections. A, 43-hour; B, 70-hour embryo. (am) Amnion. (ggv) Gastrula furrow. (il) Inner layer. (ser) Serosa.

this occurs, the head moves toward the cephalic pole, and the tail withdraws from the yolk. The head lobes now extend over on the dorsal side (Fig. 120A). The serosa, as it contracts, thickens and finally lies as a strip on the dorsal side, covering the remainder of the dorsum to form the provisional dorsal closure. The serosa soon sinks into the yolk where it

FIG. 120.—*Platthemis*. Sagittal sections. A-C, successive stages. (am) Amnion. (br) Brain. (do) Secondary dorsal organ. (nc) Nerve cord. (neurp) Neuropile. (proct) Proctodaeum. (ser) Serosa. (stom) Stomodaeum. (y) Yolk.

forms the secondary dorsal organ, an ovoid hollow mass of cells apparently attached to the end of the stomodaeum (Fig. 120B, do).

The stomodaeum which probably forms at the time segmentation takes place in the invaginated embryo is well developed when the embryo

has again reached the surface (Fig. 120A). The proctodaeum, although not so apparent as the stomodaeum, can also be distinguished at this time. While these invaginations are deepening, the ventral nerve cord is developing along the midventral line (*nc*). The neural groove appears by the fourth day (Fig. 121), and on each side of it a number of neuroblasts differentiate from the ectoderm. They undergo mitotic division, giving off daughter cells which soon form vertical columns above the neuroblasts, conspicuous at 120 hours. The neuropile appears soon after this as clear areas that are segmentally arranged (Fig. 120A).

FIG. 121.—*Plathemis*. Cross section of germ band. (*am*) Amnion. (*bl*) Blood cell. (*ch*) Chorion. (*coel*) Coelomic cavity. (*neur*) Neuroblasts. (*neurg*) Neural groove. (*ser*) Serosa. (*ysp*) Yolk spherule.

As segmentation occurs accompanied by the development of the nerve cord, the mesoderm becomes divided into two longitudinal strips, and these in turn are divided into segmentally arranged masses of cells separated from each other by the developing intersegmental grooves. As these segmental mesodermal layers continue to grow in width and length, they fold over laterally to form the coelomic sacs, one on each side of the center line in each segment (Fig. 121, *coel*). At this time cells of the inner layer are set free and take their places next to the yolk. They are considered to be the blood cells (*bl*).

After blastokinesis, the yolk, still constituting most of the egg, is formed into spherules, each apparently surrounded by a delicate membrane and containing within, a yolk nucleus. The embryo is a slender

strip lying on the ventral surface. Occasionally where one of these nuclei may be seen adjacent to a yolk globule, the part nearest the nucleus is in a liquefied condition. During the next two days, with the

FIG. 122.—*Plathemis*. Sagittal section of 13-day embryo. (*br*) Brain. (*ggl*) Ventral nerve ganglion. (*lu*) Lumen. (*proct*) Proctodaeum. (*stom*) Stomodaeum. (*wo*) Outer wall. (*ws*) Side wall of yolk spherule (*ysp*).

reduction of the yolk mass, more space is left between the yolk and the lower layer. Yolk never extends into the portion of the caudal end that is recurved under the ventral part of the embryo. The proctodaeum elongates in this region to the point of the bend where its blind end rests against the yolk mass (Figs. 120*B,C*).

As the yolk diminishes, the walls of the spherules are more clearly seen, and soon it is evident that these walls are arranged in such a manner that a provisional mid-gut is formed (Fig. 122), the outer walls (*wo*) constituting a continuous covering enclosing the yolk mass, the side and inner walls of the spherules (*ws*) further enclosing the yolk into compartments. While the provisional mid-gut is forming, the end of the stomodaeum is expanding until it finally forms a bulbous sac (*stom*) extending into the mid-intestine. In a living egg the compartments appear clearly

FIG. 123.—*Libellula*. Dorsal aspect of nine-day living embryo. (*proct*) Proctodaeum. (*stom*) Stomodaeum. (*ysp*) Yolk spherule.

defined, and the bulbous end of the stomodaeum is apparent as well as the smaller expanded end of the proctodaeum extending into the yolk (Fig. 123). Movement of the mid-gut is evident in a live egg at this stage in development.

Further reduction of the yolk in the compartments causes their walls to shrink away from the center of the mid-intestine, leaving an irregular lumen extending from the stomodaeum to the proctodaeum (Fig. 124, *lu*). This lumen is not evident throughout its entire length in *Plathemis lydia* until shortly before hatching on the fourteenth day.

The nymph of *Plathemis* emerges from the egg during the fourteenth day. The newly emerged nymph has a round bulbous head and a long slender abdomen; its legs remain in the same position under the abdomen

that they had while in the egg. The labium at this time is long and slender and lies extended back on the ventral side under the thorax and abdomen. For a short time after emergence the nymph lies quietly on its side or back, but soon the embryonic integument breaks and the nymph emerges. When it is free, the tip of the labium assumes a position in front of the head like a mask. Although the time varies between hatching and completion of the first molt, the whole procedure takes less than ten minutes.

FIG. 124.—*Plathemis*. Mid-gut of 14-day embryo. (lu) Lumen. (proct) Proctodaeum. (stom) Stomodaeum. (ws) Outer wall of yolk spherule. (ysp) Side wall of yolk spherule.

Immediately after hatching, the tubular mid-gut extends to the second or third segment of the abdomen (Fig. 125). Soon after the nymph is free of the embryonic exuviae, the mid-gut shortens by nearly one-half its previous length (Fig. 126). For the first day or two, and occasionally for as much as three days, the larva does not take food. Even after the larva first begins feeding, it is apparent that the digestive epithelium has not yet formed. The mid-gut still contains in its walls vacuolate tissue characteristic of the embryonic stages, the food being stored in the posterior end of the fore-gut.

Tschuproff, working with *Epithecā bimaculata* and *Libellula quadrimaculata*, stated that the anterior and posterior thirds of the mid-gut are formed from ectoderm cells which grow out cup-like around the yolk from the stomodaeal and proctodaeal invaginations. The middle section, on the other hand, is formed from entodermal cells within the yolk. These cells migrate to the periphery of the mid-gut where they form regenerative cell masses lying in crypts adjacent to the muscle layer and between the yolk compartments. When the mid-intestine first forms in *Plathemis*, the whole wall is made up of yolk compartments. The ectodermal end of the stomodaeum forms a bulbous invagination corresponding to the stomodaeal valve of other insects; the proctodaeum is restricted to a small ring around the anterior end of the hind-gut.

From a study of sections of *Plathemis*, *Erythemis*, and *Libellula* it seems justifiable to assume that ectodermal cells do not migrate from the stomodaeum and proctodaeum but that the definitive digestive epithelium replaces the yolk compartments progressively from both ends, the process being prolonged until nearly time for the molt at the end of the first

instar. The yolk globules disappear early in the second day. The vacuolated compartments (spherules) linger on for five days in *Erythemis* and even longer in *Plathemis*.

It is evident that Tschuproff's figure represents only an intermediate stage in the growth of the definitive digestive epithelium corresponding roughly to Fig. 126 of *Plathemis*.

PLECOPTERA

THE STONE FLY (*Pteronarcys proteus* Newman)

Miller (1939), in his work on the embryology of the stone fly, states that adults reared from nymphs mate

FIG. 125.—*Plathemis*. Longitudinal section of mid-gut at time of hatching. (lu) Lumen. (stom) Stomodaeum. (proct) Proctodaeum.

FIG. 126.—*Plathemis*. Longitudinal section of mid-gut several hours after hatching. (y.sp) Yolk spherule.

readily in captivity. A single female, during a lifetime of three weeks or less, produces a total of 500 to 1,000 eggs in batches of as many as 450

(average about 150) at a time. The eggs accumulate in a mass on the abdomen and are later deposited in the water.

The aquatic, hemispherical egg, which is 0.7 mm. in diameter, is enclosed in a thick chorion and is held to the substratum by a gummy "anchor base" attached to its flatter ventral surface. The micropyles are distributed laterally around the entire circumference of the egg. When the egg mass is placed in water, a temporary gelatinous envelope around each egg expands and pushes the eggs apart. Formation of the egg, including its gelatinous covering, is completed within the panoistic ovariole. The egg develops with its ventral surface toward the base of the ovariole and is still a primary oöcyte when extruded by the female, with the nucleus in the first meiotic metaphase. The egg is entirely filled with yolk, cytoplasm being visible only around the ventral nucleus.

Development of the embryo is complete in about five and one-half months, but under natural conditions the nymph remains dormant over winter and hatches about ten months after oviposition, the egg period being from June until the following April.

Maturation of the egg nucleus occurs at the midventer of the egg; two polar bodies are given off, undergo no further division, and soon degenerate. Cleavage is of the superficial type characteristic of most pterygote insects. There is evidence that the first six divisions are essentially synchronous. The cleavage cells reach the periphery of the yolk at random, beginning at about the 128-cell stage, but the concentration becomes greatest on the ventral surface. Probably all the cleavage cells reach the surface.

The peripheral cells of the primary epithelium (blastoderm) are widely distributed and do not form a continuous layer. Compound "primary nuclear aggregates," which seem to represent the prospective embryonic cells, appear in the yolk during this stage; they presumably arise by clumping of cells that migrate inward from the periphery. A total of 600 to 700 nuclei are present in the egg when differentiation of the embryo occurs. The embryonic rudiment is formed at the midventer of the egg, evidently by direct streaming of cells (including the primary aggregates) from the yolk to form a ventral mass which is then modified into a unilayered ventral plate, or disk. Above the disk a number of "secondary nuclear aggregates" are left which seem gradually to become dispersed in the yolk, their components separating and forming vitellophags. Most of the vitellophags, however, are derived directly from the primary epithelium as individual cells which enter the yolk at the time of ventral streaming. "Yolk cleavage" occurs later in development. Embryonic paracytes are formed during rudiment formation and early growth of the embryo.

The ventral plate invaginates to form a small spheroid embryo with a central amniotic cavity. The lower part of this spheroid develops into the amnion. The extraembryonic cells remaining at the egg periphery form the serosa, completely enclosing the egg contents. A small mid-ventral clump of residual serosal cells (grumulus) remains associated with the caudal end of the embryo during early growth as a point of attachment. A thick serosal cuticle is secreted on the outside of the serosa beneath the chorion. This is partly eroded before hatching occurs. At first the embryo lies upon the ventral serosa. As development proceeds, it arches upward in the middle and finally becomes fully immersed in the yolk, extending across the diameter of the egg. Although the embryo becomes fully immersed in the yolk, this is not accomplished tail foremost, as it is in the Odonata, but by dorsal arching of the embryo, followed by withdrawal of head and tail from the surface. The process of invagination does not involve the formation of the amnion; the latter completely covers the ventral side of the embryo before immersion begins.

Just before blastokinesis the serosa and amnion rupture in front of the head, and the embryo slips out of the yolk and turns so as to lie on its right (very rarely left) side with its venter against the side of the egg and the yolk dorsally enclosed by the reflected amnion, thus again attaining a superficial position but now extending along the circumference of the egg. The degenerate serosa forms a "dorsal organ," which probably incorporates the amnion also, as dorsal growth of the body wall progresses; both embryonic membranes are thus engulfed in the yolk and disintegrate. The embryo becomes coiled in the egg with its legs in the center and finally hatches with the aid of a cephalic egg tooth.

The inner layer, apparently representing mesoderm only, arises dorso-caudally in the spheroid embryo as a small group of median cells, by dorsal displacement and perhaps proliferation of cells from the outer (ectodermal) layer without the formation of a gastrular furrow. Further additions from below in the stages immediately following, if they occur at all, are probably limited to the basal protocephalic region (= differentiation center?). Shortly after blastokinesis, indications of gonads appear segmentally in the abdominal portions of the longitudinal lateral strands of the splanchnic mesoderm.

The embryo elongates, and protocephalon and protocorm differentiate. No primary divisions occur; segments first become demarcated in the gnathal region, and others are added posteriorly as the embryo lengthens, by successive differentiation from the unsegmented tailpiece. Labral, antennal, and intercalary pairs of coelomic cavities appear in the protocephalon, in addition to the 3 gnathal, 3 thoracic, and 10 abdominal pairs of coelomic sacs; the mesoderm of the eleventh abdominal segment shows no distinct cavities. In the abdomen the first (pleuropodia) and

eleventh pairs of appendages are most distinct; the others are rudimentary and transitory, as are also the minute intercalary appendages between the antennae and mandibles.

A thin membrane associated with distinctive cells, for which the term "ental membrane" was proposed by Miller, develops and covers the entire upper surface of the embryo, separating it from the yolk. It is attached to the marginal ectoderm, but its mode of origin is uncertain. During dorsal closure it is carried upward by the advancing body wall and encloses the yolk; it serves as a base for the spread of the cells of the definitive mid-gut epithelium.

The fore-gut and hind-gut arise from the stomodaeum and proctodaeum, respectively. The definitive mid-gut epithelium evidently arises solely from a posterior mid-gut rudiment. The latter is composed of cells that at first form the circumferential walls of the terminal part of the proctodaeum and that become differentiated only after the proctodaeum is well formed. Similar cells give rise to the three Malpighian tubes. The apical closure of the proctodaeum ruptures, and the enlarged mid-gut rudiment cells are everted to form a discoid, unilayered plate. The cells of this rudiment spread forward over the yolk side of the ental membrane and increase mitotically (but not as proliferating bands) until they enclose the entire yolk as a squamous epithelium with widely spaced nuclei. The epithelial cells become cuboidal by the time hatching occurs, but their definitive columnar form is not attained until the first post-embryonic ecdysis approaches. In the nonfeeding first instar, the mid-gut is lined by a cellular membrane that must originate either from the mid-gut epithelium or from vitellophags; this is evacuated during the first molt and replaced by a true peritrophic membrane in the second instar. Most, if not all, of the vitellophags degenerate before hatching occurs. The usual difficulty is encountered in attempting to assign the mid-gut epithelium to a specific germ layer. Its proctodaeal origin favors the view that it is of ectodermal nature in *Pteronarcys*, unless the debatable concept of "latent secondary entoderm" is evoked.

Embryonic development in *Pteronarcys*, in general, resembles most closely that of the Isoptera; orthopteroid affinities are also apparent.

EMBIARIA

Embia uhrichi de Saussure

The metamorphosis of the embiids is of a type intermediate between the gradual and complete, the young resembling the adults in the form of the body, but the wings of the males developing internally. The members of the group are widely distributed in the warmer parts of the world. Kershaw (1914), from whose paper the following account is taken, states that *E. uhrichi* feeds chiefly on the inner but dead part of the tree where

FIG. 127.—*Embia uhrichi*. Successive stages of embryo A-H. (am) Amnion. (ant) Antenna. (ceph) Cephalic lobe. (ch) Chorion. (cut) Cuticula. (ect) Ectoderm. (lb) Labium. (lr) Labrum. (md) Mandible. (mx) Maxilla. (proct) Proctodaeum. (ser) Serosa. (stom) Stomodaeum. (y) Yolk. (From Kershaw.)

it spins its web. Sometimes it eats remains of insects and other dead animal matter. The egg batch is laid on the surface of the bark or beneath a loose piece or crevice thereof. The eggs are laid with their posterior poles touching the bark, the interstices between the eggs filled up with excrement to the level of the lids; then a thin web is spun over the batch, followed by a layer of excrement; and finally another web spun over the mass. The number of eggs in a batch varies from 40 to 80, the nymphs hatching in about forty days.

The germ band at first develops about the middle of the ventral side of the egg (Figs. 127*A,B*), but later the head moves toward the posterior pole, and the band grows around the pole and up on the dorsal side. It soon reaches nearly to the anterior pole, the posterior end of the band recurving, while the head is in its lowest position at the posterior pole (Figs. 127*C,D*). At the same time the appendages have already budded out, the antennae and labrum appearing first, later the mandibles and maxillae, and finally the legs. The labrum is at first very markedly lobed (Fig. 127*D*). The amnion and serosa around the head region are in close contact, but early in the recurved stage the posterior part of the embryo sinks somewhat back into the yolk, so that, except around the head region, there is yolk between the amnion and serosa. At a later recurved stage the serosa secretes a complete outer membrane (Figs. 127*F,G*, section *i-j*) which separates from the serosa. The amnion tears or disintegrates down the median ventral line of the embryo and starts to grow afresh laterally and dorsally, fusing to the dorsal remnant of the serosa. The ventral part of the serosa also disintegrates. The remains of the two envelopes—together with some yolk that was enclosed between them—forms a substance that surrounds the appendages of the embryo up to the time of hatching. The dorsal remnant of the serosa thus serves to surround the yolk, while the amnion quickly grows around and encloses them both (Fig. 127*F*). Shortly before hatching, the remains of the serosa and amnion gather dorsally near the head (Figs. 127*F,G*) and are absorbed in the gut with the remains of the yolk just before the body wall grows dorsad, to close over to complete the dorsal wall. When the embryo is in its final position, it remains thus for 16 days while the musculature and other internal parts develop. The nymph just before hatching is enveloped in three membranes: the vitelline membrane, the membrane secreted by the serosa, and a cuticula molted by the nymph. All these are left within the eggshell on hatching. The behavior and fate of the amnion and serosa are thus similar to that of the Odonata or of *Gryllus*.

DERMAPTERA

THE EARWIG (*Forficula auricularia* L.)

The eggs of this earwig, as described by Heymons (1895), average 1 to 1.5 mm. in length, are rounded ovoid, and are slightly pointed at the

posterior end, with the micropylar area at the anterior end. Within the egg the usual vitelline membrane, periplasm, protoplasmic reticulum, and food yolk are found. The fifth day after deposition two types of cells may be seen in the yolk, the cleavage cells which later penetrate the periplasm to form the blastoderm, and yolk cells which remain behind in the yolk. After the formation of the blastoderm the yolk cells actively divide and become scattered. At the posterior end of the egg a clump of sex cells becomes differentiated and enters the yolk. When the elongated germ band has formed on the ventral side, the head lobes retract from the anterior end of the egg as the tail pushes over on the dorsal side carrying the sex cells with it. Above the gastrular furrow the cells of the inner layer are formed, with the amnion and serosa developing in a normal manner. Segmentation of head and thorax takes place before that of the abdomen, and the appendages of the eleventh abdominal segment appear before the rudimentary appendages of the intermediate abdominal segments. Mesoderm segmentation occurs simultaneously with that of the body wall. Development of the ventral nerve cord offers nothing unusual. Heymons failed to find a ganglion in the eleventh abdominal segment.

In the formation of the compound eye an inner layer of ectodermal cells gives rise to the optic ganglion which does not entirely lose its connection with the outer ectodermic layer that will form the eye plate. There is, therefore, a direct nerve connection from the beginning and not a subsequent union, as stated by Viallanes and Wheeler for the insects studied by them.

Laterally coelomic sacs develop in the mesoderm extending into the appendages. No sacs form in the short preantennal section. In the premandibular region, between the antennal and mandibular segments, the lateral mesoderm is two-layered, perhaps indicating rudimentary coelomic sacs. The walls of the coelomic cavity in the antennal segment, which is most highly developed, become very thin. The sacs in the gnathal and thoracic segments are smaller, and none forms in the eleventh segment. The dorsolateral part of the coelomic sacs represents the pericardial septum, which later develops into the segmentally arranged "wing muscles" of the heart, uniting below the heart tube as the dorsal diaphragm. Mesad of these cells groups of cells distinguished by their paler color and elongate form are found in each segment which together form the longitudinal paracardial cell strands that eventually come to lie on each side of the heart in the walls of the pericardial septum. Since the pericardial septum retracts from the epidermis, a pericardial chamber is formed in which a fat body develops. The fat body is formed from the cells at the junction of the dorsal and ventral sections of the somatic wall. Later, distinct in postembryonic life, pericardial cells also develop in addition to the paracardial cell strand. They are probably derived from middle section of the pericardial septum.

Unlike the heart, the aorta is not formed from cardioblasts but directly from the median or inner wall of the antennal coelomic sac which has extended back into the neck region. The lateral or outer wall of the antennal sacs form the peritoneal wall of the stomatogastric ganglia. As soon as the secondary dorsal organ has been absorbed in the yolk, the continuity of the heart and aorta is established. The subesophageal body is lacking in *Forficula*.

According to Heymons (1895), the mid-gut epithelium is formed from ectodermal cells arising from the blind ends of stomodaeum and proctodaeum. These cells form a single-layered ribbon with forked end from each of the invaginations. The ribbons elongate until they meet, then widen to envelop the yolk. Strindberg (1910) interpreted them as entodermal.

Before hatching, the amnion and serosa rupture and are absorbed in the yolk, as with the Odonata.

HEMIMERINA

Hemimerus talpoides

Hemimerus talpoides, an external parasite upon an African giant rat (*Cricetomys*), is remarkable in that it exhibits an intra-uterine development, the embryo undergoing its complete development in the ovary nourished by the aid of a placenta-like structure. The embryonic growth and the structure of the reproductive organs have been described by Heymons (1912); the anatomy, by Jordan (1909).

The egg follicle of the female, as in other insects, at first forms an epithelium of a single layer of cells. Later, as development proceeds, the nuclei arrange themselves in an irregular fashion in the vicinity of the egg, forming the follicular placenta, by means of which the embryo is nourished. The cells of the follicular placenta in the immediate vicinity of the nurse cell undergo an especially active proliferation whereby the latter is soon completely enveloped. The nurse cell, which lies at the apical end of the egg follicle, then becomes functionless. The growing embryo from this time on derives some nourishment from the placenta follicle but chiefly from the mass of proliferating placenta cells that surround the degenerated nurse cell, as well as from a similar placenta cell mass at the posterior end of the egg follicle.

Instead of yolk, the shell-less egg contains a fatty substance which later becomes alveolar. In spite of a lack of yolk the cleavage is not total, the cleavage nuclei migrating to the surface especially toward the posterior part of the egg where the germ disk is probably formed. Nuclei that remain behind in the interior will form the trophocytes (entoderm cells). The germ band, at first composed of a single layer of cells, in the process of

invagination is covered on the ventral side by the amnion made up of rounded cells. On the dorsal side are large trophocytes whose plasma still retains the alveolar structure of the original egg contents. The trophocytes correspond to the vitellophags, or yolk cells, of other insects, the alveolar protoplasmic envelope taking the place of the yolk. These cells, which number on an average but 8 to 10, lie in contact with the anterior placental cell mass, presumably acting as intermediaries in conveying nutriment from the placental cells to the embryo. Here and there on the outer side of the amnion certain cells develop by delamination another layer which later separates from the amnion to form a serosa-like envelope. The germ band soon elongates until head and tail nearly meet on the ventral side. Meanwhile serosa cells have pushed in between the trophocytes and the placental follicular wall, wholly separating the former from the latter. It is thus apparent that an interchange of nutritive material between the maternal tissue and the trophocytes no longer takes place, the connection between the follicular wall and embryo being established by the embryonic envelopes which henceforth take on the nutritive function. Amnion and serosa are nutritive organs and not protective envelopes as in other insects. In *Hemimerus*, therefore, these envelopes might be called "trophamnion" and "trophserosa," as in certain parasitic Hymenoptera. With the increasing nutritive activity of the envelopes the embryo develops rapidly, with a corresponding degeneration of the placenta cells. The formation of the nervous system, the arrangement of the coelomic sacs, and the development of oenocytes and other structures offer nothing remarkable.

In *Hemimerus* the revolution results in the ventral side of the embryo's being turned toward the ventral follicular wall, while the head end of the embryo after complete revolution is directed toward the anterior pole and the caudal end toward the basal end of the maternal follicle. Unlike other insects, however, the envelopes during revolution remain unbroken. The embryonic envelopes after revolution become alveolar and several-layered at both ends of the embryo and may here be designated as the "fetal placenta."

At the time of the revolution of the embryo the ectoderm closes over on the dorsal side. The posterior part of the head remains open for some time after the ectodermal closure of the remainder of the dorsal wall. Here a head vesicle, a diverticular structure peculiar to *Hemimerus*, is developed from cells of the anterior portion of the amnion and serosa and projects into the placenta. The membranous wall of the vesicle merges with a delicate mesodermal layer that lines a blood sinus which is situated in the posterior part of the head and is connected posteriorly with the dorsal blood vessel. At this stage the blood vessel is already provided with muscles so that blood conceivably may circulate through these parts

and thereby carry nutritive material from the maternal placenta through the serosal and amniotic fetal placenta to the embryo. The maternal follicular placenta as well as the fetal placenta after formation of the vesicle gradually degenerate, the products passing through the wall of the vesicle and thence into the circulatory system of the embryo. The alimentary canal is formed as in *Forficula*.

References

EPHEMERIDA: Brandt (1878), Burmeister (1848), Carrière (1886), Murphy (1922), Needham, Traver, and Hsu (1935). *Ephemera* sp.; Heymons (1896a,c). *Palingenia virgo*; Joly (1876).

ODONATA: Heymons (1896a); *Agrion puella*; Brandt (1869, 1878). *A. virgo*; Meissner (1855). *Calopteryx virgo*; Brandt (1869), Tillyard (1917). *Diplax* sp.; Packard (1868, 1871b). *Epithea bimaculata*; Tillyard (1917), Tschuproff (1903). *Gomphaeschna furcillata*; Kennedy (1936). *Libellula quadrimaculata*; Tillyard (1917), Tschuproff (1903). *Perithemis domitia*; Packard (1871b). *Platynemus pennipes*; Seidell (1926-1935). *Sympetrum pedemontanum albioni*; Munchberg (1939).

PLECOPTERA: Brandt (1878). *Pteronarcys proteus*; Miller (1939, 1940). *Sembris bicaudata*; Herold (1839).

EMBIARIA: *Embia uhrichi*; Kershaw (1914).

DERMAPTERA: *Anisolabis litorea*; Heymons (1899c). *Forficula* sp.; Husain (1927). *F. auricularia*; Brauns (1913), Heymons (1893, 1895a), Strindberg (1915c).

HEMIMERINA: *Hemimerus talpoides*; Heymons (1909, 1912), Jordan (1909).

CHAPTER XV

ORTHOPTEROIDEA (PANORTHOPTERA)

MANTARIA

THE PRAYING MANTIS (*Paratenodera sinensis*)

Hagan (1917), from whose paper the following account is taken, states that from oöthecae deposited in September the insects hatch the following spring. The egg is elongate-oval, somewhat convex ventrally, tapering to a smaller, more pointed anterior micropylar end. It averages 4.5 mm. in length. The germ disk is short, its cephalic end about two-thirds the distance from the anterior pole. After gastrulation it elongates rapidly, developing well-marked cephalic lobes anteriorly. Throughout the entire embryonic life the head end is directed toward the anterior end of the egg. The amnion and serosa develop in the usual way. Very early in the development of the embryo a compact mass of cells is at first found opposite or slightly posterior to the cephalic third of the ventral plate but later shifts slightly more posteriorly. This mass of cells is interpreted as the indusium which in this species does not develop further.

As the posterior growth of the embryo progresses, the definitive abdominal appendages become clearly recognizable in anteroposterior sequence—the first pair, finger-like pleuropodia; the others, merely prominent swellings. The stomodaeum is discernible shortly before the flexing of the telson; the proctodaeum is visible immediately after. The median groove is then a deep furrow, and meanwhile the brain and optic plates differentiate. Up to this time the embryo has been lying on the ventral side of the egg with its longitudinal axis in a straight line. The longitudinal axis now suddenly becomes curved, with head and tail still remaining in position; the middle of the embryo bends toward the lateral margin. The head then moves to the side. The entire embryo next passes laterally around the yolk, maintaining its superficial position, and finally comes to rest until hatching on the dorsal side of the egg, the ventral side of the embryo up. The embryo with a slight twisting motion has thus rotated about its longitudinal axis.

During the rotation, growth continues. By the time the embryo is in a mid-lateral position, head and thoracic appendages elongate and begin to show segmentation. Tracheal invaginations appear, and the 10 definitive abdominal segments with a telson have become evident. By the time the embryo reaches its final dorsal position, the procephalon is

clearly outlined, the optic plates are heavily pigmented, the tritocerebrum is drawn up under the procephalon, and the buccal segments have drawn forward in a more compact mass.

Late in embryonic life a fusion of amnion and serosa occur as in many insects; then contracting they form the secondary dorsal organ which encloses the yolk on the dorsal side of the embryo. Gradually the envelopes together with the yolk are carried into the mid-gut as the dorsal body wall is being completed.

Hagan did not study the earliest stages of *Paratenodera sinensis*. Giardina (1897) described these stages in *Mantis religiosa* which probably resemble those of the first-mentioned species. In *M. religiosa* three polar bodies are given off at the periphery in the middle of the ventral side. The female pronucleus leaving the periphery joins the male pronucleus on its way toward the center. The fusion nucleus that results then divides, the cleavage nuclei moving to the periphery, resulting in a blastoderm. A little behind the middle on the convex side, a compact mass of cells, the germ band, is formed but on the remainder of the surface the cells are sparsely distributed. All cleavage nuclei reach the egg surface, but later some migrate inward, first from the germ band but later from the other part of the blastoderm, thus forming, especially under the germ band, an inner layer of cells with large nuclei which divide amitotically. From this inner layer, cells free themselves to enter the yolk to become yolk cells.

Two longitudinal strips of mitotically dividing cells, which somewhat diverge posteriorly and later become two or three layers deep, form on the inner side of the germ band. The thin cells which do not take part in the formation of the germ band now start to divide amitotically to give rise to the serosa, whereas the amnion originates from the germ band by mitotic division. Giardina did not describe the further formation of the germ layers. From Rabito's account (1898) it appears that the mid-gut epithelium in *M. religiosa* arises from the blind inner ends of the stomodaeal and proctodaeal invaginations as in *Forficula*.

BLATTARIA

THE CROTON BUG (*Blattella germanica* L.)

This widely distributed cosmopolitan species has for many years been a subject for embryological investigation by a number of workers.

The eggs are enclosed in a purse-like capsule, or oötheca, within which there are two parallel spaces, in each of which there is a row of separate chambers each enclosing an egg. The oötheca is usually carried about by the female until shortly before the emergence of the young. The average number of eggs in an oötheca is about 30. The egg is elongate,

convex on one side, straight on the other, and much compressed (Fig. 128), with the micropyles scattered over a quadrant of its upper half. The first maturation division of the egg nucleus occurs before the egg is enclosed

FIG. 128.—*Blattella*. Lateral aspect of egg. A, before cleavage. B, after cleavage. (From Wheeler.)

in its oötheca. After fertilization the cleavage cells migrate to the egg surface, the blastoderm being completed in about 60 hours at 27°C. After reaching the surface some of the cleavage cells turn back into the

FIG. 129.—*Blattella*. Section through stomodaeum (*stom*) of five-day embryo. (*am*) Amnion. (*ect*) Ectoderm. (*mes*) Mesoderm. (*ser*) Serosa.

yolk to become vitellophags. Shortly afterward the embryonic rudiment forms in the middle half on the ventral surface (along the V-shaped ridge) of the egg, the blastoderm on the dorsal and lateral surface becoming thin

to form the serosa. The inner layer, or, as Chlodkowsky (1891) terms it, the primary "entoderm," is formed by a feeble invagination followed by delamination, proliferation, and migration. At the cephalic end the inner layer divides to underlie the cephalic lobes which have been formed by lateral proliferation of the germ band. The amnion forms in a normal way (Fig. 129), the tail fold appearing first (Fig. 130).

Segmentation is not evident until the rudiments of the appendages are well developed. Riley (1904) recognized six head segments: the ocular (preoral), antennal, second antennal (premandibular), mandibular, maxillary, and second maxillary (labial). The leg rudiments lie folded beneath the thorax and the anterior part of the abdomen. The rudimentary appendages of the abdomen disappear about six days after fertilization, except the pair on the first segment which persists until the envelopes rupture. The segments, as also the appendages, develop from the cephalic toward the posterior end.

FIG. 130.—*Blatella*. Frontal aspect of embryo. Amnioserosal folds (*am. ser*) extending over cephalic and caudal ends. (*ceph*) Cephalic lobes.

With the lengthening of the embryo the caudal end folds over ventrally (Fig. 131), and then the embryo shifts to a more posterior position (Fig. 132). Meanwhile, further lengthening pushes the head forward until it reaches the cephalic end of the egg. With this increase in length the amnion and serosa tear longitudinally along the mid-ventral line, the amnion reflecting back although maintaining its connection with the margin of the embryo, the serosa contracting until both amnion and serosa are drawn into the yolk on the dorsal side in the prothoracic region. While the remains of the envelopes are gathering on the

dorsal side, the lateral parts of the body wall grow upward to enclose the yolk. The dorsal growth of the body wall is accompanied by the dorsal growth of the mesoderm and the mid-gut epithelium.

When the ectodermic evaginations for the appendages of head, thorax, and abdomen appear, the mesoderm layer having become segmented acquires a lumen for each segment except the first and last. These sacs are approximately triangular in shape in cross section and more or less trilobed in the abdominal segments, the dorsal (splanchnic) part in contact with the yolk, the remaining (somatic) part largely lining the ectoderm of the appendages. Between the right and left rows of sacs there is formed a free space, the epineural sinus, just above the nerve cord. When the somatic walls of the coelomic sacs break down to form the muscles, the epineural sinus and coelomic cavities together will constitute the schizocoele (pseudocoele), or definitive body cavity, of the insect.

The muscles of the mid-gut are formed from the splanchnic (visceral) layer of the coelomic sacs. Blood cells arise from the median part of the mesodermal layer which originally connected the right and left halves. The fat body arises from a part of the lateroventral wall of the sacs, at

first only an inconspicuous mass but later filling a considerable space in the definitive body cavity. As has been described for other Orthoptera, the pericardial septum develops from the dorsad-growing part of the somatic mesoderm, the heart from the crescent-shaped cardioblasts (mesoderm derivatives at the dorsal junction of somatic and splanchnic layers). A delicate ental membrane, similar to that described for *Locusta*, *Pteronarcys*, and some other insects but heretofore not recorded for *Blattella*, has been observed by Dr. L. C. Pettit.

FIG. 131.

FIG. 131.—*Blattella*. Mid-sagittal section of amniotic fold at caudal end. (*am*) Amnion. (*ect*) Ectoderm. (*il*) Inner layer. (*ser*) Serosa.

FIG. 132.

FIG. 132.—*Blattella*. Caudal migration of nine-day embryo.

The germ cells in the roach are segregated from the median caudal groove during or shortly after segregation of the mesoderm but before mesoderm segmentation and before the formation of the coelomic sacs. Later they migrate forward, are carried dorsad, and come to lie in two strings extending from the second to the seventh segments after having passed through the splanchnic layer into the genital ridges. Here the paired anlagen of the gonads are formed.

The ectodermal stomodaeum and proctodaeum are formed in the usual way in the roach. From the lateroventral angles of these invaginations cellular ribbons arise, two from the stomodaeum growing backward, two from the proctodaeum growing forward until they meet, their outer surface in contact with the splanchnic mesoderm. The ribbons then widen and fuse, first, along the lower and then along the upper, median longitudinal line, forming the tubular mid-gut epithelium. The muscles of the mid-gut are derived from the splanchnic mesoderm. Embryologists are for the most part in agreement as to this process, but there is a distinct difference of opinion concerning to which germ layer these epithelial ribbons owe their origin. Wheeler (1889) states "that it is next to impossible to come to any definite conclusion as to the mode of origin of the entoderm in *Blatta*." Heymons (1891, 1895) maintains that the ribbons arise from the ectodermal cells of the blind ends of the stomodaeal and proctodaeal invaginations. More recently Nusbaum and Fulinski (1906) in an elaborate study on this question conclude that the cells that give rise to the epithelial ribbons are not a part of the ectodermal invaginations but have arisen from bipolar entodermal rudiments upon which the blind ends of the invaginations impinge but from which they are entirely independent. This subject is discussed in more detail in Chap. VI of this text.

With the absorption of amnion and serosa and the dorsal closure of both of the body wall and of the mid-gut, the embryo completes its development, the young making their escape about three weeks after the oötheca first appears at the vaginal opening.

Since the development of the brain, ventral nerve cord, visceral system, sense organs, integument, stomodaeum, proctodaeum, and other ectodermal derivatives in the roach closely resembles that described in this text for other Orthoptera, there is no need for repetition.

The accounts of Wheeler (1889), Cholodkowsky (1891), and Heymons (1895) on the development of *Blattella germanica* differ somewhat on minor points.

ISOPTERA

THE TERMITE (*Eutermes rippertii* ?)

The unsegmented egg, as described by Knowler (1900), is oval, about 0.5 mm. long by 0.22 mm. in diameter, enlarged at the posterior (micropylar) end and markedly convex on the ventral side. As here considered, the micropylar end is the definitive as well as the primary posterior pole, and the convex side becomes the final ventral surface. Polar bodies appear at about the middle point of the flattened dorsal surface of the yolk mass. The pronucleus returns from the dorsal side to the middle of the yolk where division takes place. The cleavage nuclei after repeated

division reach the surface, where they continue to divide much more actively in the posterior half of the egg. A few yolk cells remain in the yolk. Later a small, nearly circular germ disk forms at the posterior end of the egg; the nuclei of the cells of the remaining primary epithelium (blastoderm) are widely separated.

No gastrula invagination is formed in the embryo of this termite. At irregular points in the embryonic area, lateral as well as median, some cells are pushed below the surface, and others are separated toward the inner surface of the ectoderm by tangential divisions of its nuclei at

FIG. 133.—A, B, *Eutermes*. Median sagittal sections. (am) Amnion. (am. cav) Amniotic cavity. (antr) Anterior end of germ band. (ch) Chorion. (mes) Mesoderm. (ser) Serosa. (yc) Yolk cells.

various scattered points; an inner layer, constantly gaining in bulk, is thus formed. The amnion appears as a fold at the caudal end of the embryo, its structure at this stage not differing from that of the embryo in contrast to the remaining primary epithelium or serosa (Fig. 133A, am) which is thin, its nuclei far apart. The amnion is thus merely a specialized portion of the germ disk, or embryo. As development continues, the amniotic tail fold grows over the embryo, neither head nor lateral fold developing (Fig. 133B, am). The mesodermal collection of cells first lies under the anterior half of the germ disk. The yolk-cell nuclei are of remarkable size and apparently remained undivided from an early stage. The cells of the embryo as well as those of the amnion have become smaller by repeated divisions, whereas those of the serosa are compara-

tively large, having before this practically ceased to divide. The hind end of the embryo pushes back over the posterior end of the yolk mass just beneath the serosa; the head end remains fixed (Fig. 134). The embryo, which in this stage is not yet segmented, has acquired broad cephalic lobes. With the increase in length, the amnion becomes thinner and membranous, and, the inner layer of the embryo by proliferation of its cells increases in size (Fig. 135A), especially at the posterior end.

FIG. 134.—*Eutermes*. Unsegmented germ band. (am) Amnion. (ser) Serosa.

Soon the first traces of segmentation and appendages appear. The antennae have at this time become evident as backward processes of the cephalic lobes, postoral in position, appendages of the other anterior segments as far back as the thoracic segments arising about the same time. There are no macrosomites such as have been described for *Stenobothrus*. When the caudal end of the embryo has pushed forward along the dorsal surface of the yolk almost to the anterior end of the egg, three additional segments (meso- and metathoracic and the first abdominal) have been added (Fig. 135B).

FIG. 135A.—*Eutermes*. Median sagittal section. (am) Amnion. (am.cav) Amniotic cavity. (ect) Ectoderm. (mes) Mesoderm. (post) Posterior end of germ band. (yc) Yolk cell.

As the embryo increases in length, the caudal end sinks slightly into the yolk by a flexure much like that of the dragonfly. Appendages increase in length; the abdomen becomes segmented; stomodaeum and proctodaeum are formed; and the body walls grow dorsad. The ento-

derm appears late, after the segmentation of the germ band. Yolk cells take no part in its formation. Blastokinesis is accomplished as described and figured for the dragonfly; amnion and serosa fuse into a single membrane at one point, only to tear open over the ventral side of the embryo, the edges of these two envelopes fused, both retracting dorsally, later to form the secondary dorsal organ at the back of the head. The yolk is now contained in a sack whose ventral wall is the embryo and whose lateral and dorsal walls are formed of the amnion and serosa. The head of the embryo now slips up along the ventral surface of the yolk to the anterior end of the egg, while the caudal end comes to lie beneath the micropyles of the opposite end. Finally the yolk together with the envelopes is carried into the mid-gut, the dorsal wall closing over them. The development of organs is not described by Knowler.

PHASMATARIA

THE WALKING STICK (*Carausius morosus* Br.)

The developmental history of the walking stick has been briefly described by several workers and more extensively by Hammerschmidt (1910), Thomas (1936), Leuzinger, Wiesmann, and Lehmann (1926), the work of the three last-mentioned authors being the most detailed. As might be expected the development resembles most closely in general features that of the locust. The eggs, which measure over 2 mm. in length, are ellipsoidal and flattened laterally, with a lid-like operculum which is pushed off on emergence of the insect. At the time the egg is laid, a small number of cleavage nuclei may be found in the periplasm in the region not far from the posterior pole. These proliferate and give rise to further nuclei that migrate tangentially in the periplasm. They remain sparsely scattered over the surface except at the posterior end, where they form a small heart-shaped embryonic rudiment, which is soon composed of several layers of cells. The cells exclusive of those forming the rudiment constitute the serosa. At a later date, as described by Thomas (1936), the amnion appears around the margin of the embryo and later still covers the ventral face. While the inner layer is still forming,

FIG. 135B.—*Eutermes*. Embryo with rudimentary appendages. (abd) Abdomen. (am) Amnion. (ant) Antenna. (ch) Chorion. (lb) Labium. (md) Mandible. (mx) Maxilla. (ser) Serosa. (th 1) First thoracic leg. (y) Yolk.

other cells are given off from the embryonic rudiment to form the yolk cells. More yolk cells are now set free from the median line of the ental surface of the rudiment, which connect with each other by pseudopod-like processes to form a reticulated sheet between the rudiment and the yolk. This sheet is the yolk-cell membrane and is interpreted by Leuzinger (1925) as the primary entoderm. There may now be recognized in the embryo an outer layer, about two cells deep, which forms the ectoderm; then a layer of transversely arranged cells, the inner layer; and finally, between the latter and the yolk, the yolk-cell membrane or primary entoderm (Fig. 136A).

With the longitudinal growth of the embryo and consequent stretching, segmentation first appears when the inner layer divides transversely into metamERICALLY arranged masses. Without the formation of a distinct longitudinal furrow, the segmental masses of the inner layer each separate into two parts. From the mesal margins of the segmented parts (somites) of the inner layer, cells are liberated which pass by way of pseudopod-like plasma bridges into the yolk-cell membrane along the median longitudinal line a position from which they migrate laterally, replacing the original yolk cells of the membrane and crowding them into the yolk. The replacement cells are regarded by Wiesmann (1925) as mesodermic; the membrane itself, however, after the substitution for the original cells, is designated as the "secondary entoderm." Although Thomas (1936) stated that the definitive digestive epithelium originates from anterior and posterior mesenteron rudiments, both Hammerschmidt (1910) and Leuzinger and Wiesmann (1926) expressly deny this.

After the metameric mesoderm plates become two-layered, they acquire coelomic cavities. These coelomic cavities are unusually well developed in *Carausius* and more or less triangular in cross section, the angles in most of the segments extending out in the form of diverticula. Wiesmann recognizes coelomic sacs in the labrum and in the preantennal, antennal, intercalary, gnathal, thoracic, and abdominal segments 1 to 10 (Figs. 136B,C,D). In *Carausius*, as in *Blatta*, the eleventh coelomic sac is but feebly developed. The cavities of the labral and preantennal sacs are evanescent, and that of the intercalary sacs restricted to a small cleft. Except for the last three abdominal sacs the antennal sacs persist after all the others have broken down for the formation of fat bodies and muscles. The median walls of the antennal sac form the aorta; the outer or caudolateral walls, the fat body; the lateral walls, the sheath of the corpora allata. According to Wiesmann the subesophageal body develops from the intercalary sac. In addition to fat and body muscles, splanchnic mesoderm is formed from the coelomic sacs of the labial to the seventh abdominal segments, inclusive. Cardioblasts, from which the

FIG. 136.—*Carausius*. *A*, cross section of anterior end of second thoracic segment. *B*, longitudinal section of labral region. *C*, longitudinal section of antennal coelomic sac. *D*, cross section of labial coelomic sac. *E*, longitudinal section of the third to the sixth coelomic sacs. (*ab. 4*) Fourth abdominal appendage rudiment. (*am*) Amnion. (*ant*) Antenna. (*coel*) Coelomic cavity. (*div. 1, 2, 3, 4*) Anterior, ventral, lateral, and median diverticula. (*fr*) Vento-lateral furrow. (*gc*) Germ cell strand. (*il*) Inner layer. (*mus*) Lateral myoblast. (*mx*) Lobe of maxilla. (*mx. palp*) Maxillary palpus. (*splm*) Splanchnic mesoderm. (*ster*) Sternite. (*stom*) Stomodaeum. (*ter*) Tergite. (*yc*) Yolk cell. (*ycm*) Yolk-cell membrane. (Adapted from Leuzinger and Wiesmann.)

heart is formed, develop on the labial to the tenth abdominal segments, inclusive.

The coelomic sacs of the third to the sixth abdominal segments are formed as in the thorax, but their shape is influenced by the presence of the sex-cell mass (Fig. 136*E*). The germ or sex cells appear early as a wedge-shaped cellular mass at the posterior end of the embryonic rudiment at the time of the formation of the inner layer. When the body is fully segmented, the strand of sex cells lies dorsad in contact with the visceral wall of the third to the sixth coelomic sacs. Later the second and seventh sacs are also involved. Finally the sex-cell strands become surrounded by the compressed part of the coelomic sacs in segments three to six to form a two-layered envelope, the future gonad. The ducts of the gonad form in the posterior segments as in *Forficula*. The normal incubation period of *Carausius morosus* is five months, and development is parthenogenetic.

FIG. 137.—*Locusta*. Longitudinal section of egg 23 hours old. (cc) Cleavage cells. (yc) Primary yolk cells.

CAELIFERA

THE AFRICAN MIGRATORY LOCUST (*Locusta migratoria migratorioides* R. F.)

Maturation stages of *L. migratoria* were not studied by Roonwal (1936), but presumably they are similar to those of *Melanoplus differentialis*. In the latter species, the eggs, when ready to be laid, all are in the metaphase of the first maturation division. The first polar body sometimes divides, but whether or not it always does so has not been determined. The second polar body is given off within five to seven hours after being laid. In *M. differentialis* the maturation divisions occur in the peripheral portion of the yolk and are usually to be found between 0.4 and 0.8 mm. from the micropyle end of the yolk mass.

The earliest cleavage stage of *Locusta* studied by Roonwal (1936) was the four-cell stage which occurs about $5\frac{1}{2}$ hours after the egg is laid. The cleavage cells, large stellate masses with well-defined central nuclei, lie close to the posterior end of the egg though distinctly away from the

periphery. At about 10 hours, after several divisions, the eggs being maintained at a constant temperature of 33°C., the cleavage cells start migration to the periphery, which they reach by the 18-hour stage. Meanwhile with repeated mitotic divisions there is an anterior migration along the periphery of the egg but not through the yolk. About the twenty-third hour the cells at the posterior end of the egg form a continuous layer (Fig. 137) of primary epithelium (blastoderm). Anteriorly the cells are not contiguous until about the twenty-eighth hour (Figs. 138, 139). The cells of the germ disk, or embryonic region (*emb*), are closely packed together and columnar. Those of the extraembryonic region are elongated tangentially to the egg periphery.

FIG. 138.—*Locusta*. Cross section near posterior end. 28-hour stage. (*emb*) Embryonic portion of blastoderm. (*y*) Yolk. (*yc*) Secondary yolk cell.

The cells of the germ-disk epithelium undergo rapid division at about the thirtieth hour, with the result that the epithelium temporarily acquires an irregular two- or even three-layered arrangement of the nuclei in places (Fig. 140). At this time the mid-ventral line of the germ disk near its future cephalic end, a shallow groove, is formed on the outer surface. This groove, which lasts for about four hours or less, is called the "first ventral groove" and, according to Roonwal, is not to be confused with the gastral groove.

The yolk cells which lie immediately beneath the germ disk at the thirtieth hour are arranged in a layer (Fig. 140, *ycm*), forming the yolk-cell membrane. The cell boundaries are not visible, the nuclei being connected by protoplasmic strands forming a continuous membrane

which meets the germ disk some distance inward from the edge of the latter. By the thirty-fourth hour the membrane has degenerated, and no trace of it can be seen, thus being much more ephemeral than in *Carausius* where it has a share in the formation of the mid-gut epithelium.

FIG. 139.—*Locusta*. Embryonic region. 28-hour stage. (yc) Secondary yolk cell.

At about the thirty-fourth hour the germ disk is more markedly multilayered than before, but this condition is only temporary and disappears before the differentiation of the inner layer, a process that takes place in a unilayered germ disk. About the forty-second hour the inner layer (*il*) is seen to arise as a proliferation of cells from the roof of a deep median-ventral groove (second ventral groove, or gastral groove). This inner layer first is seen near the anterior end but extends rapidly caudad and finally extends almost the entire length of the embryo with the exception of the extreme cephalic end (Figs. 141, 145, *il*). The second ventral groove lasts but three or four hours and is not visible after about the forty-sixth hour.

The inner-layer formation in the Acrididae, according to Roonwal, occurs only by means of cell proliferation from the roof of the mid-ventral, longitudinal invagination. In *Locusta migratoria* the differentiation of the inner layer occurs from a single area on an elongated median longitudinal line proceeding from the cephalic to the caudal end

FIG. 140.—*Locusta*. 30-hour stage. (c) Cells proliferating from roof of ventral groove (vg). (y) Yolk. (yc) Secondary yolk cells. (ycm) Yolk-cell membrane.

(Figs. 142, 143, 144, *il*). The ectoderm, or outer layer, now becomes more than one-layered in places, the lateral halves of the germ band becoming thicker in the middle than on the sides.

The protoplasmic reticulum is not distinct in early stages, but with the diminishing yolk in the older stages it becomes evident. At about the sixtieth hour the yolk, which so far presents an amorphous appearance,

FIG. 141.—*Locusta*. Cross section of 45-hour germ band. (*ect*) Ectoderm. (*il*) Inner layer. (*vg*) Second ventral groove.

begins to show polyhedral differentiation in the immediate neighborhood of the embryo. By the seventy-fifth hour the entire mass is divided into polyhedral masses, which 24 to 36 hours later completely disappear.

FIG. 142.—*Locusta*. Cross section of hind region of protocerebrum of 42-hour germ band. (*am*) Amnion. (*am. cav*) Amniotic cavity. (*ect*) Ectoderm. (*il*) Inner layer. (*ser*) Serosa. (*y*) Yolk. (*yc*) Yolk cell.

Not all the cleavage cells reach the egg periphery to form the primary epithelium (blastoderm), some remaining in the yolk to form the vitellophags, or primary yolk cells, stellate cells with large round nuclei.

FIG. 143.—*Locusta*. Cross section of posterior end of 45 $\frac{3}{4}$ -hour embryo. (*am*) Amnion. (*am. cav*) Amniotic cavity. (*ch*) Chorion. (*ect*) Ectoderm. (*il*) Inner layer. (*mi*) Micropylar canal. (*ser*) Serosa.

Secondary yolk cells may arise by inward migration or by division of the primary epithelial cells, the inner product forming the secondary yolk

cells. Whether the division is amitotic or mitotic was not determined by Roonwal.

Yolk cells that do not share in the formation of the yolk-cell membrane lie singly and are stellate; others group together into clumps of two or three or more to form irregular syncytia. At about the fortieth hour the yolk-cell syncytia may contain seven or even more nuclei in each, but shortly afterward they disappear, and only single yolk cells are met with. As time goes on, the yolk cells penetrate deeper into the yolk and thus become distributed throughout the egg.

In *Locusta migratoria*, according to Roonwal, there are four main periods of activity into which the whole process of gastrulation is divided. These periods are fairly sharply demarcated, although they sometimes

FIG. 144.—*Locusta*. Cross section of 46-hour embryo. (*am*) Amnion. (*am. cav*) Amniotic cavity. (*ect*) Ectoderm. (*il*) Inner layer. (*ser*) Serosa.

overlap. The first phase occurs by modified epiboly (overgrowth) and results in the differentiation of the primary endoderm represented partly by the primary yolk cells. In the second phase the yolk-cell membrane (corresponding to a part of the evanescent primary entoderm) is formed. Multilayered condition of the germ band is an indication of activity during this phase. In the third phase the second ventral groove (part of the gastral groove) and the inner layer are formed. In the fourth phase the secondary yolk cells (part of the secondary entoderm) appear.

The embryonic envelopes, or membranes, in this species are formed in the usual way and begin to appear almost simultaneously with the differentiation of the inner layer. This is brought about by the inward folding of the lateral borders of the germ band ventrally. The cephalic fold appears first, then the caudal fold. At about the 50-hour stage the embryonic envelopes, amnion and serosa, are completed. Between the amnion and serosa at the sides there is some yolk which may even contain yolk cells, but in the middle the envelopes are nearly or quite in contact with one another (Fig. 145).

The round concave germ disk composed of long prismatic cells starts forming as a thickening of the primary epithelial cells lying at the posterior pole of the egg slightly on the ventral side (Fig. 138). The cells of the extraembryonic primary epithelium are more or less spindle-shaped with large nuclei. The germ disk afterward begins to elongate at the ventroanterior end along the ventral side of the egg. The protocorm rapidly elongates and at about the 46-hour stage is twice as long as the protocephalon. Four hours later the inner layer begins to show segmentation, especially in the thoracic regions, and the rudiment of the stomodaeum is in evidence. A little later the germ band has divided into four primary segments: a protocephalic and three protocormic

FIG. 145.—*Locusta*. Longitudinal section of 46-hour embryo. (*am*) Amnion. (*am.cav*) Amniotic cavity. (*antr*) Anterior end. (*ch*) Chorion. (*ect*) Ectoderm. (*il*) Inner layer. (*post*) Posterior end. (*ser*) Serosa. (*y*) Yolk. (*yc*) Secondary yolk cell.

elements, *i.e.*, four macromeres or macrosomites. Rudiments of three jaw and three thoracic appendages are apparent at the 52-hour stage. Definitive segmentation of the inner layer preceded that of the ectoderm. By the 75-hour stage the entire abdomen becomes externally segmented into 11 segments, thus establishing the definitive body segmentation. Eye pigment first makes its appearance shortly before the beginning of blastokinesis.

After the primary segmentation of the inner layer into four macromeres the definitive segmentation of the inner layer takes place. At the 52-hour stage the inner layer in the head and thorax is divided into segments corresponding to the three gnathal (jaw) segments and the three thoracic segments. The somites are also separated on the median line (Fig. 146) and lie somewhat obliquely, the anterior inner end of each meeting its fellow on the opposite side in the intersegmental region in front. The segmental mesoderm masses develop coelomic cavities, and

the small intersegmental anteromedian mesoderm masses (blood-cell lamella) give rise largely to the blood cells. A primary median mesoderm band is not present in *Locusta* but is formed secondarily by the extension of the blood-cell lamellae medially and by cells derived from the lower end of the median wall of the coelomic sacs (Fig. 147). The antennary

FIG. 146.—*Locusta*. Cross section of second maxillary segment. (am) Amnion. (ect) Ectoderm. (il) Inner layer.

mesoderm is the first to be differentiated into a more or less discrete segment.

In the formation of the coelomic cavities of the head and thorax the inner layer spreads laterally and becomes in large part one-layered. The ectoderm at the lateral edges of the germ band then curves dorsomedially, and the mesoderm in each segment follows suit. The free ends of the

FIG. 147.—*Locusta*. Cross section of extreme anterior end of second thoracic segment of 75-hour embryo. (am) Amnion. (bl) Blood cell. (coel) Dorsoanal pouch of first thoracic coelome. (dc) Provisional dorsal closure. (ect) Ectoderm. (mes) Mesoderm. (p2) Second thoracic leg.

mesoderm layer in each lateral half of a segment then approach each other and unite to form a coelomic sac (Fig. 148). At the time of their first appearance the cavities lie inside the rudiments of the appendages belonging to their segment and may therefore be called "appendicular coelomic cavities," each pair being formed distinctly and separately.

FIG. 148.—*Locusta*. Cross section, second maxillary segment, of 56-hour embryo. (coel) Coelomic cavity. (ect) Ectoderm. (mes) Mesoderm forming coelomic sac.

FIG. 149.—*Locusta*. Cross section of ninth abdominal segment of 72-hour embryo. (am) Amnion. (am. cav) Amniotic cavity. (dc) Provisional dorsal closure. (ect) Ectoderm. (il) Inner layer. (ser) Serosa.

FIG. 150.—*Locusta*. Cross section of second abdominal segment. (am) Amnion. (coel) Coelomic cavity. (ect) Ectoderm. (mes) Mesoderm.

FIG. 151.—*Locusta*. Cross section of fourth abdominal segment of 75-hour embryo. (am) Amnion. (coel) Coelomic sac. (dc) Provisional dorsal closure. (ect) Ectoderm. (mes) Median mesoderm.

FIG. 152.—*Locusta*. Para-sagittal section of 75-80-hour embryo. Coelomic sacs. (*ab* 1-11) Coelomic cavities of abdominal segments 1 to 11. (*ant*) Antennal, (*lb*) labial, (*md*) mandibular, (*mx*) maxillary, and (*p* 1-3) thoracic coelomic cavities. (*am*) Amnion. (*br*) Brain. (*dc*) Provisional dorsal closure. (*eps*) Epineural sinus. (*int*) Intercalary appendage. (*proct*) Proctodaeum. (*suboesb*) Subesophageal body.

Coelom formation in the first abdominal segment takes place in the same way as in the head and thorax. In the following segments with the growth of the median portion of the ectoderm the originally wedge-shaped mass of the inner layer flattens out and spreads laterally in such a way as to lose its multilayered condition and acquires instead a bilayered arrangement of its nuclei (Fig. 149). Soon the dorsal of these two layers becomes extremely thin. Meanwhile the undivided mass of the inner layer becomes constricted into segmental masses, and then between the two layers of cells a cavity appears (Fig. 150). By subsequent division of each segmental mass into a right and left half the paired coelomic sacs are formed. The medio-ventral wall of the coelomic sacs in each segment grows medially and thus secondarily forms the mesoderm bridge from which the blood cells arise (Fig. 151, *mes*).

Between 56 and 59 hours a pair of labral coelomic sacs with distinct cavities may be distinguished. Unlike those of *Carausius* (Wiesmann, 1926), they are not joined medially at this stage. By the 72-hour stage they have disappeared, leaving in their place a rather loose mass of mesoderm which still shows a paired arrangement and which soon afterward becomes connected with the mesoderm investing the stomodaeum and eventually gives rise to the labral musculature.

The antennary mesoderm is first differentiated in the 52-hour stage as a pair of mesoderm masses lying behind the stomodaeal invagination. Cavities develop in these masses 4 hours later and elongate with the growth of the antennae. In the 72-hour stage each antennary coelom has developed a long dorsorostral pouch projecting far into the head and a much

smaller dorsoanal pouch (Fig. 152), the ventral pouch completely filling the antenna. The dorsorostral portions of the two coelomic sacs, shortly before blastokinesis, approach each other; their median walls fuse and thus form the anterior portion of the cephalic aorta which functions as a blood-distributing apparatus. The median walls of the dorso-

FIG. 153.—*Locusta*. Cross section of mandibular segment of 75- to 80-hour embryo. (*am*) Amnion. (*bl*) Blood cells. (*coel*) Coelomic cavity. (*md*) Mandible. (*suboesb*) Developing subesophageal body.

anal pouch form the proximal part of the cephalic aorta; the lateral walls form fatty tissue. The walls of the ventral pouch are converted into antennary muscles. The antennary coelomic sacs are the largest in the body and form, in addition to that mentioned above, the investment of the pharyngeal ganglion and of the corpora allata.

FIG. 154.—*Locusta*. Cross section of first maxillary segment of 59-hour embryo. (*am*) Amnion. (*bl*) Blood cells. (*coel*) Coelomic cavity. (*dc*) Provisional dorsal closure. (*ect*) Ectoderm. (*eps*) Epineural sinus. (*mes*) Median mesoderm.

The intercalary coelomic cavities are first seen during blastokinesis lying between the antennary and mandibular mesoderm. They are very small and evanescent and soon disappear. Among the Pterygota they have been described in but few forms.

The mandibular coelom is first in evidence at 56 hours as a pair of small cavities lying in the hollow of the mandibular rudiments. Cells

given off from the dorsal wall (Fig. 153, *suboesb*) increase in size and meet medially to form a cluster of cells that give rise to the subesophageal body. The other cells of the coelomic sacs form muscles.

The first maxillary coelomic sacs have small rounded cavities (Figs. 152, 154), which do not develop a dorsal pouch but correspond to the ventral portion of other coelomic cavities. Their walls eventually develop into muscles of the first maxillae.

The labial coelomic cavities (Fig. 152) first appear at 56 hours. They grow rapidly so that in the 70-hour stage they already show a long dorso-rostral and a short dorsoanal pouch. The ventral pouch fills the hollow

FIG. 155.—*Locusta*. Cross section of middle of second thoracic segment of 75-hour embryo. (*am*) Amnion. (*bl*) Blood cell. (*coel.*) (1) Dorsorostral, (2) dorsoanal, (3) ventral pouch of coelomic sacs. (*dc*) Provisional dorsal closure. (*ect*) Ectoderm. (*p*) Second leg.

of the second maxillary appendage and forms the labial musculature; the dorsorostral and anal portions contribute to the formation of the splanchnic mesoderm, the lateral myoblast plate, and the fat body. This is the largest of the gnathal coelomic sacs. The small mandibular and first maxillary sacs correspond largely to the ventral portion of the labial coelom.

The coelomic sacs of the thoracic segments (Figs. 147, 155, 156) develop in a similar manner appearing first in the hollow of their appendages and lying obliquely to the long axis of the embryo. Their median, dorsoanterior ends are pointed, whereas the lateral, ventroposterior ends are rounded. In the 75-hour stage the coelomic sacs show three distinct pouches: the dorsorostral, the dorsoanal, and the ventral. The rostro-lateral coelomic walls extend medially as a thin, single-layered band over the ectoderm, each fusing with its fellow of the opposite side, forming in this way the blood-cell lamella (median mesoderm) (Fig. 147). A little later (80-hour stage) the segmental mesoderm (Fig. 156) also extends

medially, the median extension forming the ventral diaphragm. In the 94-hour stage a deep furrow develops in the lateral coelomic wall at the junction of the dorsorostral with the ventral pouch (Fig. 156), which deepens and eventually separates the dorsal from the ventral coelom. The ventral coelom gives rise to the leg musculature. At the same time, the dorsal coelomic portion (both rostral and anal) is divided by a horizontal partition into upper (dorsal) and lower (ventral) halves. Soon the intersegmental partitions between the upper portions of the dorsal pouches of the coelomic sacs disappear, with the result that there are formed two continuous lateral tubes extending from the first thoracic to the ninth abdominal segment. The somatic mesoderm thickens and forms the so-called "myoblast plate" whose dorsal edge contains cardioblasts (compare Fig. 160). The central part becomes fatty tissue except the uppermost end which forms for a time the wall

FIG. 156.—*Locusta*. Cross section of distal and of second thoracic segment showing ventrolateral furrow in coelomic wall. (*am*) Amnion. (*coel*) (1) Dorsorostral, (3) ventral pouch of coelomic sac. (*dc*) Provisional dorsal closure. (*ect*) Ectoderm. (*mes*) Median mesoderm. (*sin*) First lateral blood sinus.

of the middorsal blood sinus. After completion of the heart it gives out cells that form the pericardial cells. The upper portion of the myoblast plate forms the dorsal suspensory muscles of the heart; the inner layer, the pericardial septum. The median walls of the upper portion of the dorsal pouch form fatty tissue in the thorax and in the first, eighth, and ninth abdominal segments. In the second to tenth abdominal segments it forms the gonads as well. As for the lower portion of the dorsal coelomic pouch, its lateral walls form the vertical muscles of the body wall, and the median walls form fatty tissue.

The difference between the origin of the coelomic cavities of the first abdominal segment and that of the following ones has already been described. At the 75-hour stage (Fig. 152) there are 11 pairs of coelomic cavities in the abdomen, of which the first 10 show a division into three portions as in the thorax. The last, or eleventh, abdominal coelomic sac (Figs. 152, 157) does not show the triple division. It disappears before the 112-hour stage. It consists of a pair of long narrow sacs which run dorsally along the proctodaeum. They will form the musculature of the cerci, of the hind-gut, and of some fatty tissue. The further develop-

ment of the abdominal somites differs from that of the thorax only in so far as the former are associated with the development of the gonads and the genital ducts. The genital ducts are differentiated in the median walls of the coelomic sacs from the second to the tenth segments but subsequently undergo a concentration so as to become restricted to the third to the sixth abdominal segments. A greater part of the dorsal portions of the abdominal somites form myoblast plates and the fat body, as in the thorax. The ventral portions of segments three, four, and six to ten form coelomic ampullae which are comparable to the muscle-forming mesoderm of the thoracic legs.

In the 52-hour stage, rudiments of the labrum appear as paired swellings. Soon, however, the paired nature is no longer evident. The bifid

FIG. 157.—*Locusta*. Cross section of eleventh abdominal segment. (*am*) Amnion. (*coel*) Coelomic cavity. (*dc*) Provisional dorsal closure. (*eps*) Epineural sinus. (*ect* and *mes*) ectoderm and mesoderm of the proctodaeum (*proct*).

nature of the labrum is of secondary origin. The presence of an independent pair of coelomic cavities lying in the labrum suggests the appendicular nature of the labrum, although it is not so regarded by most morphologists. The antennary rudiments arise in the 50-hour stage. At first behind the oral aperture; subsequently, owing to the backward shifting of the latter, they come to lie in front of the mouth. Five days after blastokinesis the segmentation is established for the entire antenna. The intercalary appendages are represented by a thickening of the ectoderm between the antennae and the mandibles (Fig. 152), but no definite evagination is formed. The thickening is first seen in the 75-hour stage but disappears before hatching. The mandibles, maxillae, and labium make their appearance at the 52-hour stage and acquire their definitive form during the course of the next two or three days.

The legs are first in evidence about the time the mouth parts arise and lie on the outer edge of the primary lateral sternite. In the 100-hour

stage each leg consists of five segments: a basal piece (representing subcoxa, coxa, and trochanter) the femur, the tibia, the tarsus, and a terminal segment. By the 120-hour stage the basal segment divides into two segments, the proximal one representing the subcoxa, the tarsus becoming three-segmented. During blastokinesis the trochanter is differentiated.

A pair of appendages is formed on each of the 11 abdominal segments. Those on the first are the pleuropodia. Appendages of segments two to seven are small and disappear during blastokinesis. The eighth pair is also small and in the male disappears completely. The ninth pair persists in the female as an ovipositor valve; the tenth pair in the same sex disappears during blastokinesis. In the male the ninth and tenth pairs fuse to form the aedeagus and associated parts. The appendages of the eleventh segment form the cerci in both sexes.

The pleuropodia arise in the 53-hour stage as lateral evaginations in the same way as the thoracic appendages with which they are homologous. They attain a maximum development during blastokinesis when they are about 0.35 mm. long (Fig. 161). After blastokinesis they shrivel up, to be cast off at time of hatching.

A typical segment of the body divides into a median sternum and two lateral primary tergites. The sternum is divisible into a median part and two lateral parts which bear the appendages. This applies from the mandibular to the tenth abdominal segments. In the thorax the legs move laterally and come to lie at the junction of the tergum with the sternum, the subcoxal segment growing to form a large sclerite, the pleuron, between the tergum and the sternum. The pleuron later divides into an anterior episternum and a posterior epimeron.

The number of segments composing the head of *Locusta migratoria* is seven, as supported by the evidence from the coelomic cavities, the appendages, and the neuromeres. Furthermore, according to Roonwal, although the evidence points to the existence of a labral segment in insects, it is difficult to fit in with the general scheme of the arthropod head.

Regarding the segmentation of the abdomen in *Locusta*, it has been shown that 11 segments take part in its formation. The eleventh, like those which precede it, is provided with a pair of appendages, a pair of coelomic cavities, and a neuromere. The telson is not distinct in *Locusta*. Thus exclusive of the acron and the telson there are 21 segments in all.

When the embryo is about 59 hours old, a thin membranous provisional dorsal closure is formed (Fig. 154, *dc*). It arises from the lateral edges of the embryo at a point slightly above the origin of the amnion and covers the entire dorsum, cutting off the yolk from contact with the inner side of the embryo. Its method of formation has not been determined in *Locusta*. Graber (1888) states that in *Stenobothrus variabilis*

it arises from the lateral edges of the germ band as two flaps which spread medially toward each other and ultimately fuse into a single membrane. It is said to be of ectodermic origin. This membrane at first serves as a gliding surface beneath which the splanchnic mesoderm progresses medially. At first in close contact with each other, later the membrane and the mesoderm separate near the lateral edges of the germ band, thus forming the first pair of lateral blood sinuses. During blastokinesis the portion of the provisional dorsal closure lying between the blind ends of the stomodaeum and proctodaeum becomes free at the edges and grows around the yolk, forming a temporary mid-gut covering. The anterior and posterior ends distad of the stomodaeum and proctodaeum remain unchanged until some time after blastokinesis, when they probably

FIG. 158.—*Locusta*. Successive steps in blastokinesis. Sagittal sections. (am) Amnion. (ch) Chorion. (dc) Provisional dorsal closure. (do) Secondary dorsal organ. (gut) Mid-gut. (proct) Proctodaeum. (ser) Serosa. (stom) Stomodaeum.

degenerate, being replaced by the definitive epidermis. Middorsally the provisional dorsal membrane is fused with the amnion which now forms the second provisional dorsal closure of the embryo. The splanchnic mesoderm now grows dorsad and separates the first dorsal closure from the amnion. The former provisional dorsal closure then degenerates, leaving the inner layer of the splanchnic mesoderm as a temporary mid-gut cover until the definitive mid-gut epithelium is formed.

Shortly before the beginning of blastokinesis the amnion and serosa become secondarily attached to each other at the cephalic end of the embryo and then rupture there (Figs. 157, 158). The fate of the embryonic envelopes resembles that already described for the dragonfly.

Locusta migratoria shows a marked blastokinesis, the embryo turning along the posterior pole of the egg through an angle of 180 deg. (Fig. 158).

It thus shifts its position from the ventral to the dorsal surface of the egg; and the embryonic head, which originally pointed toward the posterior pole of the egg, turns toward the anterior pole.

The corpora allata arises soon after blastokinesis as a pair of invaginations of the lateral body wall of the embryo on either side of the intersegmental region between the mandibular and the first maxillary segments. The blind ends of these invaginations are directed medioven-

FIG. 159.—*Locusta*. Cross section of fourth abdominal segment one day after blastokinesis. (*bl*) Blood cells. (*cbl*) Cardioblasts. (*drc*) Definitive dorsal closure. (*f*) Fat. (*g*) Gonad. (*mus*) Muscle. (*mus. s*) Suspensory muscle of the heart. (*nc*) Nerve cord. (*oen*) Oenocytes. (*pd*) Paricardial diaphragm. (*splm*) Splanchnic mesoderm. (*st*) Stigmata. (*vs*) Ventral septum.

trally. They soon become rounded and eventually are severed from the outer ectoderm. They then move dorsally and posteriorly and come to lie on the stomodaeum. Their connection with the stomatogastric nervous system is purely secondary.

Of the four pairs of cephalic invaginations, the first three, respectively, arise in front of, at the level of, and behind the mandibles, and the fourth pair arises behind the first maxillae. The first and third pairs form the tentorium; the second forms the mandibular apodeme; and the fourth gives rise to the salivary glands. In the 90-hour stage a pair of small, backwardly directed T-shaped invaginations arise between the mandibles and the rudiments of the intercalary appendages. At the same time

a pair of deep medially directed invaginations arises just behind the mandibles which fuse with the T-shaped invaginations to form the tentorium. The dorsal tentorial arms arise afterward as outgrowths from the anterior

FIG. 160. *Locusta*. Cross section of fifth abdominal segment of 112-hour embryo. (bl) Blood cells. (cbl) Cardioblast. (coel) Upper and lower portions of dorsal coelome. (dc) Provisional dorsal closure. (ect) Ectoderm. (gc) Germ cells. (hs) Horizontal septum. (mus) Lateral myoblast plate. (sin) Lateral blood sinus. (splm) Splanchnic mesoderm.

tentorial arms. The mandibular apodemes arise at the 90-hour stage as a pair of deep invaginations near the middle of the inner side of the mandibular base. The lower flexor mandibular muscles become attached to them. Invaginations appearing soon after blastokinesis and proceeding backward from either side of the base of the newly formed hypopharynx on the ventral side form the salivary glands. Already one day after blastokinesis the two invaginations approach each other and finally fuse near their mouths to form the common salivary duct.

Just after the completion of blastokinesis the median area of the floor of the buccal cavity immediately in front of the labium becomes thickened to form the hypopharynx. This area arises by fusion of the sternites of the three jaw segments. As the mandibles and maxillae move closer to the mouth, the hypopharynx becomes closely associated with them.

In the 112-hour embryo the dorsomedian walls of the coelomic sacs of all segments of thorax and abdomen begin to grow medially beneath and along the provisional dorsal closure (Fig. 160). Two lateral bands of splanchnic mesoderm are thus formed. This splanchnic mesoderm is two or more cells deep, the outer, or dorsal, layer in contact with the provisional dorsal closure, and the inner thin layer with a single layer of nuclei at right angles to the longitudinal axis of the embryo. The outer layer gives rise to the longitudinal and circular muscles of the mid-gut; the inner layer soon after blastokinesis separates from the dorsal layer to form the short-lived mesentery which bounds the circumintestinal blood sinus from the outside (Fig. 164, *ib*).

FIG. 161.—*Locusta*. Longitudinal section of embryo during blastokinesis showing pleuropodium. (ab 1) First abdominal segment. (mes) Mesoderm. (th 3) Third thoracic segment.

The epineural sinus, which appears early in embryonic development between the germ band and the yolk, is bounded dorsally by the provisional dorsal closure in *Locusta* (Fig. 152), in *Stenobothrus*, and probably in some other primitive insects, although in most of the pterygotes it is open dorsally. With the growth of the embryo the sinus becomes enlarged and forms the definitive body cavity, the haemocoel.

The heart, or dorsal vessel, is formed from the cardioblasts, differentiated in the 112-hour stage as two strings of single large rounded cells lying on the dorsolateral border of the myoblast and extending through the thorax and abdomen. With further development the cardioblasts move toward the middorsal line and come to lie beneath the first lateral blood sinus. At the same time they become crescent-shaped, with the concave surface facing upward. The middorsal sinus in the posterior

FIG. 162.—*Locusta*. Cross section of heart (*h*) five days after blastokinesis. (*cbl*) Cardioblasts. (*f*) Fat. (*mus*) Muscle. (*pc*) Pericardial cells. (*pd*) Pericardial diaphragm.

region of the abdomen at the time of blastokinesis is bounded dorsally by the epidermis, ventrally by the provisional mesoderm wall of the midgut, and laterally by somatic mesoderm. The cardioblasts lie dorso-laterally close to the epidermis. Inside the sinus a few blood cells may be seen (Fig. 159). The dorsal portion of the somatic mesoderm mass (Figs. 159, 162) completely separates from the ventral part, becomes membranous, and acquires a connection with the body wall by means of fan-shaped processes. The dorsal membrane finally gives rise to intersegmentally placed suspensory muscles of the heart, and the ventral membrane to the pericardial diaphragm (Fig. 159). With the fusion of the cardioblasts the heart is provided with a wall of its own. The cephalic aorta develops from the internal walls of the dorsorostral and dorsoanal pouches of the antennary coelomic sacs, the anterior portion forming the blood-distributing apparatus, or pulsatile vesicle; the posterior portion, the aorta proper.

Three kinds of temporary embryonic blood sinuses are formed in *Locusta migratoria*: lateral blood sinuses, dorsal blood sinuses, and the circumintestinal blood sinus. Two pairs of lateral blood sinuses are

formed, the first pair arising after the formation of the provisional dorsal closure but before blastokinesis. The separation of the outer dorso-lateral end of the somatic mesoderm from the provisional dorsal closure gives rise to the two more or less spindle-shaped lateral sinuses. Later the first pair of lateral sinuses is lost by the breaking away of the provisional dorsal closure from the edges of the germ band. Later still, the two lateral blood sinuses unite into a common dorsal blood sinus (Fig.

FIG. 163.—*Locusta*. Longitudinal section of aorta (*ao*) one day before hatching. (*ant. co*) Inner wall of antennal coelomic sac. (*bl*) Blood cell. (*f*) Fat. (*g. ph*) Pharyngeal ganglion. (*mus*) Muscle. (*n*) Nerve from brain. (*tr*) Trachea. (*x*) Lateral wall of antennal coelome forming fatty tissue (*f*).

159), and finally the true heart cavity arises by the fusion of the cardioblasts from either side.

About one day after blastokinesis the provisional mesodermal mid-gut layer is invested externally by a thin mesentery (Fig. 164). The latter lies close to the former, nevertheless is separate from it except in the middorsal region. The narrow space between is the circum-intestinal blood sinus. The outer mesentery which arises from the ventral portion of the splanchnic mesoderm soon afterward disappears.

The pericardial cells first make their appearance about a day after blastokinesis, forming an irregular string of large round cells on each

side of the heart. They arise from the somatic mesoderm abutting on the ventrolateral aspect of the heart. The blood cells arise mainly from the median mesoderm but partly also at the junction of the somatic and splanchnic mesoderm or even from the splanchnic mesoderm in the pre-blastokinetic stages.

The fat body is derived from the larger part of the median and lateral walls of the dorsal section of the coelomic sacs in the thorax and abdomen

FIG. 164.—*Locusta*. Cross section of heart and upper margin of mid-gut in region of mesothorax. (bl) Blood cell. (cb) Connecting sinus between heart (h) and circumintestine blood sinus (ib). (cbl) Cardioblast. (ms) Mesentery of circumintestine blood sinus. (spl.m) Splanchnic mesoderm. (y) Yolk. (yc) Yolk cells.

and also from the lateral walls of the dorsoanal pouch of the antennary coelomic sac.

The tracheal system is first in evidence in the 112-hour stage as 10 pairs of ectodermal invaginations whose mouths form the spiracles (cf. Fig. 159, *st*). The mesothoracic and metathoracic spiracles subsequently migrate forward so that the former come to lie on the membrane between the prothorax and mesothorax, whereas the latter come to lie on the posterior margin of the mesothoracic pleuron. At the blind end of each spiracular invagination two diverticula develop: a horizontal, short mediadorsal one and a longer laterodorsal backward-directed one. Later another very short mediohorizontal diverticulum is formed from the spiracular invagination.

At about 64 hours the neuroblasts first become differentiated as a row of four, rarely five, large cells with massive rounded nuclei, lying

on either side of the median line of the ectoderm and facing the yolk. Simultaneously with the multiplication of the neuroblasts the germ-band ectoderm expands on either side of the mid-ventral line to form a pair of neural swellings (Fig. 165, *neur*). The neuroblasts divide mitotically and give rise to smaller daughter cells (*n*) which arrange themselves on the inner (dorsal) side of the neuroblasts to form the future ganglion cells (Fig. 165). At about the 112-hour stage the neuroblasts of the *median cord* (*mst*) at first lying intersegmentally shift forward and become incorporated into the ganglion of the preceding segment. The ganglion cells send out long processes that develop into the intersegmental pair of connectives and the transverse commissures of each ganglion. A thin layer of elongated cells, the neurilemma, probably arising from the

FIG. 165.—*Locusta*. Cross section of second thoracic segment of 75- to 80-hour embryo. (*mst*) Median nerve cord. (*n*) Daughter nerve cells. (*neur*) Neuroblasts. (*neurg*) Neural groove.

outlying ganglion cells, covers the neurogenic tissue dorsally. The total number of nerve ganglia belonging to the ventral chain is 17, one for each segment from the mandibular to the eleventh abdominal segments, inclusive, the last being very small.

The brain, which consists of the proto-, deuto-, and tritocerebrum, arises, except for the optic ganglion, in a manner similar to that described for the ventral chain of ganglia. The neuroblasts are at first differentiated in the 59-hour stage in the protocerebral part and slightly later in the following parts of the brain. The protocerebral rudiments occupy the entire head lobes. From the beginning the neuroblasts of each half of the protocerebrum are divided into two lobes. A third, the optic, lobe is then differentiated from the lateral ectoderm in a manner different from and independent of the other two lobes but later is connected with them. Neuroblasts do not take part in the formation of the optic lobes. On the dorsolateral edge of the head lobes there appear in the 52-hour stage thickened masses of which the peripheral nuclei are arranged in a

single row, although in the rest of the mass they exhibit no regular arrangement. This mass is the rudiment of the optic ganglion and eye plate. Several hours later the inner mass, or optic ganglion, begins to separate from the outer layer, or eye plate, the separation being completed in the 80-hour stage. Meanwhile the optic lobe becomes connected with the middle protocerebral lobe which ultimately forms the internal medullary mass of the optic lobe and the optic nerve. During blastokinesis the optic lobe acquires a secondary connection with the eye plate. The nuclei of the optic ganglion near its dorsal edge elongate and send out nerve fibers which go to the retinulae and form the postretinal fibers. The middle, or second, lobe, as noted above, forms the internal medullary mass of the optic ganglion. The median, or third, lobes form the future protocerebral lobes of the brain between which, and arising from which, runs the supra-esophageal commissure. The deuto- and tritocerebrum in mode of origin and further development are exactly comparable to the ganglion of the ventral chain. Originally they are postoral in position but subsequently shift forward in relation to the mouth so that the deutocerebrum is distinctly preoral, whereas the tritocerebrum lies beneath and behind the mouth, its lobes connected by a commissure. The deutocerebral lobes, which at first lie close together, gradually move apart, migrate forward, and lose all evidence of their original connection. The deutocerebrum, from which the antennary nerves arise, has no transverse commissure.

The stomatogastric nervous system arises in the 98-hour embryo as an unpaired group of cells on the dorsal ectodermal wall of the stomodaeum. The mesodermal coat which surrounds the stomodaeum is wanting in these regions. Afterward, when the masses are well differentiated into ganglia and separate from the stomodaeal ectoderm, the mesoderm closes beneath them to form an unbroken ring around the stomodaeum. There are formed a frontal ganglion, an unpaired occipital and paired pharyngeal ganglion arising from a common rudiment, and a third rudiment from which the paired ventricular ganglia arise. These rudiments soon are connected by the recurrent nerve. When the inner walls (*ant.co*) of the antennary coelom form the cephalic aorta, the pharyngeal ganglia (*g.ph*) become enclosed in them (Fig. 163).

The fore-gut develops in the 52-hour stage as an invagination near the cephalic end of the embryo (Figs. 166A,B). At the time of its first appearance its blind end is free from cells of the inner layer but shows an outgrowth of cells that eventually form the mid-gut epithelium. Later the blind end secondarily acquires a covering of inner-layer cells which form the stomodaeal musculature. In the 120-hour stage the blind end broadens out and becomes thin, rupturing when the mid-gut epithelium is completed. The hind-gut develops as a proctodaeal invagina-

tion (Fig. 166*C, proct*) in a manner similar to the stomodaeal invagination but at the caudal end of the body. It is first in evidence about 7 hours after the appearance of the stomodaeum. The six Malpighian tubules, of ectodermal origin, first appear in the 117-hour stage.

The definitive mid-gut, according to Roonwal, arises from the ectoderm, *i.e.*, from a proliferating mass of cells that come from the ectodermal cells at the blind ends of the stomodaeal and proctodaeal invaginations. These masses become cup-shaped, the edges of the anterior growing toward the edges of the posterior cup until their edges meet, enclosing a part of the mid-gut yolk. The yolk, previous to this period, has become enclosed first by the provisional dorsal closure soon after blastokinesis and

FIG. 166.—*Locusta*. Sagittal sections. A, stomodaeum of 52-hour embryo. B, stomodaeum of 56-hour embryo. C, proctodaeum of 70-hour embryo. (am) Amnion. (ect) Ectoderm. (lb) Labium. (lr) Labrum. (md) Mandible. (mes) Mesoderm. (mx) Maxilla. (proct) Proctodaeum. (stom) Stomodaeum.

then by the splanchnic mesoderm which grows around the yolk outside the provisional dorsal closure, thus cutting off the little that remains of the extraembryonic yolk. The provisional dorsal closure then degenerates, leaving the thin splanchnic mesoderm as the second provisional mid-gut cover until four days after blastokinesis. One day later (two days before hatching) the cell masses at the blind ends of the stomodaeum and proctodaeum quickly spread over the entire yolk to form the definitive mid-gut epithelium. At the same time, the stomodaeal and proctodaeal membranes rupture, thus connecting the lumen of the mid-gut with those of the fore- and hind-guts.

In the 56-hour-old embryo the dorsal walls of the mandibular coelom (Fig. 153) give out large, rounded, loosely arranged cells which spread mediadorsally and soon form an arched structure, the subesophageal body. It ultimately comes to lie beneath the stomodaeum, losing its connections with the coelomic walls. The cells of the subesophageal body reach a

maximum size during blastokinesis, after which they gradually become smaller. The subesophageal body is still in evidence in the freshly hatched grasshopper, where it occupies a small space beneath the anterior end of the crop. Roonwal agrees with Heymons in regarding this body as excretory in function.

The germ cells are first distinguishable in the 112-hour stage (Fig. 160) as cells that are larger and whose nuclei are poorer in chromatin than those of the adjacent mesoderm. They lie in the median walls of the dorsal pouch of the coelom of the second to the fifth abdominal segments. They are at first segmental but afterward extend into the intersegmental regions as well. Soon they can be traced as far back as the tenth abdominal segment. Each gonad rudiment is spindle-shaped and composed of five parts: a terminal filament, a dorsal cell mass, a central cell mass consisting of the germ cells and mesoderm cells, a small ventral cell mass lying below the central mass, and the follicular cells which limit the gonad rudiment from the outside. In the male the dorsal cell mass becomes incorporated into the central cell mass which forms the testes proper. The ventral cell mass gives rise to the gonadal part of the vas deferens which shows no lumen at the time of hatching. In the female the dorsal cell mass forms the germarium, and the central cell mass contains the oögonia and the interfollicular cells. The ventral cell mass forms the egg calyx, and the follicular cells give rise to the outer membrane of the ovarioles and of the egg calyces. The gonadal portion of the genital ducts, as noted above, are formed of the ventral cell mass. In many of the abdominal segments the ventral coelomic pouches form ampullae which usually remain connected for some time with the rest of the coelomic walls by means of solid strands. In the female the ampullae are formed in the third and fourth and the sixth to the tenth abdominal segments. All these, except the pair belonging to the ninth segment, have a distinct lumen until sometime after blastokinesis. Strands that connect the ampullae disappear sooner or later. Portions of the strands in the seventh and eighth segments give rise to the paired mesodermal oviducts in the female; in the male they form, together with the strands of the ninth abdominal segment, the paired vas deferens. The ampullae also eventually disappear in the female; the pair belonging to the eighth, though, lasts longest, apparently not taking part in the formation of the end portion of the paired oviducts. The acquisition of a lumen in the entire mesoderm portion of the oviduct is a postembryonic development.

In the male the definitive genital opening lies in the intersegmental region between the ninth and tenth abdominal sterna, the former constituting the subgenital plate. The tenth abdominal appendages shift forward and fuse with the ninth, and together they form the aedeagus, the ejaculatory duct, and associated structures. The ampullae of the

tenth abdominal segment are very large. As they develop, they move medially and eventually open into the ejaculatory duct. The male accessory glands arise as invaginations of the walls of these ampullae.

About a day after blastokinesis the embryo secretes a cuticular membrane all around its body which is shed just after emergence. Hatching and intermediate molting are dependent on humidity but not influenced by light. Hatching in *Locusta migratoria* occurs 7 days after blastokinesis, or 13 days after egg deposition.

THE DIFFERENTIAL LOCUST (*Melanoplus differentialis*)

As described by Nelsen (1934), the embryonic rudiment of *Melanoplus differentialis* is at first a short, pyriform, posteriorly placed germ disk; then it becomes short T-shape, then progressively longer as segments are differentiated from the cephalic toward the posterior end. A blastoporic groove forms in the germ disk, and soon the inner layer begins to form, not only by invagination and delamination but also during these processes by division of the inward-moving cells. A tubular invagination does not form. The mid-gut rudiment is derived from the ends of the inner layer associated with the blind ends of stomodaeum and proctodaeum, although Nelsen does not deny the possibility of ectodermal material's migrating inward with the entoderm. The mid-gut epithelium thus develops from anterior and posterior rudiments. Aside from the material that is segregated for the formation of mid-gut epithelium, the inner layer constitutes the mesoderm. Mesoderm material in the head and thoracic regions begins to differentiate before the abdominal region has attained its caudal limits of growth. Mesodermal segmentation corresponds to ectodermal segmentation, with paired coelomic cavities appearing in the appendage-bearing segments.

The germ cells are segregated from the lateral margins of the ectoderm of the abdominal region at the time the segmentation of the latter begins. They ultimately become separated from the ectoderm cells where these join the amnion and migrate in a passive manner on to the coelomic sacs where they become associated with the inner walls of the sacs. When the coelomic sacs coalesce with each other, the germ cells and the splanchnic wall mesoderm cells form two continuous cell strands from the first to the eighth abdominal segments, inclusive, although some cells may be located posterior to the eighth segment.

Recently Stuart (1935) working with the same insect arrived at a different conclusion regarding the origin of the mid-gut epithelium. He says that shortly before hatching, the yolk cells move peripherally to form a temporary lining upon the inner surface of the mesodermic components of the mid-gut. About the time the insect hatches, each yolk-cell nucleus divides into a dozen or more smaller nuclei which Stuart

designated as the "presumptive mid-gut epithelial nuclei." Each of these nuclei then appropriates a portion of the yolk-cell cytoplasm, and thus are formed the definitive mid-gut epithelial cells.

References

MANTARIA: Bruce (1887), Graber (1890*b*, 1891). *Empusa egena*; Bugnion (1923). *Mantis religiosa*; Bugnion (1923), Giardina (1897), Rabito 1897*a*), Viallanes (1891). *Paratenodera sinensis*; Hagan (1917). *Sphodromantis guttata*; Williams and Buxton (1916). *Stagmomantis carolina*; Cockerell (1898), Rau (1913), Wheeler (1893*a*).

BLATTARIA: *Blatta sp.*; Nusbaum (1890*a*), Wheeler (1891*a*, 1893*a*). *Blattella germanica*; Blochmann (1887, 1892), Cholodkowsky (1888–1892), Faussek (1911), Heymons (1891, 1895*a*), Hummel (1835), Nusbaum (1883), Nusbaum and Fulinski (1906), Patten (1884), Riley (1904), Wheeler (1889*b*). *Diploptera dytiscoides*; Hagan (1939). *Parcoblatta virginicus*; Glaser (1920). *Periplaneta americana*; Glaser (1920). *P. orientalis*; Blochmann (1892), Fraenkel (1921), Gresson (1931), Hallez (1885, 1886), Heymons (1895*a*, 1905), Korschelt (1886), Mercier (1906), Miall and Denny (1886), Nusbaum (1886).

ISOPTERA: *Eutermes rotundiceps*; Strindberg (1913*b*). *E. rippertii?*; Knower (1896, 1900). *Termes*; Ahrens (1935).

PHASMATARIA: *Bacillus rossii*; Heymons (1897*c*, 1899*a*). *Carausius morosus*; Ashbel (1931), Hammerschmidt (1910), Leuzinger, Wiesmann, and Lehmann (1926), Strindberg (1914*b*), Thomas (1936), Zokolska (1917). *Clitumnus artemis*; Cappe de Baillon (1928). *Menezenus semiarmatus*; Cappe de Baillon (1928). *Phasma ferula*; Müller (1825). *Phyllium scythe*; Murray (1864).

SALTATORIA: *Caelifera*; Bezrukov (1923), Cappe de Baillon (1925). *Amphitornus sp.*; Caruthers (1931). *Decticus bicolor*; Korschelt (1886). *D. marginalis*; Korschelt (1886). *Ectobia livida*; Heymons (1895*a*). *Gomphocerus haemorrhoidalis*; Korschelt (1885). *Gryllotalpa vulgaris*; Graber (1888, 1890*b*, 1891*b*), Heymons (1895*a*), Korotneff (1883, 1885, 1894), Nusbaum (1890*a*), Nusbaum and Fulinski (1909), Rathke (1844), Weismann (1882). *Gryllus abbreviatus*; Murray (1926). *G. campestris*; Heymons (1893*b*, 1895*a*). *G. domesticus*; Heymons (1893*b*, 1895*a*). *G. luctuosus*; Wheeler (1893*a*). *G. mitratus*; Oka (1934). *G. vulgaris*; Dohrn (1876), Graber (1888, 1889*b*), Heymons (1893*b*). *Locusta migratoria*; Roonwal (1936, 1937). *L. viridescens*; Hallez (1886). *L. viridissima*; Harold (1839). *Mecostethus sp.*; Caruthers (1931). *Melanoplus sp.*; Wheeler (1891*a*). *M. allanisi*; Packard (1883). *M. differentialis*; Baden (1936, 1937), Bodine (1935), Cole and Jahn (1937), Else (1938), King and Slifer (1934), McNabb (1928), Nelsen (1931, 1934), Slifer (1931–1938), Slifer and King (1932, 1934). *M. spreata*; Packard (1883). *Nemobius fasciatus*; Murray (1926). *Oecanthus sp.*; Graber (1888*d*), Nusbaum (1890*a*). *O. niveus*; Ayers (1884), Nusbaum (1890*a*). *Orthoptera*; Snodgrass (1937), Stuhlmann (1886). *Orchelimum vulgare*; Wheeler (1893*a*). *Stenobothrus sp.*; Graber (1888*d*, 1890*d*), Leydig (1889). *S. variabilis*; Graber (1888*b,c*, 1889*b*, 1890*b*). *Tachycines asyramorus*; Krause (1934, 1938). *Trimerotropis*; Caruthers (1931). *Xiphidium ensiferum*; Heymons (1894*b*) Wheeler (1890, 1891*a*, 1893*a*).

CHAPTER XVI

OLIGONEPHRIDIA

COPEOGNATHA, ANOPLURA, THYSANOPTERA, HEMIPTERA COPEOGNATHA

A VIVIPAROUS PSOCID (*Archipsocus fernandi*)

This psocid, which is found among dry leaves in Ceylon, has been studied by Fernando (1934) with respect to its development. The abdomen of a gravid female may contain more than a dozen embryos in all stages of development, which remain in the ovarian tubules and finally pass down the common oviduct to the exterior. The mature ovum, which

FIG. 167.—*Archipsocus*. Ovum in ovariole (ovt). (pr) Periplasm. (trc) Trophocyte. (y) Yolk.

FIG. 168.—*Archipsocus*. Sagittal section. (bld) Dorsal blastoderm. (ent) Anterior (a) and posterior (p) entoderm rudiments. (gb) Germ band. (gc) Germ cells. (trc) Trophocyte.

measures 57.6 microns in length, has neither yolk nor chorion and entirely fills the ovarian tubule in which it lies. As the egg travels down the ovarian tubule, cleavage begins. The first division results in the production of two nuclei, which come to lie in the center of the egg, embedded in the central cytoplasm. When about six nuclei (blastomeres) are produced, they are found embedded in the periplasm (Fig. 167), with two nuclei surrounded by cytoplasm, remaining in the center and giving rise to the vitellophags (trc trophocytes). The egg now elongates, the periph-

eral nuclei by repeated division soon forming a primary epithelium (blastoderm). The vitellophags meanwhile have also increased in number. The primary epithelium thickens ventrally, and at the anterior and posterior ends within and close to the epithelium some small cells whose nuclei stain more lightly than the epithelial cells constitute the entodermal rudiments (Fig. 168, *ent*). In addition, at this time, the primordial germ cells are found at the posterior end (Fig. 168, *gc*). Certain cells, which wander into the central nutritive mass from the ectoderm, may be considered as forming a middle entodermal mass.

After the development of the entoderm, the mesoderm and the ectoderm begin to differentiate. The sides of the ventral germ band become thickened by rapid multiplication of cells, resulting in the

FIG. 169.—*Archipsocus*. Cross section. (*ent*) Entoderm. (*lp*) Lateral plate. (*mp*) Median plate. (*trc*) Trophocyte.

FIG. 170.—*Archipsocus*. Sagittal section. (*am*) Amnion. (*ent*) Entoderm. (*gc*) Germ cells. (*ser*) Serosa. (*ovt*) Wall of ovary.

formation of a median plate and two lateral plates (Fig. 169, *mp*, *lp*). Meanwhile, cells are proliferated along the entire length of the median plate. The mesal edges of the lateral plates then grow toward each other until they meet on the median line without the formation of a gastrular furrow. The lateral plates form the ectoderm; the median plate, the mesoderm.

The germ band now becomes flexed (Fig. 170). Head and tail folds appear which grow around the embryo to meet ventrally and thus complete the amnion (*am*) and serosa (*ser*).

Later, body segmentation and rudiments of the appendages appear. The antennae, the mandibles, and the three thoracic appendages are first conspicuous, followed later by the other mouth appendages. Ten distinct segments are to be found in the abdomen. The stomodaeal and proctodaeal invaginations now take place, the inner end of the stomodaeal

invagination abutting on the anterior entoderm rudiment. Cells of the middle entodermal mass arrange themselves in the form of a layer between the nutritive yolk mass and the mesodermal cells on the ventral side. In the nutritive mass are entodermal cells as well as trophocytes (vitellophags). Stomodaeum and proctodaeum are surrounded by mesodermal cells from which the muscles arise. The anterior entoderm rudiment becomes arranged in a layer that, in conjunction with the blind inner end of the stomodaeum, forms a small vesicle, or sac (Fig. 171), projecting into the nutritive mass. A similar but much smaller sac appears at the blind end of the proctodaeum. Amnion and serosa by this time have disappeared entirely, though Fernando (1934) does not

FIG. 171.—*Archipsocus*. Sagittal section of stomodaeum (*stom*). (*br*) Brain. (*ent*) Entoderm. (*mes*) Mesoderm. (*ser*) Serosa. (*trc*) Trophocyte. (*ves*) Vesicle.

state in what manner this is accomplished. The dorsal organ lies above the stomodaeum. Between the dorsal organ and the brain is the remnant of the anterior entodermal mass loosely adherent to the dorsal surface of the stomodaeum. Along the ventral surface of the nutritive mass is the layer of entodermal cells from the middle rudiment. Meanwhile dorsally the entodermal cells in the nutritive mass arrange themselves in a dorsal layer. The nutritive mass is thus gradually enclosed by entodermal cells (Fig. 172) with the help of the entodermal cells situated at the tip of the proctodaeum. At this time the mid-gut is attached to the stomodaeum, and internally the mid-gut encloses the anterior entodermal vesicle (Fig. 172, *ent. ves*) which was derived from the major part of the anterior entodermal rudiment. The vesicle elongates toward the posterior end where it comes in contact with the smaller posterior vesicle, thereby forming a tube. Meanwhile the nutritive mass is

absorbed. The inner entodermal tube derived from the vesicles now undergoes disintegration, leaving as the definitive mid-gut epithelium (*mge*) the cells originating from the middle entodermal mass.

Since the nutritive mass is so small in this viviparous psocid, additional food material is obtained through a pseudovitellus in a manner

FIG. 172.—*Archipsocus*. Sagittal section of anterior part of mid-gut enclosing inner entodermal vesicle (*ent. ves*) at anterior end. (*br*) Brain. (*mes*) Mesoderm. (*mge*) Definitive mid-gut epithelium. (*nc*) Nerve cord. (*stom*) Stomodaeum.

similar to viviparous (ovoviviparous) aphids. Fine cytoplasmic processes pass from the cells of the serosa into the walls of the ovarian tubule wherever the embryo comes in contact with it. In the posterior region the wall of the ovarian tubule is unusually thick, the boundary between it and the serosa (Fig. 173, *ser. ovt*) being obliterated. It is here that

FIG. 173.—*Archipsocus*. Sagittal section showing connection between serosa and ovariole (*ser. ovt*) at the posterior region of the embryo. (*ovt*) Ovariole. (*p*) Thoracic leg. (*proct*) Proctodaeum. (*ser*) Serosa. (*ser. ovt*) Fusion of serosa and ovariole. (*y*) Yolk.

on the embryonal side the nutritive mass is continuous with the serosa, thus establishing a means for the embryo to obtain nutriment from the ovarian tubule. A somewhat similar connection is found in the anterior region just in front of the brain. This connection is temporary. When amnion and serosa disappear and the definitive dorsal ectoderm develops, the embryo is disconnected from the maternal wall. The embryo then

rapidly passes down the ovarian tubule and finally out by the common oviduct.

The secondary dorsal organ makes its appearance directly above the stomodaeum after the rupture of amnion and serosa. It is formed by an intucking of the ectoderm (Fig. 174), by which the contents of the organ come in close contact with the wall of the ovarian tubule. Finally, the ectodermal aperture is closed, and the dorsal organ is absorbed along with the nutritive mass.

Blastokinesis does not take place during development.

FIG. 174.—*Archipsocus*. Cross section of secondary dorsal organ. (br) Brain. (ent) Entoderm. (ovt) Ovariole. (stom) Stomodaeum.

SIPHUNCULATA, THE SUCKING LICE

THE HEAD LOUSE (*Pediculus humanus capitis*)

The egg of the head louse is ovoid, somewhat narrowed posteriorly, with an operculum, or cap, at the anterior end containing the micropylar openings. The union of the pronuclei occurs in the anterior third of the egg. Schölzel (1937) found that at the 256-cell cleavage stage the cleavage nuclei are uniformly distributed over the yolk, placed at an average distance of 10 to 15 microns from the periplasm. When the nuclei reach the periphery, they continue dividing mitotically, forming a complete blastoderm. The vitellophags which remain behind in the yolk in the main have smaller nuclei and do not undergo mitotic division. On the posterior third of the egg the blastoderm cells are deeper than elsewhere, especially in the area where the germ band appears. At the posterior end of the egg at the time of deposition a mass of symbiotic plant cells are found. These become imbedded in a depression in the thickened germ band. Above them in the plasma, which still separates them from the yolk, a peculiar aster-like plasmic radiation develops (Fig. 175). The germ band now invaginates into the yolk, carrying at its upper, open, or caudal, end the mass of symbionts which become enclosed in an irregular syncytium formed by the germ band, the "aster" meanwhile degenerating. The break that existed at the place where the

symbionts were located in the germ band at the caudal junction of the germ band and amnion closes when the symbionts, enclosed in their syncytial envelope (mycetom), pass out of the germ band into the yolk at the anterior end of the egg. The germ band meanwhile is reflexed at its caudal end (Fig. 176). The amnion, at first thick and indistinguishable from the germ band, becomes a thin membrane. The part of the blastoderm not concerned in forming the germ band and the amnion is the serosa, in which, owing to stretching of the membrane, the nuclei lie far apart. The germ band broadens, acquires broad head lobes, and

FIG. 175.—*Pediculus*. Sagittal section. (gb) Germ band. (myct) Mycetom. (ser) Serosa.

FIG. 176.—*Pediculus*. Sagittal section. (am) Amnion. (ect) Ectoderm. (gb) Germ band. (mes) Mesoderm. (myct) Mycetom. (ser) Serosa.

then separates from the serosa. The mycetom now lies wholly free in the yolk (Fig. 177, *myct*) under the micropyle. At the time of invagination of the germ band, the cleavage of the yolk into spherules begins, first at the posterior pole, then at the anterior pole, and finally in the center. Vitellophags within the spherules reduce the yolk to a homogeneous mass.

When the germ band has become flexed (Fig. 176), the inner layer begins to develop on its dorsal, or yolk, side in the form of isolated cell islands along the median line. These cell islands enlarge and finally fuse into an inner layer which represents the entoderm and mesoderm. While the inner layer is forming, first the proctodaeum (Fig. 177) and then the stomodaeum make their appearance. The anterior and posterior mesenteron rudiments are derived from the inner layer (Fig. 180).

Segmentation of the germ band begins about the time the proctodaeum forms. Twenty-one segments are evident: one oral, one intercalary, one antennal, three gnathal, three leg, eight abdominal, and four proctodaeal segments, the last four later fusing into an anal segment. The intercalary segment is less distinctly developed than the others. The mandibles are smaller than the maxillae which in turn are smaller than the paired second maxillae (labium). According to Schölzel (1937), the hypopharynx is a derivative of the sternum of the mandibular and first maxil-

FIG. 177.—*Pediculus*. Sagittal section. (*am*) Amnion. (*emb*) Embryo. (*entm*) Ental membrane. (*myct*) Mycetom. (*ser*) Serosa.

FIG. 178.—*Pediculus*. Sagittal section of embryo during revolution. (*am*) Amnion. (*entm*) Ental membrane. (*gl*) Prothoracic gland shortly before degeneration. (*myct*) Mycetom. (*ser*) Serosa.

lary segment. This is not in agreement with the interpretation of Fernando (1934).

The germ band, which in the stage shown in Fig. 176 is attached to the serosa, becomes free (Fig. 177) by the time the segmentation is recognizable and the anlagen of the appendages appear. The amnion separates the germ band from the yolk on the ventral side. Dorsally it is separated from the yolk by a membrane that is fused with the posterior part of the head of the embryo and at the caudal end with the proximal part of the hind-gut (Fig. 177, *entm*). In cross section it appears that in the middle section of the body the amnion and the dorsal membrane ("ental membrane") just mentioned arise from the same lateral region of the germ band. Revolution of the embryo is initiated by a secondary fusion of the amnion with the serosa at the place where the original invagination

at the cephalic end of the embryo occurred and where the envelopes rupture. Shrinkage of the envelopes and a revolution of the embryo then take place (Fig. 178), the dorsal (ental) membrane becoming thick with closely approximated cells (*entm*), the amnion and serosa enclosing the yolk. When, with the shortening of the embryo, the revolution is completed, the serosa has become greatly contracted in the neck region to form the secondary dorsal organ (Fig. 179, *do*) which later is absorbed with the yolk, the amnion forming a provisional dorsal closure. Subsequently the dorsal wall of the embryo is completed by the dorsad-growing ectoderm, the amnion being absorbed in the yolk. An embryonic ventral neck gland is developed in *Pediculus* as described for some other insects also. The mycetom, which before revolution is located at the anterior end of the egg, after revolution is carried posteriorly to a position in the yolk in the region of the future mid-gut (Fig. 179, *myct*). As soon as the anlage of the mid-gut is formed, the mycetom is pushed into the still irregularly formed mid-gut epithelium, developing there a pocket, or diverticulum. The diverticulum at first encloses some yolk in addition to the mycetom. Its connection with the mid-gut becomes so constricted that only a narrow canal unites them, through which the syncytium composing the mycetom and the yolk is discharged, leaving the symbionts behind in the pocket. The canal then closes, the syncytium later degenerating in the yolk. The diverticulum, or pocket, containing the symbionts, enveloped by a layer of mesoderm cells, may now be designated as the "second mycetom" and forms the structure that in the larval louse has been called the "stomach disk."

The development of the nervous system, as described by Schölzel (1937), offers nothing especially characteristic. Tracheal invaginations were observed by him on the margins of abdominal segments three to eight and dorsally on the metathorax, but none was observed on the mesothorax. The stomodaeum becomes greatly elongated as develop-

FIG. 179.—*Pediculus*. Sagittal section of embryo after revolution. (*am*) Amnion. (*do*) Secondary dorsal organ. (*entm*) Ental membrane. (*myct*) Mycetom. (*nc*) Nerve cord. (*proct*) Proctodaeum. (*stom*) Stomodaeum.

ment proceeds, attaining the region of the metathorax. On the blind end of the proctodaeum the buds of four Malpighian tubules appear which reach a considerable length before the hatching of the insect. They form as solid strands which later acquire a lumen. The reproductive organs are not recognizable as such until the revolution of the embryo. What Melnikow (1869) considered to be the germ cells at the posterior end of the egg was probably the mass of symbionts. After revolution a small ventrally located anlage of the genital ducts is formed which remains at this stage of development until the first larval instar. The visible differentiation of the germ cells apparently occurs in larval life.

FIG. 180.—*Pediculus*. Sagittal section of caudal end. (*am*) Amnion. (*mge*) Mid-gut epithelial rudiment. (*proct*) Proctodaeum. (*ser*) Serosa.

The mouth parts in the fully developed embryo, according to Schölzel (1937), are readily homologized with those of the adult. The ventral "bristle," provided with a lumen, is developed from the second maxillae. From the hypopharynx there is developed the "dorsal bristle" of Vogel or sucking tube of Sikora and a ventrally located thin sclerotized tube, designed as the "middle bristle" by Vogel or the "salivary duct" by Sikora. Dorsad of the bristles is the anterior part of the pharynx with its dilator muscle. The first maxillae are, according to Schölzel, greatly reduced. Fernando (1933), however, considers the dorsal stylet as developing from the first maxillae, whereas the salivary duct alone is derived from the hypopharynx.

MALLOPHAGA, THE BITING LICE

The eggs of the Mallophaga are uniformly smaller than those of the Siphunculata and are rather variable in form. The species parasitic on mammals resemble those of the Siphunculata in form and manner of attachment to hair, whereas those which live on birds are obviously modified to adapt them to a different environment. The eggs of most

of the species have a glabrous surface. The anterior end, as with the egg of the sucking lice, is provided with an operculum that bears the micropylar openings, and at the posterior end there is a stigma with a fine canal which nearly or actually penetrates the chorion.

THE PIGEON LOUSE (*Lipeurus baculus* L.)

As with the sucking lice the infection of the eggs of the pigeon louse with symbionts takes place during a late period of oögenesis. The symbionts wander singly from the mycetocytes up the egg tube (ovariele) and thence into a depression at the posterior pole of the egg. With the invagination of the germ band the symbionts are carried more deeply into the yolk (Fig. 181) but without the close association with the germ band characteristic of *Pediculus*. The germ band and its envelopes are formed as in *Pediculus*. Yolk cells penetrate the mass of symbionts, the yolk meanwhile having become divided into spherules. At the time the anlage of the mid-gut epithelium makes its appearance, forming in the same way as in *Pediculus*, the symbiont masses, each with a yolk cell as nucleus, become surrounded by a membrane, thus forming mycetocytes. In the male embryos the mycetocytes migrate through the mid-gut epithelium and into the fat bodies. Ries (1931) failed to find mycetocytes in the fat of female embryos and therefore assumed that they all pass into the ampullae of the reproductive organs, where they may readily be demonstrated in the young female. Here they are binucleate in contrast to those found in the embryo and the larva.

Fusion of serosa and amnion before rupture of the membranes, revolution of the embryo, formation of the dorsal organ, and final absorption of this in the yolk take place as with *Pediculus*.

THE GUINEA-PIG LOUSE (*Gyropus ovalis* N.)

The development of the guinea-pig louse, as described by Strindberg (1916), resembles in most particulars that of the pigeon louse described by Schölzel (1937). The former, however, in common with *Menopon*, *Trichodectes*, and *Gliricola*, appears to lack symbionts.

FIG. 181.—*Lipeurus*. Sagittal section of germ band. (am) Amnion. (gb) Germ band. (ser) Serosa. (sym) Symbionts. (yc) Yolk cells. (From Ries.)

The blastoderm is composed of uniformly deep, nearly cubical cells. With the formation of the germ band, which extends from the posterior end of the egg to beyond the middle on the ventral side, the remaining blastoderm cells become thinner. The invagination of the germ band occurs near the caudal end of the egg. The inner layer is formed on both the germ band and the amnion when the germ band is partly invaginated. Later the inner-layer cells which have been formed on the yolk side of the amnion are liberated as paracytes which later degenerate in the yolk. The yolk has meanwhile undergone a secondary cleavage into yolk spherules, as described for Coleoptera, Lepidoptera, and some other insects. When the caudal end of the embryo has invaginated nearly to the anterior end of the egg, it becomes strongly flexed ventrally. Before the head of the embryo has lost its connection with the periphery, the large head lobes have developed. Stomodaeum and proctodaeum appear after the embryo is completely immersed in the yolk. At the blind end of the proctodaeum two buds appear which represent the anlagen of the four Malpighian tubules. Strindberg states that the tracheal invaginations appear on the prothorax and on abdominal segments two to seven.

Coelomic sacs are formed by the bending over of the outer margin of the mesoderm segments. In all there are 19 pairs, of which that of the tritocerebral segment is smallest and lacks a cavity. According to Strindberg it develops into the subesophageal body which later appears to degenerate before the emergence of the insect from the egg.

Before the revolution of the embryo the mid-gut epithelium makes its appearance, covering the blind end of the stomodaeal invagination and later that of the proctodaeum, the epithelial rudiments growing toward each other until they meet. The dorsal closure of the mid-gut occurs simultaneously with the definitive closure of the body wall. Late in embryonic life, the yolk spherules, which heretofore were approximately spherical, become more or less angulate: the division lines between them become obliterated, the margin remaining distinct only in the periphery of the yolk. Yolk-cell nuclei are now found singly or in groups adjacent to the mid-gut epithelium: but since by this time the mid-gut epithelium has already formed as a very thin layer, the yolk-cell nuclei do not give rise to this epithelium as in *Lepisma*.

The revolution of the embryo takes place as described for *Pediculus*, the amnion and serosa secondarily fusing at the cephalic end of the embryo and then rupturing to permit the eversion of the embryo.

THYSANOPTERA

THRIPS (*Thrips physapus* L.)

The development of *Thrips physapus* has been briefly described by Uljanin (1874). The species occurs in the blossoms of the Cichoriaceae

and related plants. The germ band forms on the posterior half on the concave side of the reniform egg. The caudal end then pushes into the yolk, and gradually the entire embryo becomes wholly immersed. The head, somewhat curved up but located not far from the posterior end of the egg, moves toward the surface, pushing the amnion against the serosa. At this point a rupture occurs. The subsequent behavior of the embryo in rotating into its original position of head foremost while emerging from the embryonic envelopes does not differ in essential features from that of the Homoptera and numerous other insects. Shortly before the fusion of the amnion and serosa, and before revolution, a rupture of the chorion occurs at the cephalic end through which the nymph later emerges. Here we have another instance of a break in the eggshell occurring long before hatching of the insect.

HOMOPTERA, APHIDIDAE

The Egg of the Viviparous Parthenogenetic Generations.—The Aphididae have a type of development known as “heterogamy,” or cyclic reproduction. This is characterized by an alternation of parthenogenetic generations with a sexual generation. In the north where the winter interrupts the production of young or in hot climates where there is a dry season, a single egg is laid by the female of the sexual generation which tides over an unfavorable period. In the north in the spring there hatches from the overwintering egg a female, known as the “stem mother,” which will parthenogenetically and viviparously produce young females. When the young have become mature, they in turn will produce parthenogenetic viviparous females, and so on for several generations. For many species these are wingless except for a spring and a full migrant generation which are winged parthenogenetic viviparous females. The last of the parthenogenetic generations of the season will give birth to true sexual forms, male and female. After mating, the female will deposit the single overwintering egg, completing the cycle.

The eggs of the viviparous generations undergo their complete embryonic development in the vitellarium of the ovariole (egg tube). These eggs have a scanty yolk, and they lack a chorion, the follicle of the ovarian tube taking its place. Development is rapid; partially developed young may be found in the ovariole before the mother is mature.

That the embryonic development of various species of aphids differs only in minor particulars has been shown by Toth in his comparative study of the parthenogenetic generations of 28 species representing 19 genera. The early phases of oögenesis in parthenogenetic aphids have been studied by Will (1883), Blochmann (1887), Stevens (1905), Tan-reuther (1907), Hirschler (1912), Toth (1933), and others, Blochmann first pointing out that the parthenogenetic eggs extrude only a single polar

body, whereas Stevens stated that there is but one maturation division without reduction. In the second and third cleavage stages (Fig. 182) Toth found no nuclei in the egg center. In the four-nucleate stage the egg follicle still retains its connection with the nutritive chamber by means of plasmatic strands as in the acrotrophic type of egg tube generally (Fig. 182), but shortly afterward the embryo is completely cut off from the nutritive, or end, chamber. In the fourth or fifth cleavage one of the dividing nuclei may lie with the axis of its spindle perpendicular to the egg surface, thus giving rise to a nucleus surrounded by plasma lying in

FIG. 182.—*Aphis sambuci*. Cleavage. (fol) Egg follicle.

FIG. 183.—*Myzus galeopsidis*. Blastoderm. Eighth cleavage. Chromatin elimination in the mycetoblasts.

or near the center of the egg. Up to this time cell division has been synchronous.

In the seventh cleavage stage near the posterior end of the egg are several cells, distinguished by their larger size and more abundant chromatin, that have not divided (Fig. 183). Here one finds three kinds of cells: blastoderm and yolk cells distinguishable from each other only by their position and the larger cells noted above which represent the future mycetocytes (Fig. 183, *myct*). The cell walls begin to appear in this stage. The future mycetocytes next unite into a syncytial mass in the posteromedian part of the egg. By this time the blastoderm is completed, and the cell walls are distinct (Fig. 184). Two types of blastulae may occur: one completely closed and the other open at the posterior end (Fig. 185). These forms may even occur in the same species. As development in the open type of blastoderm proceeds, the mycetom (syncytial mass of mycetoblasts) in contact with the egg follicle pushes up into the blastocoele. The mycetom anlage in its further growth crowds against

the yolk-cell syncytium (*yc*) which then covers the mycetom like a cap (Fig. 185) and eventually becomes an envelope (Fig. 186). If, on the other hand, the blastoderm is closed, the mycetom anlage in its outward

FIG. 184.—*Aphis sambuci*. Blastoderm. After the eighth division. (*myct*) Mycetoblasts.

FIG. 185.—*Hyadaphis* sp. Blastoderm. Anlage of mycetom. (*bld*) Blastoderm. (*fol*) Egg follicle. (*myct*) Mycetom. (*yc*) Yolk-cell syncytium.

FIG. 186.—*Doralis fabae*. (*bld*) Blastoderm. (*myct*) Mycetom. (*ycc*) Yolk-cell cap.

growth pushes the blastoderm cells aside to effect an opening. Thus the end result is the same in establishing a connection between the mycetom plasma and the egg follicle (Fig. 186).

When the stage of the blastoderm development just described is reached, the maternal symbiotic organism passes into the mycetom plasma. Contrary to the views of Hirschler (1912), Toth states that he has never observed symbionts in the summer eggs of aphids before blastoderm formation. As already described, the yolk-cell syncytium gradually grows around the mycetom, becoming thinner and membranous. From the inner surface of the syncytium, partition walls arise which divide the mycetom syncytium into mycetocytes (Fig. 187). The walls begin development at the anterior pole of the egg but not until the invasion of the microorganisms (symbionts) is complete and the infection pore is closed (Fig. 187).

FIG. 187.—*Hyadaphis* sp. (gb) Germ band. (gc) Germ cells. (myct) Mycetom. (ser) Future serosa. (ycc) Yolk-cell cap.

After the invasion of symbionts into the interior of the blastoderm has begun, the margin around the opening is turned inward. When the mycetom is filled with microorganisms, the egg follicle closes, which prevents more symbionts from entering. Following this the blastoderm also closes. Meanwhile the germ band which has formed on one side of the blastoderm backs further into the interior, dragging with it the portion of the blastoderm that is to form the amnion.

The germ cells become evident when the invagination of the caudal end of the germ band into the interior is well under way and the invasion of symbionts is nearly completed. Rapid cell division takes place until a mass of cells is formed at the tip of the tail (Fig. 187), the mass being pushed passively inward toward the anterior pole. As development proceeds, the caudal end of the germ band is reflected, the band assuming an S-shaped figure (Figs. 188C,D,E). About this time the beginning of the body segmentation and the invagination of the stomodaeum are in evidence. The proctodaeal invagination occurs later.

The development of the mesoderm and the formation of the mid-gut have been described by Hirschler (1912) for *Rhopalosiphum nymphae* and *Aphis rosae*. In these insects the inner layer develops along the median longitudinal line of the germ band by the overgrowth of the lateral ectoderm bands without the formation of a distinct gastrular furrow. This inner layer forms a single layer of cells. Distinct clumps of cells at each extremity of the inner layer, such as described for the Lepidoptera, are not found in the aphids.

As development progresses, the inner layer divides on the medium longitudinal line, leaving a space between. Almost immediately the transverse divisions appear to form the mesodermal metameres. A median cell strand is not present except that at the posterior end and also

FIG. 188.—Median sections of stages A-E of the viviparous *Aphis pelargonii*. (a) Union of amnion and serosa. (am) Amnion. (am.cav) Amniotic cavity. (amf) Amniotic fold. (antr) Anterior end of embryo. (b.cv) Primary body cavity. (fol) Follicular epithelium. (post) Posterior end of embryo. (ser) Serosa. (ser.ceph) Cephalic serosa. (y) Primary yolk. (y2) Ovarian yolk. (yc) Yolk cells. (Adapted from Will.)

for a short distance behind the head lobes at the anterior end. Between the lateral bands of the inner layer there are a few cells arranged singly or a few in a chain, cells that Hirschler says correspond to the median cell strand of other insects. Therefore he considers them as the secondary entoderm rudiments. They are found anteriorly from the stomodaeal

invagination to the first thoracic segment and posteriorly in the last three abdominal segments.

Before the differentiation of the inner layer has been completed, the beginnings of the stomodaeal and proctodaeal invaginations appear almost simultaneously. At this time the germ band has already become greatly elongated and flexed into an S shape. The stomodaeal invagination is clothed on the ventral side with mesodermal cells which, however, do not cover the blind end. Near the blind end are entodermal cells which Hirschler is convinced are not derived from the ectodermal stomodaeum.

FIG. 189.—*Aphis pelargonii*. Section of embryo through the germ cells (gc). (am) Amnion. (ent) Entoderm. (gc) Germ cells. (mes) Mesoderm. (mst) Median nerve cord. (ser) Serosa. (ser. ceph) Cephalic serosa (= serosa and amnion). (y) Yolk. (Adapted from Will.)

Later, after revolution, when the stomodaeum has increased in length until it has nearly reached the abdomen, the blind end is in contact with the mesenteron rudiment, an entodermal cell strand that lacks a lumen. In a similar manner the proctodaeal invagination impinges upon the posterior mesenteron rudiment which is composed of few cells and which Hirschler maintains cannot have arisen from ectodermal cells of the blind end of the proctodaeum. As development proceeds, the blind ends of the two invaginations are nearly in contact, with only a small entodermal strand composed of few cells and lacking a lumen lying between them. This strand represents the fused anterior and posterior rudiments or immature mid-

gut. Later still the blind ends of the stomodaeum and proctodaeum come in contact, with no evidence of the mid-gut rudiment remaining. Since there is no evidence of their degeneration, Hirschler ventures the opinion that the few cells of the mid-gut rudiment have migrated on to the stomodaeum and proctodaeum and later form a suspensorium. Subsequently the ectodermal cells at the blind ends of the invagination break down, thereby establishing continuity of the alimentary canal. The posterior part of the stomodaeum by this time has enlarged, forming a functional mid-gut. Hirschler therefore concludes that the yolk cells take no part in the formation of the embryo, that the gut owes its origin chiefly to the ectodermal stomodaeum and procto-

daecum, and that the gut suspensorium alone is derived from the secondary entoderm.

The account and figures given by Hirschler of the development of the embryonic envelopes are not so clear as those given by Will (1888) for *Aphis pelargonii*. In *A. pelargonii*, at the place where the serosa joins the amnion (Fig. 188*B*) and where the serosa joins the head lobe, the amniotic fold (Fig. 188*D*, *amf*) will appear. This fold is two-walled at the base (Fig. 188*E*, *a*), but beyond this point the amnion fuses with the serosa into a single membrane which continues around the head lobe to form what Will has designated as the "cephalic-serosa" (Figs. 188*E*; 189, *ser. ceph*). The structure thus differs in that only the serosa covers the head instead of both amnion and serosa as in many insects.

The other later processes of development—the rupture of the cephalic embryonic envelope, the evagination of the embryo through the opening

FIG. 190.—*Toxoptera*. (*bld*) Blastoderm. (*y*) Yolk. (*y 2*) Ovarian yolk (mycetom). (*yc*) Yolk cells.

FIG. 191.—*Toxoptera*. (*bld*) Blastoderm. (*y*) Primary yolk. (*y 2*) Ovarian yolk (mycetom). (*yc*) Yolk cells.

thus produced, and the rotation of the germ band—occur in the same way as described for the Libellulidae.

The Egg of the Oviparous Sexual Generation.—The modes of development described above apply to the viviparous parthenogenetic summer generations of aphids. Since the development of the oviparous sexual winter generation differs in some particulars, a brief abstract of the account of Webster and Phillips (1912) of the embryology of the stem mother of the grain aphid (*Toxoptera graminum*) will serve as an example.

The eggs are broadly ellipsoidal, with a slight reniform tendency. At oviposition they are pale yellow, changing in a few hours to a faint greenish color, some days later turning black. The chorion is tough and leathery, with a smooth and shining surface. A vitelline membrane is present. At the posterior end is the large, dense, almost spherical granular mycetom (termed by Webster and Phillips "ovarian yolk") (Fig. 190). The blastoderm forms more rapidly at the anterior than at the posterior pole. Some of the cleavage nuclei remain in the yolk to form yolk cells,

and later some of these yolk cells migrate into the mycetom. At the posterior end the mycetom remains uncovered at first by the forming blastoderm (Fig. 191), but later the blastoderm begins to thicken and

FIG. 192.—*Toxoptera*. (am) Amnion. (gb) Germ band. (ser) Serosa. (y) Yolk. (y 2) Ovarian yolk (mycetom). (yc) Yolk cell.

FIG. 193.—*Toxoptera*. Sagittal section. (am) Amnion. (gb) Germ band. (po) Polar organ. (y) Yolk. (y 2) Ovarian yolk (mycetom). (ser) Serosa. (yc) Yolk cell.

FIG. 194.—*Toxoptera*. Sagittal section of germ band. (am) Amnion. (ect) Ectoderm. (ent) Entoderm. (mes) Mesoderm. (ov) Developing ovary. (po) Polar organ. (ser) Serosa. (y) Yolk. (yc) Yolk cell.

invaginate, pushing the mycetom into the yolk. The mycetom is carried inward until it lies well toward the middle of the egg, forming the base of a cone the body of which consists of germ band and amnion (Fig. 192).

The germ band now releases itself from the blastoderm, leaving behind the grumulus ("polar organ" of Webster and Phillips), a cluster of cells imbedded within a mass of protoplasm (Fig. 193). The amnion meanwhile has become thin and membranous (*am*), the attenuated blastoderm forming the serosa (*ser*). As development proceeds, the germ band becomes much flexed (Fig. 194), the anterior and posterior ends lying nearly in contact with each other, both pointing toward the posterior pole. By this time the germ layers have differentiated, the entoderm being thin and less compact than the ectoderm, forming an almost continuous sheet over the inner surface of the germ band. At this stage the body segmentation becomes apparent, and the mycetom assumes a more anterior position in relation to the embryo. Between the mycetom and the germ band a group of cells that have apparently separated from the mesoderm give rise to the gonads (Fig. 194, *ov*). The primary yolk divides into yolk spherules, each with one or more yolk cells. The embryo next changes its position so that when viewed from the side it has the form of the figure 6 with the stem directed toward the posterior end of the egg. The mycetom now lies in the region of the first abdominal segment between the dorsal side of the embryo and the yolk, and just behind it is the spherical gonad. Cephalic, thoracic, and abdominal regions are sharply marked, each distinctly segmented, the first with five, the second with three, and the last with nine segments (Fig. 195).

FIG. 195.—*Toxoptera*. Ventral aspect. (*abd* 1-9) Abdominal segments 1-9. (*ant*) Antenna. (*lb*) Labium. (*lr*) Labrum. (*md*) Mandible. (*mx*) Maxilla. (*p* 1) First thoracic leg bud. (*stom*) Stomodaeum.

In the next stage the abdominal region changes its position by folding back dorsally over the mycetom (Fig. 196). The proctodaeum has by this time been formed as well as the stomodaeum, and the mid-gut is in the course of formation above and resting on the mycetom. This is the stage in which most of the embryos pass the winter.

In the spring the embryo advances in the yolk toward the posterior pole until the amnion in the dorsocephalic region comes in contact with

the serosa. These membranes thereupon fuse as with the Odonata, following which the embryo reverses its position until the head comes to lie at the cephalic end of the egg, the embryonic envelopes accumulating in the cephalic region, later to form the second dorsal organ. In this revolution the grumulus is carried cephalad on the dorsal side of the embryo and finally merges with and shares the fate of the embryonic envelopes. Soon after the dorsal closure the insect emerges from the chorion.

FIG. 196.—*Toxoptera*. Sagittal section. (*abd*) Abdomen. (*am*) Amnion. (*lr*) Labrum. (*ov*) Rudimentary ovary. (*po*) Polar organ. (*ser*) Serosa. (*stom*) Stomodaeum. (*y*) Yolk. (*y 2*) Degenerating ovarian yolk (mycetom). (*yc*) Yolk cell.

HOMOPTERA

Siphanta acuta

The eggs of this species, as described by Muir and Kershaw (1912), are long, cylindrical, flattened on the ventroanterior surface where the micropylar area is situated, pointed at the anterior, and rounded at the posterior end. The eggs are laid in batches of about 60, with the ventral side uppermost, one overlapping the other. Twenty-four hours after the egg is laid, the blastoderm is distinct, and a thickening along the dorsoposterior area indicates the germ band. At about the thirtieth hour the posterior end of the germ band begins to invaginate (Fig. 197) and is entirely invaginated about the fortieth hour (Fig. 198), whereupon the amniotic

FIG. 197.—*Siphanta*. Sagittal section at 30 hours. (*bld*) Blastoderm. (*dr*) Dorsal side. (*gb*) Germ band. (*mi*) Micropylar area. (*post*) Posterior end.

FIG. 198.—*Siphanta*. Sagittal section at 40 hours. (*am*) Amnion. (*ch*) Chorion. (*dr*) Dorsal side. (*gb*) Germ band. (*ind*) Indusial thickening. (*mi*) Micropylar area. (*post*) Posterior end. (*ser*) Serosa.

FIG. 199.—*Siphanta*. Sagittal section at four days. (*am*) Amnion. (*ch*) Chorion. (*dr*) Dorsal side. (*emb*) Embryo. (*ind*) Inner (2) and outer (1) indusium. (*mi*) Micropylar area. (*post*) Posterior end. (*ser*) Serosa.

FIG. 200.—*Siphanta*. Ventral aspect at five days. (*am*) Amnion. (*ch*) Chorion. (*ind*) Inner (2) and outer (1) indusium. (*mi*) Micropylar area. (*post*) Posterior end. (*ser*) Serosa.

cavity closes. The embryo now lies on the dorsal side of the amniotic cavity (Figs. 199, 200) with its caudal extremity toward the anterior and its cephalic extremity toward the posterior end of the egg, its ventral surface turned toward the ventral aspect of the egg. In this position the embryo develops until about the fifth day, when revolution takes place. On the second day, before the amniotic cavity closes, an "indusial thickening" appears on the anterodorsal area of the blastoderm, similar to that described by Wheeler in *Xiphidium* (Fig. 36, *ind*). Muir and Kershaw did not follow the development of the indusium in detail, but they state

FIG. 201.—*Siphanta*. Lateral aspect at 12 days. (*ch*) Chorion. (*cut*) Cuticula. (*dr*) Dorsal side of egg. (*emb*) Embryo. (*ind 1*) Outer indusium. (*mi*) Micropylar area. (*ser*) Serosa.

that later two indusial envelopes develop, so it may be assumed that these are formed from the two walls of the indusial sac as in *Xiphidium* (Figs. 36, 37, *ind*). The outer indusial envelope (Figs. 199, 200, 201, *ind.1*) becomes closely applied to the serosa, except at the two poles, and remains intact until the hatching of the nymph; the inner indusial envelope (Figs. 199, 200, *ind.2*) joins the amnion near the head of the embryo and takes on the usual functions of the serosa during the revolution of the embryo. Between the fifth and sixth days the amnion and the inner indusial envelope break open near the head of the embryo, and the revolution begins. The head of the embryo leaves the amniotic cavity and moves upward to the dorsal side of the egg, toward the original position of the germ band. When the head is well on the dorsal side, the entire embryo, including the amnion and the inner indusial envelope, begins to revolve around the longitudinal axis of the egg. The emergence from the amniotic

cavity continues at the same time (Fig. 200) until the embryo lies on the ventral side of the egg in the normal position of insects during the later stages of embryonic development.

An embryonic cuticle covers the embryo, entirely sheathing all appendages. A thickening at the cephalic portions of this cuticle forms the "egg burster." Thus the mature embryo is enveloped in three coverings, apart from the chorion; *viz.*, the serosa (Fig. 201, *ser*), forming the outer covering; the outer indusial envelope (Fig. 201, *ind.1.*); and the "embryonic cuticle" (Fig. 201, *cut*). Although this was not seen by Muir and Kershaw, it seems possible that the amnion and the inner indusial envelope, after rupturing, are absorbed in the yolk and thus undergo the same fate as the amnion and serosa of the Odonata.

Rudiments of mouth parts and legs which are apparent on the second day are not fully developed until the ninth day, although segments of the legs are indicated on the fourth day, and the abdomen is then fully segmented. Muir and Kershaw maintain that the mandibles and maxillae arise as in other insects, the former being articulated in an approximately normal position. The maxillary seta does not represent the palpus but may be a development of the palpiger or the combined lacinia and galea. The maxillary plate represents the cardo and stipes.

HETEROPTERA

THE MILKWEED BUG (*Oncopeltus fasciatus* Dall.) AND THE FIRE BUG (*Pyrrhocoris apterus* L.)

Oncopeltus fasciatus, a member of the family Lygaeidae, feeds on the milkweed plant. It is easily reared in the laboratory, since it will feed on the seeds of the host plant and will continue to lay its eggs throughout the year. It therefore is an excellent species for morphological and embryological study.

The egg is elongate-oval, with a pearly white chorion about 1 mm. long. After fertilization, the nucleus divides, and the cleavage nuclei migrate toward the periphery of the egg. About eight hours after the egg has been laid, they may be seen about two-thirds of the way to the surface. Two hours later they are almost within the peripheral cytoplasm, those on the side reaching the periphery before those at the ends, and the nuclei migrating toward the posterior pole reaching their destination last of all. Some nuclei remain in the yolk to form the vitellogophs.

By the fourteenth hour the nuclei are all in the thin cytoplasm at the surface. They are widely spaced in the cytoplasmic layer which is very irregular in thickness. As they increase in number by mitotic division, this irregularity disappears. During the next few hours cell walls appear, and a thin one-layered epidermis of small flattened cells is formed. By the twentieth hour the blastoderm appears thinner on the dorsal side which is the first indication of the differentiation of the serosa from that part of the blastoderm which will form the germ band. The formation of the germ band corresponds in most respects to the development of the fire bug (*Pyrrhocoris*) as worked out by Seidel in 1924. On the second day after egg deposition in *Pyrrhocoris* the germ band, together with the anlage of the amnion, develops in the form of two longitudinal lateral, anteriorly diverging plates made up of cubical cells, the remaining blastoderm being thinner and destined to form the serosa. This ventral germ band extends cephalad over the anterior pole and caudad to the posterior pole where the two lateral strips converge and fuse. At the posterior pole an invagination of the germ band takes place, the tail end of the developing embryo backing into the yolk to form, together with the amnion, a

dorsoventral flattened sack, one wall of which is the embryo, the other the amnion. At first the amnion and the embryo show a similar cell structure

FIG. 202.—*Pyrrhocoris*. Ventral aspect. (hl) Head lobe.

except at the posterior end at the point of invagination. There the amniotic cavity runs out into two furrows (Fig. 202), the inner wall of the invagination representing the prolongation of the amnion, the outer wall the anlage of the germ band. The continuation of the germ band anteriorly is represented by the two ends of the lateral plates, or head lobes, which are still distinctly separated (Fig. 204, hl). When the tail of the invaginating embryo reaches the cephalic end of the egg, it bends and grows caudad until head and tail nearly meet (Fig. 203A). At the point of invagination two amniotic folds appear (Fig. 203A, amf)

which fuse, with the result that the embryo lies completely separated from the serosa (Fig. 203B). Nearly the same stage in development of *Oncopeltus* is represented by Fig. 204, a

FIG. 203.—*Pyrrhocoris*. Sagittal sections. Diagrammatic. A, elongation of embryo. B, shortening of embryo. (am) Amnion. (am. cav) Amniotic cavity. (amf) Amniotic folds. (il) Inner layer. (proct) Proctodaeum. (ser) Serosa. (stom) Stomodaeum.

sagittal section of an embryo before it has attained its greatest length and while the head lobes (hl) are still on the surface.

The head lobes at this time appear in cross section as two thickened areas continuous with the serosa (*ser*), forming the covering enclosing the yolk (Fig. 205*C*, *hl*). In a section closer to the pit through which the embryo is pushing into the yolk (Fig. 205*B*) the two furrows representing the cephalic end of the amniotic cavity are evident (*am. cav*). Still farther cephalad the relation that the head lobes (*hl*) bear to the germ band (*gb*) and the amnion (*am*) is apparent in Fig. 205*A*. The mass of cells separated from the two amniotic furrows represents that point in the embryonic envelopes where the amnion and serosa join (*am. ser*).

Before the head lobes have withdrawn from the surface at about 32 hours, the gastrular groove appears, and the inner layer forms from the invaginating ridge (Fig. 204). The formation of the inner layer is uneven. At one point in the middle region it appears flattened out with the groove already obliterated beneath it (Fig. 206*B*, *il*); at other points it appears as invaginating masses of cells (Figs. 205*C*, 206*A*, *D*); and at the anterior and posterior ends it appears as a definite ridge with a groove in the ectoderm. Figure 206 *C* shows the inner layer consisting of only three cells with the groove in the ectoderm entirely obliterated. The inner layer forms in a similar manner in *Pyrhocoris*. According to Seidel these alternate thicker and thinner masses of cells of the inner layer represent an indication of early segmentation. The number of segments that develop in the embryo as indicated by the masses of cells is 20, of which 6 are head segments, 3 thoracic segments, and 11 abdominal segments.

The Heteroptera differ from most other orders in the position assumed in the egg by the embryo when it invaginates into the yolk. It is clear from Fig. 204 that the ventral side of the germ band is directed inwardly and that when appendages appear they extend into the yolk, the inner layer and developing mesenteron ribbons (Fig. 208, *mge*) lying on the outer side of the germ band near to the surface of the egg. This position

FIG. 204.—*Oncopeltus*. Sagittal section. (*am*) Amnion. (*ect*) Ectoderm. (*hl*) Head lobe. (*il*) Inner layer. (*ser*) Serosa.

FIG. 205.—*Oncopeltus*. Cross sections at different levels. (*am. cav*) Amniotic cavity. (*am. ser*) Amnioserosa. (*gb*) Germ band. (*hl*) Head lobe. (*il*) Inner layer. (*ser*) Serosa.

FIG. 206.—*Oncopeltus*. Cross sections. (*am*) Amnion. (*ect*) Ectoderm. (*hl*) Head lobe. (*il*) Inner layer. (*ser*) Serosa.

is retained until after blastokinesis, when the embryo comes again to the surface and the yolk lies in the developing mid-gut lumen.

The formation of the two layers of the germ band does not take place simultaneously; nevertheless, it is to be regarded as a single step in the development of the embryo. The outer layer constitutes the ectoderm; the inner one, the meso- and entoderm. The vitellophags are to be regarded as early segregated, abortive entodermal cells. Following the appearance of the inner layer there are differentiated from this layer mesenteron rudiments, two cell masses from which the mid-gut lining will be formed.

Soon after the three germ layers have been differentiated, the germ band attains its maximum length, and the amniotic folds (Fig. 203A, *amf*)

FIG. 207.—*Pyrrhocoris*. Cross section of germ band. Differentiation of middle strand (*mds*). (*am*) Amnion. (*ect*) Ectoderm. (*il*) Inner layer. (*mds*) Middle strand. (*par*) Paracytes. (*ser*) Serosa.

close over the orifice of invagination. Even before the germ band has completely invaginated, the stomodaeum and then the proctodaeum become evident (Figs. 203A, B, *stom*, *proct*). The amniotic cavity at the edges is slightly expanded segmentally (Fig. 205C, *am. cav*). In consequence of this the lateral parts of the germ band together with the inner layer are bent. Before the formation of the other organs the ectoderm gives rise to a median strip on each side of which four longitudinal rows of neuroblasts are formed. Tracheal invaginations occur at this time, and near these the oenocytes arise. Four evaginations from the tip of the proctodaeum, two lateral and two ventral, represent the rudiments of the Malpighian tubules. As soon as the middle ectodermal strip is formed, the cells of the inner layer that lie above it break down except at the extremities where these cells later are largely utilized for the formation of the mid-gut.

The inner layer now consists of two uninterrupted longitudinal strands, one on each side of the median line. The inner layer lines the

edges grow dorsad. It should be remembered that the amnion now in large part forms an envelope around the yolk and that there is greater space for the development of the organs. As development progresses, the lateral edges of the body wall close over on the dorsal side, appendages attain their definitive shape, the cuticula is formed, and red pigment appears in the eyes and on the sides of the abdomen.

Going back now to the time of stomodaeal invagination, it will be observed that, as this invagination deepens, it breaks through the underlying inner layer, forcing the extreme anterior end of this layer into the antennal segment (Fig. 210A). The part of the inner layer that lies immediately behind the stomodaeum is not arranged in a single layer of cells, as is the remainder (Fig. 210A), but forms an irregular mass which later separates from the more posterior portion and grows over the tip of the stomodaeum (Fig. 210B). This compact mass forms the anterior mesenteron rudiment which slowly grows in the form of two posteriorly directed ribbons from which in part the mid-gut epithelium will develop (Fig. 210C).

FIG. 209.—*Pyrrhocoris*. After blastokinesis. Retracted serosa (*ser*) covering the head.

FIG. 210.—*Pyrrhocoris*. Sagittal sections of anterior end. A, early stage. B, later stage. Median sagittal section. C, parasagittal section of same age as B. (*am*) Amnion. (*il*) Inner layer. (*mds*) Median strand (middle plate). (*mge*) Mid-gut epithelium. (*pa*) Paracytes. (*stom*) Stomodaeum.

At the posterior end of the germ band the inner layer is distinctly thicker than that at the anterior end. A posterior portion of it, in contact

with the developing proctodaeum (Fig. 211, *mge*), develops into the posterior mesenteron rudiment. As with the anterior mesenteron rudiment, two ribbons of cells, here anteriorly directed, grow out from the posterior rudiment and, fusing with the anterior ribbons, later spread around the yolk to form the mid-gut epithelium. In the main, the observations of Karawaiew (1893) regarding the development of the mid-gut agree with those of Seidel (1924). In *Pyrrhocoris* the middle longitudinal section (middle strand) of the inner layer breaks down. In this insect the inner layer may thus be regarded as composed of a middle section (middle strand), anterior and posterior mesenteron rudiments, and two lateral mesoderm strands.

FIG. 211.—*Pyrrhocoris*. Sagittal sections. A, fifth (v) and sixth (vi) abdominal segments. (*gc*) Germ cells. B, proctodaeum (*proct*). (*mge*) Mid-gut epithelial rudiment. (*neur*) Neuroblasts.

At the time the mesenteron ribbons are approaching each other in *Pyrrhocoris* and shortly before the differentiation of the lateral bands of the mesoderm, one may observe the germ cells (Fig. 211A) emerging dorsally from the mesoderm in the intersegmental region between the first to the eighth segments. Prior to this period the germ cells had not become sufficiently differentiated to be distinguished from adjacent mesoderm cells. The germ cells near the median abdominal segments are recognizable as such a little earlier than those of either the anterior or the posterior segments, a fact that, in the opinion of Seidel (1924), indicates that the germ cells were differentiated before the formation of the germ layers. On the inner (dorsal) side of the somatic mesoderm the metameric genital ridges develop. Each of these ridges soon shows a differentiation into an upper, middle, and lower part. The upper part, or end chamber, will form the envelope for the reception of the germ cells; the middle part will form the ovarian tubes or the testicular follicles; and the lower part will form the duct. After blastokinesis the seven genital anlagen on each side in abdominal segments two to eight unite to form

FIG. 212.—*Anasa*. Parasagittal section. (am) Amnion. (am.cav) Amniotic cavity. (br) Brain. (f) Fat. (lb) Labium. (md) Mandible. (mes) Mesoderm. (mge) Mid-gut epithelium. (mx) Maxilla. (p) Thoracic legs. (proct) Proctodaeum. (ser) Serosa.

ovaries or testes. The upper and middle parts remain unchanged during subsequent embryonic development, but the lower parts fuse to form the definitive oviduct or sperm duct.

The sequence in the development of *Pyrrhocoris* on the basis of a 12-day developmental period may be stated as follows: During the first day the 240-cell stage in the primary epithelium is reached. On the second day the lateral plates of the germ band are formed, and the invagination of the band begins. During the third day the inner layer is differentiated, the germ band has attained its greatest length, the amnion is formed, buds of the appendages appear, segmentation of head and body takes place, and the stomodaeum is invaginated. On the fourth day the embryonic envelopes fuse; the proctodaeum forms; the neuroblasts appear; the thoracic appendages become segmented; the embryo shortens; tracheae, Malpighian tubules, anterior mesenteron rudiment, and the gland of the first abdominal segment appear. On the fifth day the posterior mid-gut rudiment and the germ cells become evident. On the sixth day there take place the formation of the commissures of the ventral nerve cord; preparation for blastokinesis; definitive shortening of the embryo; rupture of embryonic envelopes at the head end; differentiation of musculature, fat bodies, cardioblasts, and genital ridges; enclosure of germ cells in the genital ridges and further differentiation of gonads; anlage of stink glands; completion of blastokinesis, the serosa forming the cephalic part of the temporary dorsal closure, the amnion the dorsal part of the temporary dorsal closure; and the growth dorsad of the laterad edges of the embryo. On the seventh day the serosa sinks into the yolk. On the eighth day the fusion of the head parts, the definitive dorsal closure, specialization of the mouth parts, development of egg tooth, and cephalization of ventral nerve cord take place.

The red pigment in the eye and on the sides of the body appears on the ninth day. During the next three days completion of claws and mouth parts, the shift of the gonads to their definitive position, and finally the bursting of the chorion and escape of the nymph occur.

A POLYCTENID (*Hesperoctenes fumarius* Westw.)

This species belongs to the family Polycetenidae which is closely related to the Cimicidae. It occurs in the West Indies where it is parasitic on bats. The viviparous manner of reproduction and the associated modifications in structure both in the mother and in the offspring render this form very remarkable. The following brief abstract is taken from a paper by Hagan (1931).

The mature ovum within the ovariole lacks a chorion, for no egg-follicle cells envelop it. Cleavage is complete, each blastomere lying in the periplasmic region. The process of segmentation seems to be that

typical for related insects. The germ band soon becomes long and rather flat, though multilaminar, due to the superimposed condition of the ectodermal cells. The embryo assumes a characteristic S shape, with the cephalic lobes flexed sharply dorsally, so that this region lies directly in contact with the mandibular region (Fig. 213). Typical segmentation furrows have appeared as transverse ectodermal invaginations. The definitive mesoderm layer seems not to be involved in the early segmentation. Appendages arise as paired ectodermal thickenings. At first the mandibular, maxillary, and labial swellings are equal in size to the thoracic evaginations. The pleuropodial rudiments are indistinguishable from the thoracic evaginations, but the abdominal anlagen are insignificant, appearing more like segmental swellings. Mesodermal tissue invades the ectodermal evaginations very early.

FIG. 213.—*Hesperoctenes*. Sagittal section. (am) Amnion. (ceph) Cephalic region. (p2) Second thoracic leg. (pleur) Pleuropodium. (tel) Telson. (From Hagan.)

Just before revolution of the embryo the embryonic envelopes are intact except that the amnion is not visible opposite the pleuropodia. About the time the prothoracic appendages are almost half the body length, the embryo becomes considerably shorter and broader. At this time the embryo undergoes a reversal, so that when it again comes to assume a position in which its length lies parallel to that of the mother, its cephalic region is directed forward in the maternal body. After revolution the embryonic envelopes rupture and become located anteriorly. This is accompanied by a dorsal growth of the body walls and their fusion along the middle line, excepting in the head region. Up to this time there is no sign of a mesenteron. Stomodaeal and proctodaeal invaginations are irregularly one-layered, the latter with four Malpighian tubules. Aggregations of cells at the inner extremities of the stomodaeal and proctodaeal invaginations suggest the presence of formative entodermal cells. Similar cells scattered through the formative haemocoele presage the beginning of the definitive mesenteron. Hagan did not follow the formation of the mid-gut epithelium. About the time of the revolution of the embryo the pleuropodia invaginate (Fig. 214, *pleur*) and extend

into the embryo until their inner ends touch each other. After blastokinesis, the embryo rapidly approaches the definitive nymphal type. The embryonic envelopes become enclosed in the mesenteron, whereupon the closure of the dorsal wall is completed. The pleuropodia then extend their cell tips to enclose the embryo in a cytoplasmic sheath which Hagan has termed the "pleuropodial extensions" (Fig. 214, *pleur. e*); the enclosed space he terms the "pleuropodial cavity" (*pleur. c*). From the initiation of blastokinesis until the completion of the pleuropodial extensions the embryo lies free in the maternal reproductive tract

FIG. 214.—*Hesperoctenes*. Cross section after blastokinesis. (*ant*) Antenna. (*ect*) Ectoderm. (*ggl*) Ganglion. (*mes*) Mesoderm. (*neurp*) Neuropile. (*oen*) Oenocytes. (*p*) Thoracic legs. (*pleur*) Pleuropodium. (*pleur. c*) Pleuropodial cavity. (*pleur. e*) Pleuropodial extension. (*sin*) Haemocoele. (*trc*) Trophocyte. (*tro*) Mouth parts. (From Hagan.)

without attachment to the mother and without protective covering, an unusual condition.

The nutritive function is performed by several structures. The fat-like substance that accumulates in the egg comes from the epithelium of the tubule. The nurse-cell body seems to be derived from the follicular epithelium, the usual source of the egg follicle. The serosa develops from the blastoderm and, functioning as a trophoserosa, absorbs the nurse-cell nutrients. The trophocytes (vitellophags) elaborate in succession the substances available to them within the serosa, the pleuropodial cavity, and the mesenteron. Finally, the pleuropodia take over this function and continue to supply the embryo with nutriment until shortly before its extrusion from the mother. In so doing they function in a manner

analogous to the placenta of the mammals and are therefore termed by Hagan "pseudoplacenta."

References

- COPEOGNATHA: *Archipsocus fernandi*; Fernando (1934). *Hyperetes guestphalicus*; Jensch (1936).
- SIPHUNCULATA: *Haematomyzus elephantis*; Ries (1931, 1932). *Haematopinus* sp.; Schölzel (1937). *Lignognathus tenuirostris*; Ries (1931, 1932), Schölzel (1937). *Pedicinus* sp.; Schölzel (1937). *Pediculus* spp.; Schölzel (1937). *P. capitis*; Fernando (1933), Melnikoff (1869), Ries (1931, 1932). *Phthirus pubis*; Harold (1839), Schölzel (1937). *Polyplax spinosus*; Ries (1931).
- MALLOPHAGA: *Goniodes* sp.; Melnikoff (1869). *Gyropus* sp.; Schölzel (1937). *G. ovalis*; Strindberg (1916a). *Lipeurus* sp.; Melnikoff (1869), Schölzel (1937). *L. baculus*; Ries (1931, 1932). *Trichodectes* sp.; Schölzel (1937). *T. canis*; Melnikoff (1869). *T. climax*; Strindberg (1916a).
- THYSANOPTERA: Jordan (1888). *Thrips physapus*; Ulljanin (1874), Uzel (1895).
- HOMOPTERA (Coccidae): Hovasse (1930), Leadoro (1921), Lemoine (1892), Poluszynski (1911), Richter (1928), Strindberg (1919a), Walczuch (1932). *Aspidiotus* sp.; Brandt (1869), Teodora (1921). *A. nerii*; Metschnikoff (1866b). *Crypticeria rosae*; Hughes-Schrader (1930). *Cryptococcus* sp.; Emeis (1915), Walczuch (1932). *Echiniceria anomala*; Hughes-Schrader (1932). *Eriococcus* sp.; Walczuch (1932). *Icerya* sp.; Walczuch (1932). *I. purchasi*; Hughes-Schrader (1930), Pierantoni (1914); Shinji (1919). *I. montserratensis*; Hughes-Schrader (1930). *I. littoralis*; Hughes-Schrader (1930). *Lakshadia* sp.; Walczuch (1932). *Lecaniodiaspis pruinosus*; Shinji (1919), Walczuch (1932). *Lecanium* sp.; Brandt (1869), Emeis (1915), Teodora (1921). *Lepidosaphes* sp.; Emeis (1915). *Margarodes polonicus*; Fijalkowska (1928). *M. vitium*; Canto (1896). *Monophlebus* sp.; Walczuch (1932). *Orthezia* sp.; Walczuch (1932). *Phenococcus* sp.; Walczuch (1932). *Pseudococcus* sp.; Emeis (1915), Schrader (1923), Walczuch (1932). *P. mcdanieli*; Shinji (1919). *Pulvinaria* sp.; Teodora (1921). *P. innumerabilis*; Brues and Glaser (1921). *Saissetia oleae*; Marshall (1935). *Tachardiella* sp.; Walczuch (1932).
- HOMOPTERA: Pflugfelder (1937), Šulc (1910). *Aleyrodes* sp.; Lemoine (1892). *A. vaporariorum*; Cary (1903). *Cicada* sp.; Heymons (1899b), Richter (1928). *Psylla mali*; Speyer (1929). *Siphanta acuta*; Muir and Kershaw (1912).
- HOMOPTERA (Aphididae): *Aphids*; Baker (1921), Balbiani (1866, 1870), Heymons (1893b), Hirschler (1911), Lawson (1939), Lemoine (1893b), Metschnikoff (1866b), Shull (1930, 1931), Stiles (1939), Toth (1933, 1935), Uichanco (1924), Will (1883, 1888b), Zacharias (1884). *Aphis* sp.; Brandt (1869, 1878), Klevenhusen (1927), Leydig (1850), Witlaczil (1884). *Aphis rosae*; Brass (1883), Hirschler (1912), Leuckart (1858b), Stevens (1905), Will (1883, 1888a). *A. rosarum*; Will (1883). *A. caryae*; Burnett (1854). *A. oenotherae*; Stevens (1905). *A. pedi*; Leuckart (1858b). *A. pelargoni*; Will (1883, 1888a). *A. salicis*; Will (1883, 1888a). *A. saliceti*; Will (1888a). *A. sambuci*; Graber (1889b). *Callipterus* sp.; Wilaczil (1884). *Chaetophorus* sp.; Wilaczil (1884). *Drepanaphis* sp.; Hottes (1928), Uichanco (1924). *Drepanosiphum* sp.; Uichanco (1924), Wilaczil (1884). *Dryobius* sp.; Wilaczil (1884). *Eriosoma* sp.; Uichanco (1924). *Lachnus* sp.; Hottes (1928), Uichanco (1924). *Longistigma* sp.; Uichanco (1924). *Macrosiphum tanacetii*; Uichanco (1924). *M. sp.*; Klevenhusen (1927). *Melanozanthus salicis*; Tannreuter (1907). *M. salicicola*; Tannreuter (1907). *Monellia* sp.; Hottes (1928). *Myzocallis* sp.; Hottes (1928). *Myzus* sp.; Uichanco (1924). *Pemphigus* sp.; Leydig (1889), Witlaczil (1884).

Phylloxera sp.; Lemoine (1892). *P. punctata*; Lemoine (1887, 1893a). *P. vastatrix*; Lemoine (1893a). *Pterocallis* sp.; Klevenhusen (1927). *Pterochlorus* sp.; Klevenhusen (1927). *Rhopalosiphum nymphaeae*; Hirschler (1912). *Schizoneura* sp.; Klevenhusen (1927). *Stomaphis* sp.; Klevenhusen (1927). *Symydobius* sp.; Hottes (1928). *Tetraneura* sp.; Klevenhusen (1927). *Toxoptera graminum*; Phillips (1915), Webster and Phillips (1912).

HETEROPTERA: Glasgow (1914), Pflugfelder (1937). *Belostoma flumineum*; Hussey (1926). *Cimex dissimilis*; Heymons (1899b). *Corixa* sp.; Brandt (1869), Metschnikoff (1866). *Hesperoctenes fumarius*; Hagan (1931). *Hydrometra* sp.; Brandt (1869), Henking (1888a). *Lygaeus apterus*; Harold (1839). *Naucoris cimicoides*; Heymons (1899b). *Nepa* sp.; Wheeler (1890b). *N. cinerea*; Heymons (1899b), Korschelt (1885, 1886). *Notonecta glauca*; Heymons (1899b), Korschelt (1885, 1886), Pedaschenko (1890). *Notostira erratica*; Johnson (1937). *Pentatoma rufipes*; Strindberg (1917a). *Pristhesancus papuensis*; Muir and Kershaw (1911). *Pyrhocoris apterus*; Graber (1888b), Henking (1888a, 1890b, 1891b, 1892), Heymons (1899b), Karawaiew (1893), Korschelt (1885, 1886), Niklas (1935), Seidel (1924), Wielowiejski (1885). *Ranatra fusca*; Hussey (1926). *R. linearis*; Korschelt (1885, 1886). *Reduviid* sp.; Galliard (1934). *Reduvius personatus*; Korschelt (1886). *Rodnius prolixus*; Mellanby (1936), Wigglesworth (1924).

CHAPTER XVII

NEUROPTERA AND COLEOPTERA

NEUROPTERA

THE ALDER FLY (*Sialis lutaria* L.)

The eggs of this insect are usually found attached to the leaves of water plants. The developing egg, as described by Strindberg (1915), undergoes cleavage and forms a primary epithelium (blastoderm) in a normal way, yolk cells remaining behind in the outward migration of the cleavage nuclei. The germ band forms ventrally on the posterior two-thirds of the egg. The nonembryonic part of the blastoderm, which will form the serosa, is composed of two parts: the anterior part, covering the anterior third of the egg made up of columnar cells; and the posterodorsal part, made up of thin flat cells. A deep posterior and a shallow anterior amniotic fold develop. As they become progressively longer, the flat dorsal serosa cells become greater in extent at the expense of the deep anterior serosa cells. Soon amnion and serosa are completed. Meanwhile the embryo elongates; the inner layer forms through immigration or through a feebly indicated invagination along the median longitudinal ventral line proceeding from behind forward. As interpreted by Strindberg, the anterior end of the inner layer forms chiefly the anterior entoderm rudiment; the middle part, the mesoderm; and the posterior end, the posterior entoderm rudiment. The mesoderm is segmentally arranged, the lateral edges of each somite being reflexed to form the coelomic

FIG. 215.—*Sialis*. Longitudinal section. (am) Amnion. (br) Brain. (fg) Frontal ganglion. (mge) Mid-gut epithelium. (proct) Proctodaeum. (ser) Serosa. (stom) Stomodaeum. (yc) Yolk cells.

sacs. The subesophageal body, according to Strindberg, arises without question from the mesoderm of the tritocerebral segment of the head.

The development of the central nervous system, the stomatogastric system, the endoskeleton of the head, and the tracheal system offers nothing remarkable.

The stomodaeum appears before the proctodaeum. Both, however, from the start are clothed with mesoderm which is derived from a part of the anterior and posterior ends of the inner layer. Those terminal masses, according to Strindberg (1915), without doubt also contain another type of cells, the flattened entodermal cells which will invest the

FIG. 216.—*Sialis*. Cross section of second thoracic segment. (*cbl*) Cardioblasts. (*dc*) Provisional dorsal closure by amnion. (*do*) Secondary dorsal organ. (*f*) Fat body. (*ggl*) Thoracic ganglion. (*mge*) Mid-gut epithelium. (*mus*) Muscle.

blind ends of the stomodaeal and proctodaeal invaginations (Fig. 215, *mge*). From each of these entodermal masses a pair of ribbons will arise which laterally cover the yolk. In section (Fig. 216, *mge*) these sheets appear as two thin crescents, each covered outwardly by the splanchnic mesoderm. These lateral sheets elongate, those from the stomodaeum meeting those from the proctodaeum, then widening to enclose the yolk, first dorsally, then ventrally. The membranes at the blind ends of the stomodaeum and proctodaeum in *Sialis* break down to establish the communication between fore- and mid-, and mid- and hind-guts, shortly before hatching. The rupture of amnion and serosa takes place about as in the caddis fly, the serosa and the amnion forming the secondary dorsal organ (*do*) which later is absorbed in the yolk.

The development of this species has recently been described by DuBois (1938) with special emphasis on the behavior of the embryo under experimental conditions.

THE PEARL-EYE (*Chrysopa perla*)

In brief papers dealing with *Chrysopa perla*, Tichomirowa (1890, 1892) states that the eggs of this European insect are found on the leaves of the linden, maple, wild cherry, and other plants. The incubation period is about nine days. Yolk cells, which are left behind in the outward migration of the cleavage cells, begin active division immediately following the completion of the blastoderm. From the blastoderm the ectoderm and the embryonic envelopes will arise. The yolk cells represent the primary entoderm from a part of which the entoderm is derived. But the greater part is said to develop into mesoderm at the time of the formation of the feebly marked gastral furrow. The germ-band thickening begins to form at the posterior pole even before cell walls appear and is marked by the crowding together of the nuclei in two irregular layers.

Bock (1939) in an extended account of the development of the same species states that the inner layer arises by invagination along the median line and then spreads out to form the coelomic sacs on each side. A single-layered middle strand lying between the coelomic sacs gives rise to blood cells and the secondary vitellophags. The secondary vitellophags enter the yolk but Bock was unable to trace their subsequent history. Amnion and serosa arise in the usual way. Cells liberated from the visceral layer of mesoderm wander singly over the yolk surface toward the median ventral line of the germ band to form the anlagen of the mid-gut muscle layers. Later the anlagen of the mid-gut epithelium develop into cellular ribbons one on each side closing over the yolk first dorsally and then ventrally.

COLEOPTERA

Stylops

The stylopids, or twisted-winged insects, are small insects that live parasitically within the bodies of bees, wasps, and some Homoptera. Their presence is indicated by the projecting of the body from between two of the abdominal segments of the host insect. The projecting part of the female is the head end, a flat disk-like plate; that of the male is the rounded and tuberculate head end of its puparium. The male flies for a brief period; the female remains with only its head end projecting from the host, its body still enclosed in the skin of the last larval instar. A free-flying male fertilizes the female in whose abdominal cavity the eggs are liberated. Here the eggs develop into the triungulinids, or first instar larvae, which escape from the body of the female through unpaired median genital apertures on the second to fifth abdominal segments. The apertures open into the space between the venter of the female and the puparium which functions as a brood chamber. The triungulinids

escape through a slit between head and prothorax of the puparium and then crawl over the body of the host wasp or bee. The triungulinid now finds a larva or a nymph of its host species, quickly bores into it, and begins its parasitic life. It undergoes its metamorphosis within the body of its host, there completing the life cycle. The finding of the host larva by the triungulinid is easily understood in case of the social insect hosts, since the original host may carry it to the nest, but in other cases it is possible the triungulinids creep over flowers visited by the host and thus make the transfer.

Immature eggs of *Stylops* are more or less spherical. Later they may be found free in the body cavity of the female instead of in the ovary.

FIG. 217.—*Stylops*. Two-cell stage.

FIG. 218.—*Stylops*. Four-cell stage.

Surrounding the egg is a syncytial membrane which contains a few nuclei, and outside this are a few scattered cells. A chorion is lacking as in viviparous aphids. The eggs are small: those of *Stylops parvula* measure 43 microns in diameter, those of *S. ovina* 56 microns, the average being 50 microns. The sparse yolk is a fatty substance with but little albuminoid matter. The species studied by Noskiewicz and Poluszynski (1927) is not parthenogenetic. Polyspermy is common. In maturation the nucleus migrates to the surface where two polar bodies are formed; then the pronucleus goes back toward the center of the egg to meet the male pronucleus. Schrader (1924) has demonstrated that in *Acroschismus wheeleri*, also, unfertilized eggs do not develop. Immediately after the union of the male and female pronucleus, cleavage begins (Figs. 217–219), giving rise to the two-, four-, and eight-cell stages. Cleavage does not extend to the central yolk. In either the 16- or the 32-cell stage the nucleus of one daughter cell migrates into the central yolk mass. Seven strictly synchronous divisions take place, the nucleus within the yolk also undergoing two divisions, thus forming 120 or 124 blastomeres and a four-nucleate yolk syncytium. Further cell division gives rise to a partial

inner layer which has the effect of crowding the yolk into an eccentric position (Fig. 220). The definitive number of nuclei in the yolk syncytium is four; subsequent division affects the blastomeres only (Figs. 221, 223). At first the cells in the interior are rather loosely arranged (Fig. 221); but as development continues, they become deeper and more or less wedge

FIG. 219.—*Stylops*. Eight-cell stage.

FIG. 220.—*Stylops gwynanae*. 64-cell stage.

shaped. The cells in the interior squeeze in between the peripheral cells (Figs. 222, 223) without multiplying in number, and the yolk is pushed into a peripheral position. The shift in the position of the yolk from the morphological ventral position of the germ band to the dorsal position is

FIG. 221.—*Stylops praecocis*. 128-cell stage.

FIG. 222.—*Stylops praecocis*. Section through yolk (y).

characteristic for the Strepsiptera. An inversion of cell polarity thus occurs. The interior is filled with a granular mass which appears to be a secretion from the peripheral cells. The embryonic rudiment now elongates more or less in one dimension accompanied by a lateral flattening, the cavity becoming reniform (Fig. 224). The layer adjacent to the yolk

becomes the embryonic rudiment; the other layer, the envelope. This peculiar condition, where the yolk, instead of lying inside the vesicle formed by the primary epithelium (blastoderm) comes to lie outside of it, was first described by Brues (1903) for *Xenos peckii*.

FIG. 223.—*Stylops praecocis*. Beginning of germ band (*gb*). (*am*) Amnion. (*y*) Yolk.

FIG. 224.—*Stylops praecocis*. Longitudinal section. (*gb*) Germ band. (*y*) Yolk.

Noskiewicz and Poluszynski homologize the envelope of *Stylops* with the envelope of *Isotoma*, concluding that it represents both amnion and serosa. Since it has the appearance, however, of the amnion alone, for convenience it is here designated as the "amnion." Multiplication of cells in the embryonic rudiment is indicated by the mitotic figures.

FIG. 225.—*Stylops gwynanae*. Longitudinal section. (*am*) Amnion. (*gb*) Germ band. (*y*) Yolk.

FIG. 226.—*Stylops praecocis*. Longitudinal section. (*am*) Amnion. (*antr*) Anterior end. (*par*) Paracyte cell. (*post*) Posterior end. (*y*) Yolk.

If, as some embryologists insist, the yolk cells are to be regarded as the primary entoderm, the sphere of cells first formed should not properly be called a "blastoderm," since some of its cells form the envelope, taking no part in the formation of the embryonic rudiment. For convenience, however, the term "blastoderm" will be used. The digestive epithelial

cells, which arise later from the tip of the stomodaeal invagination and which will surround a portion of the yolk somewhat as in the Odonata, may then be designated as the *secondary* entoderm.

The embryo elongates and at the same time decreases in diameter in the dorsoventral direction (Fig. 225). A lower layer develops diffusely without the formation of a gastrula furrow (Fig. 226); the head (*antr*) and tail end (*post*) are at this time differentiated, the former less thickened than the latter. The amnion-like envelope becomes progressively thinner; the yolk, owing apparently to pressure, becomes longer and thinner. At this stage one observes in the amniotic cavity small structureless masses which stain differently from adjacent cells (Fig. 226, *par*).

FIG. 227.—*Stylops nycthemerae*. (*am*) Amnion. (*antr*) Anterior. (*post*) Posterior end. (*vent*) Venter. (*y*) Yolk.

FIG. 228.—*Stylops*. (*am*) Amnion. (*antr*) Anterior end. (*i. am*) Inner and (*o. am*) outer section of amnion. (*par*) Paracyte. (*post*) Posterior end.

These are interpreted by Noskiewicz and Poluszynski as either symbionts or, more probably, paracytes.

Further proliferation of the cells of the embryo produces an ingrowth of the caudal end whereby apparently a pressure is exerted on the yolk. In Fig. 227 the yolk is shown partly divided, a small one- or two-nucleated portion at the center, a larger portion at the surface (Fig. 227, *y*).

In the development of viviparous or parasitic insects Noskiewicz and Poluszynski (1927) say that if the yolk has preserved its primary entodermal potentiality, it will not degenerate before it has served its function in relation to the development of the mid-gut epithelium, even though it may have been considerably reduced in size. If, however, the potentiality has been lost, one of two things may happen: either it degenerates quickly and completely, or it will be used in the formation of a secondary envelope. For example, in *Stylops* and *Halictoxenus* a small part of the yolk aids in the formation of the mid-gut epithelium; on the other hand, the larger part of the yolk in the former insect degenerates; in the latter it contributes to the formation of the trophamnion-like envelope.

The fragment of yolk that lies in the periphery takes no further part in furnishing nutriment to the embryo; the one- or two- nucleated inner part, however, continues to function. The embryo as it lengthens rolls up (Fig. 228), the amnion stretching, becoming thinner and membranous in appearance, and finally fusing at the point of tangency whereby it is divided into an inner part (*i*) and an outer part (*o*), the latter forming an envelope which soon ruptures and disappears. Within the amniotic cavity an occasional paracyte (*par*) may be seen. Since the embryo in elongating rolls up spirally, a part of the caudal end is hidden by the head

FIG. 229.—*Stylops*. At maximum dorsal curvature. (*gc*) Germ cells. (*i. am*) Inner section of amnion. (*proct*) Proctodaeum. (*stom*) Stomodaeum. (*y*) Yolk.

FIG. 230.—*Stylops*. (*gc*) Germ cells. (*i. am*) Inner section of amnion. (*proct*) Proctodaeum. (*stom*) Stomodaeum. (*th*) Thoracic segments.

lobes. A diagram of a sagittal section at the time of maximum length is shown in Fig. 229.

In this stage (Fig. 229) stomodaeum, proctodaeum, and three head and three thoracic segments are in evidence, as well as the single mass of germ cells (*gc*), the latter therefore late in differentiating. By this time only the inner part of the amnion, which forms the temporary dorsal wall of the embryo, remains; the larger outer part (Fig. 228, *o*) has already ruptured and disintegrated. Division of the amnion into two parts, one forming the temporary dorsal wall of the embryo, and the other an outer envelope, in a somewhat similar fashion has already been described for the lepidopteran *Diacrisia virginica*, where, however, it occurs at a much later period. After the rupture of the outer amnion in *Stylops*, the segmentation of the abdomen and the development of the thoracic appendages take place. The part of the yolk that remained outside the embryo soon disappears.

Counter rotation, or the unrolling of the embryo, takes place rather gradually. The head rapidly enlarges; the head lobes decrease in size; the abdomen becomes shorter and sturdier (Fig. 230); and the dorsal amniotic membrane shortens (*i*). The shortening of the body continues until the embryo is no longer in a spiral but lies with the head in contact

with the tail (Fig. 231). By this time the brain (*br*) and the ventral nerve cord are well differentiated. The shortening of the body with the consequent shrinking and thickening of the dorsal amniotic membrane gives rise to the so called "dorsal organ" which now forms a pear-shaped mass lying in the neck region (Fig. 231, *do*), its anterior end still attenuated. Soon the cells bordering the dorsal organ by proliferation form first the definitive closure of the dorsal wall posteriorly and laterally and finally anteriorly, the dorsal organ becoming smaller and smaller until it finally disappears.

The cells of the proctodaeum at the time the dorsal organ is still present (Fig. 231) are large, with well-marked nuclei, but Noskiewicz and

FIG. 231.—*Stylops gwynanae*. (*br*) Brain. (*do*) Dorsal organ. (*gc*) Germ cells. (*i. am*) Inner section of amnion. (*mes*) Mesoderm. (*neurp*) Neuropile of subesophageal ganglion. (*proct*) Proctodaeum. (*stom*) Stomodaeum. (*y*) Yolk.

Poluszynski observed no proliferation of cells at the extremity that could be interpreted as mid-gut epithelium. As development continues, the proctodaeal cells diminish in size and finally resemble adjacent cells. At the inner end of the stomodaeum at this time proliferating cells are seen (Fig. 231, *stom*) which as time goes on push in under the yolk as well as over it until only a small section just below the dorsal organ remains uncovered. Shortly afterward the wall separating stomodaeum and mid-gut ruptures, thus establishing continuity. No evidence was found by these investigators to warrant the assumption that the mid-gut was formed either from entoderm rudiments located at the tips of the stomodaeal or proctodaeal invaginations or from cells from a middle strand of the inner layer, though the latter possibility was not denied. Be that as it may, the fact remains that the mid-gut epithelium arises from cells

located at the tip of the stomodaeal invagination, however these cells may be interpreted.

In the genus *Xenos*, according to Hoffman (1913), cells from the proctodaeum also contribute to the building up of the mid-gut epithelium.

When the dorsal organ is much reduced and the dorsal wall closes, the caudal end of the body tends first to straighten (Fig. 232) and then to curve ventrad, so that finally the dorsal surface of the body is directed outwardly (Fig. 233). In the stage shown in Fig. 233 the communication between the mid-gut (ventriculus) and the vesicle-like hind-gut is not yet

FIG. 232.—*Stylops*. (br) Brain. (do) Dorsal organ. (drc) Definitive dorsal closure. (gc) Germ cells. (mge) Mid-gut epithelium. (nc) Nerve cord. (neurp) Neuropile. (proct) Proctodaeum. (stom) Stomodaeum. (y) Yolk.

FIG. 233.—*Stylops*. (br) Brain. (gc) Germ cells. (mge) Mid-gut epithelium. (neurp) Neuropile. (p) Thoracic legs (dotted). (proct) Proctodaeum. (stom) Stomodaeum. (y) Yolk.

established. It is probable that the intestine remains imperforate. The development of the mesoderm, which is but feebly represented in *Stylops*, was not studied by Noskiewicz and Poluszynski (1927).

THE ALFALFA SNOUT BEETLE (*Brachyrhinus ligustici*)

The alfalfa snout beetle (*Brachyrhinus ligustici*) is an introduced species which probably came about forty years ago from central Europe where it is widely distributed. The adult is wingless, which probably accounts for the fact that it has spread so slowly. However, it multiplies in very large numbers in small, restricted areas and does serious damage to alfalfa. It develops parthenogenetically, males not having been found in the United States.

The egg is in most cases oval in shape but sometimes almost spherical, averaging 0.85 mm. in length. When laid, it is creamy white and is covered with a sticky substance to which the soil particles adhere. After the first day the color changes first to a dull yellow and gradually to a light

brown. The yolk consists of globules of varying size which are surrounded by cytoplasm which, however, is not arranged as a reticulum at this time. The periplasm (Figs. 234, 235) surrounding the yolk in some cases seems to consist of two layers: an outer one which stains more lightly than the inner layer. At the posterior pole of the egg an irregular

FIG. 234.—*Brachyrhinus*. Section through oösome. (*pr*) Periplasm.

mass, sometimes saucer shaped, can be seen lying partly in the periplasm and partly in the yolk. This is the oösome, or germinal cytoplasm. The vitelline membrane is difficult to make out, and the chorion is so thin and elastic that it can easily be removed after being pricked with a needle.

The location of the pronucleus at the time of oviposition has not been determined with any degree of certainty. In several eggs prior to the

FIG. 235.—*Brachyrhinus*. Section through oösome. (*pr*) Periplasm.

formation of the polar bodies it has been observed near one end of the egg (Fig. 236); in others, during meiosis in the periphery about halfway between the ends of the egg.

A marked thickening occurs in the peripheral cytoplasm surrounding the pronucleus in which the polar body is given off, after which the nucleus

immediately migrates back into the yolk of the egg without giving off a second polar body. Immediately after the polar body has separated from

FIG. 236.—*Brachyrhinus*. Nucleus (nu) and polar body (pb) 15 minutes after egg laying.

the pronucleus, the chromosomes appear distinct enough to indicate that there is no reduction in number. In several cases about 25 chromosomes

in both the nucleus and the polar body have been counted. Later counts made in cleavage nuclei migrating into the periphery during blastoderm formation confirm this number as being equal to the somatic number of chromosomes, indicating that parthenogenesis in this beetle is the diploid type.

About the time the nucleus is again near the center of the egg, the polar body divides, and one of the resultant nuclei is pushed out under the vitelline membrane and entirely cut off from the cytoplasm (Fig. 237). In the meantime the first cleavage division has taken place, and the daughter nuclei are migrating toward the periphery.

FIG. 237.—*Brachyrhinus*. Polar body.

Between the ninth and the twelfth hours there are 16 to 32 in the yolk. At 18 hours the daughter nuclei have increased in number and have reached

a point about two-thirds the distance toward the periphery. At the thirtieth hour they appear in the periphery but quite widely separated from one another. Each division during this migration has been synchronous, but very few spindles appear, most of the nuclei being in the prophase or in the resting stage.

During cleavage, the remaining polar body grows very large, several times the size of the cleavage nuclei. In all cases a nuclear wall to which the chromatin material tends to adhere can readily be seen. After the very earliest stages of polar-body formation the chromosomes lose their

FIG. 238.—*Brachyphimus*. Disintegrating polar body (pb). (cc) Cleavage cell.

characteristic form and appear simply as a large mass of irregular threads, much more in quantity than in the nucleus. In some cases the polar body has been observed to divide, but no spindles are formed, a large portion of the polar body splitting off and a mass of chromatin material passing from one part to the other. The polar body sometimes remains as a large vacuolated cell in which the chromatin material gradually disintegrates and disappears. This process extends over a considerable period. The polar body is still discernible in the yolk at 30 hours when the cleavage nuclei have already reached the periphery (Fig. 238). At the 32-hour stage, when there are many more cleavage nuclei in the periphery but before any cell walls have formed around them, a large mass of cytoplasm

still exists in the yolk, but by this time the chromatin material has disintegrated almost entirely (Fig. 239). The cleavage nuclei in the area nearest this last remnant of the polar body are not so numerous as in other regions of the periphery, and no cell walls have begun to form, although they are well along in development on the opposite side of the egg. This would indicate that as long as the polar body lasts, its presence prevents the cleavage nuclei from entering the periphery.

The oösome is an irregular mass of granular material located at the posterior pole of the egg. When

FIG. 239.—*Brachyrrhinus*. Longitudinal section of blastoderm (bld). (gc) Germ cells. (pb) Polar body.

stained with either iron haematoxylin or Delafield's haematoxylin it appears much darker than the rest of the cytoplasm of the egg. It may form a saucer-shaped disk lying between the yolk and the cytoplasm (Fig. 234) or a smaller but very thick mass extending for some distance into the yolk (Fig. 235). In either case it is not homogeneous but contains large globules or irregular bodies of material which stain much lighter and appear to be identical in composition with the peripheral cytoplasm. Yolk globules also are scattered through the germinal cytoplasm but not to the same extent as the lighter staining material.

As they approach the posterior pole, some of the cleavage nuclei come into contact with the germinal cytoplasm (oösome) which breaks up and gathers around them in large masses. They move on to the periphery but do not leave the walls of the forming blastoderm (Fig. 239). They are the germ cells, and their development from this point is entirely distinct from the other cleavage nuclei. The blastoderm cells, as they increase in number and acquire walls first on the outside, then on their lateral faces, become columnar in form except where they are interrupted by the germ cells and where they are retarded by the disintegrating polar body. Before the inner walls of the blastoderm have formed, the germ cells move inward to form a syncytium between the yolk and the blastoderm cells (Fig. 239). When the cleavage nuclei move out from the center of the egg, several of their number are left behind to become yolk cells. Others, as they reach the germinal cytoplasm, seem to gather up

some of the material there but, instead of continuing with the germ cells, wander back into the yolk where they become scattered. In several eggs a mass of dark-staining granular material in the anterior pole of the egg is evident. It is not so extensive as the oösome, but it may be that yolk cells move inward from the anterior pole carrying this material with them. Lassmann (1935) working with the sheep tick has observed that the yolk cells stream inward from both the anterior pole and the posterior pole near the region of the germ cells. A similar situation may exist in this species, although the evidence is not conclusive. After the blastoderm is complete, many cells may be seen migrating back from the periphery as if they were simply crowded out. These correspond to the paracytes of other workers, but there is no evidence to indicate that they disintegrate in the yolk (Fig. 240).

When the inner walls of the blastoderm are complete, the blastoderm consists of a thick layer of closely packed columnar cells. The outer ends of these cells, between the nuclei and the periphery, are dense; the inner ends are uniformly vacuolated. The primary dorsal organ appears at this time as a mass of cells that invaginate into the yolk along one side of the blastoderm leaving a groove on the outside surface (Fig. 241). The

FIG. 240.—*Brachyrhinus*. Longitudinal section of forming blastoderm. (cc) Cleavage cell.

FIG. 241.—*Brachyrhinus*. Cross section of primary dorsal organ (do).

groove is very short, but the cellular invagination extends in a longitudinal direction for about one-tenth the length of the egg. The ridge of cells is capped by a dark-staining granular mass of cytoplasm. As in

Donacia (Hirschler, 1909) and *Euryope* (Paterson, 1932), the primary dorsal organ lasts but a short time. It appears when the blastoderm is complete at the thirtieth hour but disappears before the ventral plate has become enclosed by the amniotic folds.

The thickening of the posteroventral blastoderm to form the germ band occurs about the thirty-fifth hour. The amniotic folds develop from the edges of the germ band and eventually fuse along the middle line to enclose the germ band with two envelopes, the amnion on the ventral

FIG. 242.—*Brachyrhinus*. Longitudinal section. (am) Amnion. (ect) Ectoderm. (il) Inner layer. (ser) Serosa. (sub. ser) Subserosa.

side, and the serosa enclosing the contents of the egg. The germ band now invaginates into the yolk, moving inward from the posterior pole tail first until only the head lobes remain at the surface (Fig. 242).

The embryo now begins to lengthen and at the same time to withdraw from the yolk. It withdraws in a lateral direction so that if the egg is viewed from one side, the embryo appears somewhat S shaped with the tail still immersed in the yolk. When the withdrawal process is complete, the tail lies diagonally over the side of the yolk while the head and the fore part of the embryo still lie in a vertical plane at the posterior pole of

the egg. As the tail grows toward the anterior pole, it has a tendency to return to the middorsal line. In the meantime the head has grown along the ventral side of the egg until when the embryo reaches its greatest length, the head and tail are close together at the anterior pole (Fig. 252).

While the embryo increases in length, the amnion grows laterally between the yolk and the serosa until the folds from the caudal half of the embryo meet and fuse with those from the anterior half, enclosing the embryo everywhere within two membranes. The last point of fusion is near the tail where the inner portion of the amnion joining the head and tail remains connected with the outer amniotic envelope by a thin strand

FIG. 243.—*Brachyrrhinus*. Third-day embryo. Head and first two thoracic segments.

FIG. 244.—*Brachyrrhinus*. Third-day embryo. Second and third thoracic segments and abdomen.

of amniotic tissue. The amnion and serosa remain intact until the larva cuts through them in the process of hatching.

After blastokinesis, when the tail has reached the surface and the embryo has straightened out, segmentation begins, becoming evident when the embryo reaches its greatest length. Figures 243 and 244 represent an embryo three days old showing the gastrular groove complete from the stomodaeum to the proctodaeum with segmental grooves plainly showing for slightly more than half the length of the germ band. The gnathal appendages, as yet consisting of simple lobes only, are present, as is also a single pair on the first thoracic segment. Antennae are also visible, but there is no differentiation between antennae, mouth parts, or the single pair of thoracic lobes. The labrum appears as a simple flap above the mouth opening. Paterson reports that two lobes appear

in the head that later fuse to form the labrum, but these lobes are not present in *Brachyrhinus*. As segmentation progresses toward the posterior end, the appendages of the head and thorax become more pronounced, and the embryo begins to reduce its length (Fig. 245). This occurs on the fourth day.

FIG. 245.—*Brachyrhinus*. Fourth-day embryo.

The gastrular furrow which is completed on the third day marks externally the invaginating ridge of cells that will become the inner layer (Fig. 246). The inner layer becomes arranged in transverse segmented masses when segmentation occurs; and when the neural groove appears, these masses are further divided along the center line. It is probable that at this time cells that will become blood cells are liberated along the middle strand. The inner layer soon separates, irregularly at first, into

two layers, and on the fourth day at the lateral extremities of each

FIG. 246.—*Brachyrhinus*. Cross section through abdomen. Lower-layer formation. (am) Amnion. (ect) Ectoderm. (gastr. fr) Gastrular furrow. (il) Inner layer. (ser) Serosa. (sub. ser) Subserosa.

segmental mass of the inner layer the coelomic sacs appear (Fig. 247,

coel). At this time the neural groove is deep, and ectodermal cells on each side differentiate to form the neuroblasts. The tracheal system has also started, developing tracheal invaginations (*tr*) occurring in eight segments of the abdomen. Later on, two pairs of tracheal openings will

FIG. 247.—*Brachyrhinus*. Cross section through the thorax of 90-hour embryo. (*coel*) Coelomic cavity. (*neurg*) Neural groove. (*tr*) Tracheal invagination.

be evident in the thorax. These appear clearly on the eighth day (Fig. 248).

Between the fourth and the eighth days, the embryo grows laterally around the yolk and becomes shorter until the caudal end lies at the posterior pole of the egg. At first the gnathal and thoracic appendages as well as the antennae are elongate and slender (Fig. 245). Soon they

FIG. 248.—*Brachyrhinus*. Eight-day embryo.

FIG. 249.—*Brachyrhinus*. Ten-day embryo.

become reduced to mere lobes, and processes identical with them appear on abdominal segments one to eight (Fig. 248) on the eighth day. Two days later the abdominal lobes disappear (Fig. 249). By the eighth day the gnathal segments have moved cephalad and have begun their fusion with the head lobes. At this time the intersegmental sutures have

disappeared. By the tenth day they have fused with the head lobes to form the definitive head, their appendages now being grouped around the mouth (Fig. 249).

FIG. 250.—*Brachyrhinus*. Ten-day embryo. Dorsal aspect showing dorsal closure.

During the time that the appendages have been developing, the neuroblasts through continued divisions produce the neural cells that will form the ventral nerve cord (Fig. 247). Ganglia appear in each segment, and the neuropile is apparent by the sixth day (Fig. 251). The coelomic sacs disappear at this time, the mesoderm now consisting of the somatic layer next to the body wall and the splanchnic layer lying immediately under the developing mid-gut ribbons (Fig. 251, *mge*). As the nerve cord develops, the ectodermal wall beneath it becomes very thin so that from the ventral side the ganglia and the two longitudinal connectives of the nerve cord can be plainly seen through the integument (Fig. 249).

On the eighth day the body wall of the embryo together with the mid-gut ribbons has grown around the yolk until about three-quarters of the yolk is covered. Two days later the two edges of the advancing body wall have met in the anterior and posterior ends leaving only a small area of the yolk still exposed (Fig. 250).

FIG. 251.—*Brachyrhinus*. Cross section of abdomen of six-day embryo. (*ect*) Ectoderm. (*mge*) Mid-gut epithelial ribbon. (*nc*) Nerve cord. (*neurp*) Neuropile. (*splm*) Splanchnic mesoderm.

A few hours later this, too, is covered. The embryo remains in the egg after the dorsal wall is complete for several days before hatching occurs.

The stomodaeum is formed at the time of segmentation and appears as a shallow pit on the third day when the embryo reaches its greatest

FIG. 252.—*Brachyrrhinus*. Sagittal section of three-day embryo. (*am*) Amnion. (*ect*) Ectoderm. (*il*) Inner layer. (*stom*) Stomodaeum. (*yc*) Yolk cell.

FIG. 253.—*Brachyrrhinus*. Sagittal section of six-day embryo. (*myct*) Mycetom. (*stom*) Stomodaeum.

FIG. 254.—*Brachyrhinus*. Section of stomodaeum (*stom*). (*myct*) Mycetocytes.

FIG. 255.—*Brachyrhinus*. Sagittal section of advanced stage. (*am*) Amnion. (*myct*) Mycetocytes. (*nc*) Nerve cord. (*ser*) Serosa. (*stom*) Stomodaeum. (*sub.ser*) Subserosa. The open space between embryo and subserosa is unnatural. It is caused by shrinkage.

length (Fig. 252). As the embryo shortens, the pit deepens, and a mass of cytoplasm appearing in the yolk gathers on its tip (Fig. 253). This is the first appearance of the developing mycetom. Soon nuclei appear to migrate into this mass to make up the mycetocytes. As the end of the stomodaeum grows thin, the mycetocytes gather in a mass, forming a cap over the tip of the stomodaeum (Fig. 254). This mass of cells soon moves from the end of the stomodaeum to form a ring around the stomodaeum close to the mid-gut walls. Before the embryo hatches, this ring

FIG. 256.—*Brachyrhinus*. Cross section of abdomen of eight-day embryo. (*cbl*) Cardioblasts. (*ect*) Ectoderm. (*g*) Gonad. (*mge*) Mid-gut epithelium. (*nc*) Nerve cord. (*somm*) Somatic mesoderm. (*splm*) Splanchnic mesoderm.

breaks up into separate masses of cells which migrate through the walls of the mid-gut and come to lie outside the mid-gut in close proximity to the walls of the stomodaeum. This cell mass, which is described more fully in Chap. XI, carries symbiotic organisms.

The yolk, at first a homogeneous mass containing a great many nuclei and structureless masses of cytoplasm, after blastokinesis becomes divided into compartments by a reticulum. This reticulum seems to form a provisional mid-gut wall which separates the yolk from the epineural sinus on the ventral side. On the dorsal side the provisional mid-gut wall is formed by a part of the amnion (Fig. 255). After the mid-gut ribbons have begun their development, they form along the surface of the membrane enclosing the yolk (Fig. 251).

The mid-gut ribbons apparently develop from the ends of the stomodaeum and proctodaeum. They extend beneath the yolk and grow posteriorly and anteriorly until they meet and fuse. As they lengthen they also widen out, eventually closing in under the yolk to form a trough. On the sixth day they are already well developed but have not met along

FIG. 257.—*Brachyrhinus*. Sagittal section of ten-day embryo. (br) Brain. (h) Heart. (mge) Mid-gut epithelium. (nc) Nerve cord. (proct) Proctodaeum. (stom) Stomodaeum. (x) Loop of mid-gut.

the mid-ventral longitudinal line (Fig. 251). Two days later the trough of the mid-gut is completed ventrally, and the embryo has grown more than halfway around the yolk toward the dorsal side (Fig. 256).

The dorsal wall of the mid-gut and the dorsal wall of the ectoderm are completed at the same time. For several days the mid-gut walls apparently continue to grow, for in an embryo shortly before hatching there appears a fold on the ventral side of the mid-gut that extends deeply into the yolk (Fig. 257).

On the tenth day the heart is completed on the dorsal side, extending anteriorly where it bends ventrad to end beneath the brain (Fig. 257). The cells of the mycetom at this time appear in a ring around the stomodaeal valve but are still in the mid-gut.

The subserosa begins its development early. It appears as a secretion of the serosa cells at the time the tail of the embryo is deeply imbedded in the yolk (Figs. 242, 258). After blastokinesis, as the embryo attains its greatest length, the amnion grows over the interval between the head and the tail in two loops. These meet and fuse so that the embryo everywhere is enclosed in a double-walled sac consisting of the serosa

FIG. 258.—*Brachyrhinus*. Section of serosa (*ser*) at an early stage. (*sub. ser*) Subserosa.

outside and the amnion inside, with the subserosa lying between (Fig. 255). The subserosa becomes hard and leathery and serves as a protective cover for the embryo. After the dorsal wall is completed, the embryo remains enclosed in the subserosa for several days before emerging. When hatching occurs, the leathery cover is split open, and the larva emerges. Thus it is apparent that both the amnion and the serosa together with the subserosa are preserved to the end of the embryonic period.

References

- NEUROPTERA: *Chrysopa* sp.; Bruce (1887), Packard (1871a), Tichomirowa (1890a). *C. ocellata*; Packard (1872), Smith (1922). *C. perla*; Tichomirowa (1892). *Mantispa pagana*; Brauer (1855). *Osmylus chrysops*; David (1936), Hagen (1852). *Sialis lutaria*; DuBois (1936, 1938), Strindberg (1915).
- STREPSIPTERA: *Acroschismus wheeleri*; Hughes-Schrader (1924). *Halictoxenus* sp.; Noskiewicz and Poluszynski (1927). *Stylops parvula*; Noskiewicz and Poluszynski (1927, 1935). *Xenos nigrescens*, *pallidus*, *peckii*; Brues (1903). *X. bohlsi*; Hoffmann (1914).
- COLEOPTERA: Mansour (1927, 1934b), Scheinert (1933), Stuhlmann (1886). *Acilus* sp.; Patten (1887, 1888). *Adimonia tenaceti*; Henking (1890b, 1891b, 1892). *Adoxus vitis*; Joubert (1882). *Agelastica alni*; Fulinski (1911), Henking (1890–1892), Lécaillon (1897), Petrunkevitch (1898), Smreczynski (1938). *Anomala aenea*; Rittershaus (1925). *Attelabus rhois*; Packard (1872). *Baris maculipennis*; Mansour (1930). *Brachyrhinus ligustici*; Butt (1936). *Bromius vitis*; Joubert (1882). *Bruchus quadrimaculatus*; Brauer (1925), Brauer and Taylor (1934, 1936). *Calandra callosa*;

Wray (1937). *C. granaria*; Inkmann (1933), Tichomiroff (1890a, 1892, 1900). *C. oryzae*; Mansour (1927, 1930), Pierantoni (1927), Tarsia (1933), Tiegs and Murray (1938). *Calligrapha bigsbyana*, *lunata*, *multipunctata*; Hegner (1908–1911). *Carabus cancellatus*; Kirschner (1927). *Chrysomela festuosa*, *hyperici*; Strindberg (1913b, 1917a). *C. marginalis*, *marginata*; Friederichs (1906). *C. menthastri*; Lécaillon (1897). *C. varians*; Reithfeldt (1925). *Cicindela hybrida*; Hirschler (1932). *Clytra laeviuscula*; Lécaillon (1897, 1898). *Coccinella septempunctata*; Strindberg (1917a). *Colymbetes fuscus*; Will (1884). *Corynodes pusis*; Paterson (1936). *Crioceris asparagi*; Hirschler (1932). *Curculionids*; Mansour (1927). *Dermestes lardarius*; Canzanelli (1936). *Donacia* sp.; Henking (1890–1892), Köl liker (1843), Melnikow (1869). *D. crassipes*; Brandt (1878), Friederichs (1906), Hirschler (1907a, 1908, 1909b). *D. serica*; Henking (1890–1892). *Doryphora*, see *Leptinotarsa*. *Dytiscus* sp.; Leydig (1889). *D. marginalis*; Blunck (1914), Korschelt (1912), Saint Hilaire (1895). *Elatér pectinicornis*; Meissner (1855). *Epilachna chripomelina*, *E. capensis*; Strassburger (1936). *Euryope terminalis*; Paterson (1931, 1932). *Galerucella luteola*; Provasoli (1932). *Gastroides polygoni*; Henking (1890–1892). *G. viridula*; Hirschler (1909). *Gastrophysa polygoni*; Packard (1872). *G. raphani*; Lécaillon (1897–1898). *Hydrophilus* sp.; Deegener (1900), Graber (1888b, 1890, 1891), Heymons (1895b). *H. piceus*; Hallez (1886), Heider (1885, 1889, 1890), Korschelt (1885, 1886), Kowalewsky (1871). *H. aterrimus*; Megušar (1906). *Hylobius* sp.; Mansour (1930). *H. abietis*; Scheinert (1933). *Hylurgops pinifex*; Packard (1883). *Lampyrus* sp.; Henking (1888a). *L. bellieri*; Bugnion (1922). *L. splendida*; Henking (1890, 1891b, 1892). Meissner (1855). *Lasioderma serricorne*; Canzanelli (1924). *Leptinotarsa decemlineata*; Hegner (1908–1911, 1915), Wheeler (1889b, 1891a), Wieman (1910). *Lina aenea*; Henking (1890–1892). *L. populi*; Lécaillon (1897, 1898). *Lina tremula*; Graber (1889b). *Liparus germanus*; Scheinert (1933). *Luciola cruciata*; Okada (1935). *Meloe* sp.; Bruce (1887), Graber (1891), Leydig (1889). *M. cicatricosus*; Newport (1851). *M. proscarabaeus*; Nusbaum (1889–1890). *M. scabriusculus*; Friederichs (1906). *Melolontha vulgaris*; Graber (1888, 1889b, 1890b, 1891a), Herold (1839), Tur (1920), Voeltzkow (1889b). *Micromalthus debilis*; Barber (1913), Scott (1938). *Mysis 13-punctata*; Packard (1872). *Oryzaephilus surinamensis*; Koch (1931). *Passalus cornutus*; Cody and Gray (1938). *Photinus consanguineus*; Williams (1916). *Photuris pennsylvanica*; Hess (1922), Williams (1916). *Phyllobius glaucus*; Smreczynski (1934). *Phylloperla horticola*; Rittershaus (1925). *Rhagonycha fulva*; Friederichs (1906). *Rhizotrogus solstitialis*; Korschelt (1885). *Silpha obscura*; Smreczynski (1931, 1932). *Sitona lineata*; Rieth (1935). *Telephorus* sp.; Graber (1890b). *T. fraxinus*; Packard (1872). *Tenebrio molitor*; Ewest (1937), Henking (1888a, 1890b, 1891b, 1892), Jackson (1939), Saling (1907), Selys-Longchamps (1904). *Tribolium confusum*; Hodson (1934). *Xyleborus coelatus*; Packard (1883).

CHAPTER XVIII

HYMENOPTERA

THE BARBERRY SAWFLY (*Hylotoma berberidis*)

The brief account of this sawfly given by Graber (1890) indicates that it differs in several particulars from the aculeate Hymenoptera as described by various authors. The eggs, which are laid in small clumps on the leaves of the barberry, are much elongated and distinctly convex on the ventral side. The germ band is elongated, occupying nearly the full length of the egg after two days' incubation. It lies on the ventral side of the egg, its caudal end slightly curved into the yolk. At this time the amnion and serosa are fully formed; the head lobes are conspicuous and distinctly wider than the body, which as yet shows no segmentation. A little later the caudal end of the germ band grows around the posterior end of the egg for a short distance. In the three-day-old embryo, rudiments of head and thoracic appendages appear, the stomodaeum is evident, and the antennae arise postorally in position. About a half day later the antennae migrate forward, the body segmentation becomes distinct, and the nerve cord is formed.

At this time also the stomodaeum and proctodaeum are well developed, each with mid-gut epithelial rudiments at the blind end, these rudiments each developing into two parallel ribbons. Meanwhile, the embryo has shortened so that the anal opening is at the posterior pole of the egg. Four days after egg deposition the two thoracic and the eight abdominal spiracles are clearly in evidence as well as the abdominal appendages, the homologues of the thoracic legs. Soon after this the abdomen again begins to lengthen, this time curving ventrad, so that shortly before hatching the posterior end of the abdomen reaches the thorax. After four days the dorsal wall closes, without the rupture of either amnion or serosa and with only a portion of the amnion taking part in a provisional dorsal closure as in *Diacrisia* and some Coleoptera. Both embryonic membranes persist until the time of hatching.

A HESSIAN-FLY PARASITE (*Platygaster hiemalis*)

This proctotrupoid parasite of the Hessian fly deposits its eggs in the eggs of the host. The early development of the parasite takes place in the host egg and in the young host larva during the fall, the parasite passing the winter within a well-developed host larva, which remains on the wheat plant.

Leiby and Hill (1923) state that this species develops both monembryonically and polyembryonically. Both fertilized and unfertilized eggs

FIG. 259.—*Platygaster*. Egg of parasite (e) under the blastoderm (bld) of the host egg.

will develop, the fertilized eggs presumably giving rise to females. The egg is somewhat larger than a single blastoderm cell of the host egg (Fig. 259). If the egg is inseminated, the sperm can be seen in a curved or arched position (Fig. 260A). Never more than one sperm is found in one egg. The so-called "germ-cell determinant" (oösome) is apparently lacking. The nucleus is regularly found near the center of the newly deposited egg. Later it increases in size and gives off two polar bodies. After the second division the second polar body is seen at the anterior end, near the first polar body. The

oöcyte nucleus (later the female pronucleus) after the ninth hour may be found in the posterior half of the egg, increasing in size. After the second maturation the male pronucleus becomes spherical and about the six-

FIG. 260.—*Platygaster*. A, egg one hour after deposition. B, male and female pronuclei about to fuse. C, egg one to two days old. (nu) Nucleus. (nu. f) Fusion nucleus. (nu. p) Paranuclear mass. (nu. pr) Pronuclei. (sp) Sperm.

teenth hour fuses with the female pronucleus (Fig. 260B). The fusion nucleus is now in the posterior region of the egg, whereas the polar nucleus (nu.p) made by the fusion of the two polar bodies lies in the anterior

region. Unlike that of *P. dryomyiae* as described by Silvestri (1916), the first polar body does not divide during the second maturation. Between the tenth and twelfth hours the polar nucleus (the fused polar bodies) increases in size to become the "paranuclear mass" (Fig. 260C). Just before cleavage of the fusion nucleus the paranuclear mass divides amitotically to form two subequal masses (Fig. 261A).

About the twenty-fourth hour two regions are recognized when the central part of its posterior half becomes distinctly differentiated from the remainder of the egg (Fig. 260C). This differentiated region contains the fusion nucleus (cleavage nucleus) and is called the "embryonic

FIG. 261.—*Platygaster*. Parasitic body. A, about two days old. B, three days old. (emb) Embryonic region. (nu. p) Paranuclear masses.

region," later giving rise to the embryos. The remainder of the egg containing the polar nucleus constitutes the polar region. Between the first and second days the eggs, five to eight in number, deposited by the parasite in the host become somewhat dispersed throughout the developing host if they were deposited in the host egg. If the eggs were deposited in a well-developed embryo of the host or in a recently hatched host larva, they become scattered in the body cavity of the host at an earlier hour. The eggs begin to increase in size soon after the first day, and therefore the egg stage may be regarded as past; henceforth the developing structures may be regarded as parasite bodies. These are lodged in the salivary glands, fat, or other host tissue, portions of which soon encompass the parasite bodies. After being more or less surrounded by host tissue, an elaboration of the paranuclear masses in the polar region takes place by the absorption of substances from the host. The polar region, including

that part surrounding the embryonic region, may now be designated as the "trophamnion."

The first cleavage of the embryonic nucleus is completed at about the third day (Fig. 261*B*), two embryonic nuclei being then visible in the embryonic region. By the fifth day a second cleavage has taken place, producing four nuclei, the parasite having meanwhile considerably increased in size and usually become wholly surrounded by host tissue.

About the sixth day after oviposition the parasite body becomes more elongate, and each of the two paranuclear masses (*nu. p*) as well as the two

FIG. 262.—*Platygaster*. Section through twinning stage of the parasite body. About six days old. (*am. t*) Trophamnion. (*emb*) Parasitic body. (*host*) Host tissue. (*nu. p*) Paranuclear mass.

parasite bodies (*emb*) divides, thus forming four of each (Fig. 262). Each half of the embryonic region is now a true germ and is structurally the same as a three-day-old parasite body after the first cleavage. No further major division of the embryonic region or later developing blastula stages takes place, but each germ develops directly into the blastula and later embryo stages and finally into a larva. The original egg (or parasite body) therefore develops into *twin* parasites, structurally independent of each other, held together solely by the host tissue (*host*) that surrounds them. The nuclei of each germ undergo repeated divisions until a blastula (*emb*) is formed which at first is spherical (Fig. 263*A*), the paranuclear masses (*nu. p*) of the trophamnion (*am. t*) having become

distinctly crescentic in shape (Fig. 263A). Owing probably to an unfavorable location within the host, some parasite eggs fail to develop.

Parasites continue their development from the blastula stage during the fall months (Fig. 263B), until in early winter they are in an advanced

FIG. 263.—*Platygaster*. A, early blastula stage. B, later blastula stage. (am. t) Trophamnion. (emb) Blastula stage of developing embryo. (host) Host tissue. (nu. p) Paranuclear masses.

embryo stage in which they exhibit larval characteristics (Fig. 264). During this interval all the embryos that have arisen by the twinning process become separated structurally from each other, although a twin pair may still be located side by side. Each embryo is found in an embryonic cavity, the outer wall of which is the trophamnion. During the development of the embryo the trophamnion is relatively thick and contains many small or two large, conspicuous paranuclear masses. The parasites pass the winter as well-formed embryos distributed between the fat bodies of the host. Meanwhile the host becomes fully grown and encased in a puparium on the wheat plant.

FIG. 264.—*Platygaster hiemalis*. Embryo (emb) within the trophamnion (am. t). (nu. p) Paranuclear mass.

In the spring the parasites continue their development. The embryos straighten out from their previous U-shaped form and are now recognizable as young larvae. While this development is taking place, the

trophamnion becomes relatively thinner, and its paranuclear masses are absorbed until the former is represented merely by a very thin membrane surrounding the young larva. In late spring the young larvae rupture the trophamnionic membrane and begin to feed on the body content of the host. By the time the content of the host is devoured, the larval parasites are full grown. The parasites remain as pupae or adults in the carcass of the host, emerging as adults in early fall.

Some eggs develop monembryonically. In this case the embryonic region does not divide into two parts, the germ forming a single blastula, as in some other platygasterids. Egg structure, maturation, and fecundation of *Platygaster hiemalis* are similar to that of *P. dryomyiae* as described by Silvestri, though Silvestri (1937) considers twinning in the former as questionable.

Platygaster vernalis (*P. zosine* Walker), another parasite studied by Leiby and Hill (1924), differs from *P. hiemalis* in that it develops only by the polyembryonic process, one egg giving rise to approximately eight individuals. There is but one generation annually. The adult parasites emerge from their pupal chambers within the host carcass in the spring and oviposit in the eggs of the spring brood of Hessian flies. The larval and pupal stages are completed by late August.

A single egg is deposited in the egg of the host in such a way that it always becomes lodged in the mid-gut of the embryo host where development to the primary larval stage of the parasite is completed. Maturation is similar to that of *P. hiemalis*, the two paranuclear masses being the product of the polar bodies. The embryonic nucleus divides, each daughter nucleus becoming differentiated into a germ. Growth of the trophamnion permits each one-celled germ to divide until each reaches the blastula stage. Organogeny of the parasite then follows, whereupon the trophamnion becomes vacuolated, thinned, and finally breaks down to release the parasites in their primary larval stage. The liberated primary larvae within the stomach of the full-grown larval host now feed directly on the host's tissues. When the parasite larva is mature, it pupates inside the host puparium to emerge the following spring.

THE CABBAGE-LOOPER PARASITE (*Litomastix floridana*)

Litomastix floridana (*Paracopidosomopsis floridanus*), a chalcid parasite of the common cabbage looper (*Autographa brassicae*) studied by Patterson (1921), deposits its egg in the host egg at any time but does not parasitize the young caterpillar after hatching. It lays one or two eggs at each oviposition in any part of the host egg. Unless the egg is included in the tissues of the embryo host, it will not complete its development. Eggs develop whether fertilized or not, those laid by virgin females always

producing male broods. The history of cleavage as well as of the embryonic cells is the same in fertilized and unfertilized eggs.

The freshly deposited egg is a pear-shaped cell, surrounded by a thin but tough membrane (Fig. 265) and averaging 0.155 mm. in length. The nucleus (*nu*) is near its anterior end. In fertilization the sperm enters the

FIG. 265.

FIG. 266.

FIG. 267.

FIG. 268.

FIG. 269.

FIG. 265.—*Litomastix*. Fertilized egg. (*os*) Oosome. (*nu*) Nucleus. (*sp*) Sperm.

FIG. 266.—*Litomastix*. Fertilized egg after second maturation division. (*A1*) Outer nucleus of first polar body. (*A2*) Inner nucleus of first polar body. (*B1*) Second polar body nucleus. (*B2*) Female pronucleus. (*os*) Oosome. (*sp*) Sperm.

FIG. 267.—*Litomastix*. (*A1*) Outer nucleus of first polar body. (*B2*) Female pronucleus. (*nu. p*) Polar nucleus (= *A2* + *B1*). (*os*) Oosome. (*sp*) Sperm.

FIG. 268.—*Litomastix*. With two cleavage nuclei. (*A1*) and (*A2*) First polar bodies. (*B1*) Second polar body. (*nu*) Cleavage nuclei. (*os*) Oosome.

FIG. 269.—*Litomastix*. Two-cell stage. (*A1*) First polar body nucleus. (*nu. p*) Polar nucleus. (*nu*) Cleavage nucleus. (*os*) Oosome.

egg at any point on the surface of the posterior region. Polyspermy never occurs. Within the egg is the oosome ("germ-line determinant"), a nucleolus-like body (*os*). Maturation is identical in fertilized and unfertilized eggs. The first maturation division results in reducing the number of chromosomes from sixteen to eight. The second division, but without reduction, follows immediately upon the first or may even precede it (Fig. 266*A1,A2,B1*). The result of these two divisions is the formation of three polar bodies (*A1,A2,B1*) and the oötid (*B2*), the latter forming the female pronucleus.

The second polar body (*B1*) and the inner nucleus (*A2*) of the first polar body now fuse to form the polar nucleus, or the so-called "paranucleus" (Fig. 267, *nu. p*), the outer nucleus (*A1*) of the first polar body later undergoing dissolution. That only two and not all three polar bodies enter into the formation of the polar nucleus (paranucleus) is proved by the fact

FIG. 270.

FIG. 271.

FIG. 272.

FIG. 273.

FIG. 270.—*Litomastix*. Eight-cell stage. (*amt*) Trophamnion. (*bls*) Embryonic blastomere. (*bls.os*) Blastomere with oosome. (*nu. p*) Polar nuclei.

FIG. 271.—*Litomastix*. 14-cell stage. (*amt*) Trophamnion. (*bls*) Blastomere. (*bls.os*) Blastomere with oosome. (*nup*) Polar nuclei.

FIG. 272.—*Litomastix*. 60-cell stage. (*amt*) Trophamnion, or polar membrane. (*nup*) Polar nuclei.

FIG. 273.—*Litomastix*. 221-cell morula. (*amt*) Trophamnion. (*c*) Embryonic cells. (*csp*) Spindle cells. (*myc*) Mesenchyme cells of host.

that the diploid number of 16 chromosomes and not the triploid number is present.

The egg is inseminated by a single sperm, which after having entered the egg loses its tail, only the head being transformed into the male pronucleus (Fig. 267, *sp*). During the fusion of the male and female pronuclei the oosome moves from its original more or less central position

to the side of the fusion nucleus. The fusion nucleus now undergoes mitotic division (Fig. 268) which is soon followed by a division of the adjacent cytoplasm to form two blastomeres (Fig. 269), the upper undivided part of the egg constituting the pole region (trophamnion) with its polar nucleus (Fig. 269, *nu. p*). The oösome without change becomes associated with one of the daughter nuclei (Fig. 268) and is thus included in the blastomere formed about that nucleus (Fig. 269, *os*). In the second division, or four-cell stage, the oösome again accompanies one of the blastomeres, usually one of the upper ones. With the third division, producing the eight-cell stage, the oösome also divides so that two cells now contain oösome substance (Fig. 270, *bls. os*). Meanwhile the polar region gradually grows around the lower, or embryonic, region (Fig. 270) with the polar nucleus beginning actively to divide (*nu. p*). In the fourth division all the embryonic cells divide except the two that contain the oösome substance. The result is the production of a 14- instead of the typical 16-celled stage. Before this time the oösome has broken down, and its material is spread around the nucleus throughout the cytoplasm of each of the two daughter cells (Fig. 270, *os*). It is clear that the oösome substance retards division of the cells containing it. In the fifth division all the blastomeres divide, thus producing 28 cells, four of them containing oösome substance. The polar region now has formed as a definite and complete membrane, the trophamnion (*amt*), around the blastomeres (Fig. 271). After this all synchrony in division is lost. The polar nuclei in the trophamnion in part migrate toward the posterior end of the morula-like embryonic region, the trophamnion itself becoming more envelope-like (Fig. 272). By the time the blastomeres number more than 200 (Fig. 273), there may be some spindle-shaped (*csp*) and some polyhedral-shaped cells (*c*) in the morula-like mass. In this stage the trophamnion is of uniform thickness (Fig. 273, *amt*) about the embryonic mass, and its nuclei are fairly evenly distributed.

In *Litomastix truncatellus* Silvestri (1937) recognizes the oösome substance as the germ-line determinant that is distributed to the few embryonal cells destined to become sex cells. Leiby (1929) reached the same conclusion with reference to the oösome substance in *Copidosoma gelechiae*. Patterson (1921), however, was unable to follow the history of the cells containing the oösome substance beyond the 70-cell stage. He believes that this substance has ceased to function as a germ-line determinant in the polyembryonic egg owing to the increase in complexity of development. The first steps leading to the organization of the polygerm may be observed as early as the 220- to 225-celled stage (Fig. 273). Some of the cells assume a spindle shape (*csp*) and pushing in between groups of embryonic cells and fusing with other spindle cells form nucleated membranes (Fig. 274, *csp*) around the clumps of embryonic cells. Thus

several clumps of embryonic cells, each clump surrounded by a nucleated membrane, form a polygerm, the entire mass enclosed in the trophamnion (Fig. 274). A lengthening of the polygerm follows. Ingrowths from the trophamnion (polar membrane) eventually surround each primary mass to become the outer envelope, or membrane, of each mass. The number of embryonic cells included in each primary mass is extremely variable, ranging from 4 or 5 to as many as 50 cells. Embryonic cells are constantly dividing, so that a primary mass with few cells soon has that number increased. Likewise, the number of primary masses within the polygerm is variable, ranging from 15 to 20.

In the completed polygerm each primary mass thus consists of several embryonic cells surrounded by a relatively thick inner membrane, and

FIG. 274.—*Litomastix*. Section of young polygerm. (*amt*) Trophamnion. (*c*) Embryonic cells. (*csp*) Spindle cells forming an inner membrane.

the various primary masses are more or less separated from one another by ingrowths from the trophamnion. Soon after the polygerm is formed, the primary masses begin to multiply by fission. The division is initiated by a constriction of the inner membrane, followed by a corresponding constriction or ingrowth of the trophamnion, resulting in the formation of secondary masses. A subsequent similar division of the secondary masses results in the formation of tertiary masses, the latter in turn dividing several times to produce the definitive components each of which becomes the embryo of a parasite.

The formation of the tertiaries may begin as early as the end of the fourth day and continue through the sixth day. From the seventh to the tenth day the multiplication of the tertiary masses and their components goes on with great rapidity, forming a complex structure by the eleventh day.

The components later may completely separate from each other, becoming scattered throughout the body cavity of the host and forming new centers of proliferation. The rate of their distribution to various parts of the body cavity of the host to a very great extent depends upon their relation to the host tissues. If the polygerm is imbedded in adipose or other tissue, the scattering of the tertiary masses and their components may be greatly delayed. On the other hand, if the polygerm happens to lie free within the body cavity, the dispersal of its components may begin very early, even as early as the primary stage. Eggs of the parasite may be laid in any part of the host egg, but they dis-

integrate if they happen to be placed in the yolk or the intestine of the host embryo. In the newly hatched caterpillar host the egg may be found in any part of the body cavity or imbedded in the tissues adjacent thereto. It is most frequently found in nervous or adipose tissue. The tissue not only serves as a source of nutriment for the growing polygerm but also holds the embryonic masses together and thus delays their dispersal. The usual time for dissociation and dispersal is during the period in which secondary and tertiary masses are being formed, *i.e.*, from the fourth to the tenth day. In adipose tissue the masses may remain connected until the eleventh day or even later. At the end of the fourteenth day the tertiary components begin to form embryonic masses. Each mass will form a typical morula stage from which a single sexual embryo will arise. By the sixteenth to the eighteenth day the embryos become well organized, the inner and outer envelopes thinning out to form a double-walled, transparent capsule about each embryo (Fig. 275). The parasites reach the larval stage between the twenty-second to the twenty-seventh day. They then escape from the capsules into the body cavity of the caterpillar host. Once free, the larvae proceed to devour the contents of the host, eating first the fatty tissue and finally the various internal organs, the last to disappear being the nervous system and the intestine, leaving only the cuticular layer of the body wall. The larvae pupate about the twenty-eighth day. Emergence of the parasites under laboratory conditions occurs on the forty-seventh day.

FIG. 275.—*Litomastix*. Advanced stage of the development of the sexual embryos (*emb*).

Among the embryos that develop, certain individuals are found that lack reproductive, respiratory, and circulatory systems and in which no Malpighian tubules are produced. They are asexual embryos which will never undergo metamorphosis and are nonviable. In *Litomastix* asexual embryos can be recognized in young polygerms 70 to 72 hours old. The young asexual embryo differs from other embryonic masses in having a larger number of cells and in having a relatively thicker inner membrane. They arise during both the secondary- and tertiary-mass stages. Although some polygerms produce asexual embryos at a very early stage, nevertheless the majority of such embryos do not appear until after dissociation has taken place. The asexual larvae apparently perform no function, invariably degenerate, and do not live over three days

as free larvae. They disappear at least a week before the sexual larvae are set free from their envelopes.

FIG. 276.—*Apis*. Early cleavage stage. Longitudinal section. (cc) Cleavage cells. (y) Yolk.

THE HONEYBEE (*Apis mellifica* L.)

The egg of the hive bee is elongate cylindriform, slightly convex ventrally and concave dorsally, with a finely sculptured reticulate surface. The micropylar area is apparently located at the anterior end, since the cleavage cells first form near the cephalic pole of the egg (Fig. 276). The cells multiply rapidly and migrate toward the surface where they form the blastoderm. A few remain behind to form the primary yolk cells. As the cleavage cells approach the surface of the egg, their nuclei

assume a peripheral position in the cells. The inner ends of the cleavage cells at first remain united below the cortical layer, thus forming an inner cortical layer (Fig. 277). The inner cortical layer is in part absorbed

FIG. 277.—*Apis*. Cross section. (bld) Blastoderm. (dr) Dorsal strip. (yc) Yolk cell.

by the blastoderm cells and in part remains to form a pellicle over the yolk. At first the blastoderm is of nearly uniform thickness but soon becomes differentiated into a thicker ventral and a thinner dorsal por-

FIG. 278.—*Apis*. Sagittal section of anterior end of egg. (*dr*) Dorsal strip. (*gb*) Germ band. (*yc*) Yolk cell.

FIG. 279.—*Apis*. Cross section. (*lp*) Ectodermal lateral plate. (*mp*) Mesodermal middle plate. (*ser*) Serosal cells.

tion (Figs. 277, 278). Along the dorsal mid-line is a strip of cells differing from the remainder in being especially thin and flat and in maintaining a close relation with the yolk (Fig. 277).

The mesoderm is formed from a median longitudinal area of the ventral blastoderm, the middle plate (Figs. 279, 280, *mp*) which separates from the blastoderm on each side of it. These lateral parts constitute the lateral plates (*lp*). The middle plate sinks below the surface (Fig. 281A) while the lateral plates approach each other and finally are united

FIG. 280.—*Apis*. Cross section. (*dr*) Dorsal strip. (*lp*) Ectodermal lateral plate. (*mp*) Mesodermal middle plate. (*ser*) Serosal cells.

along the ventral mid-line to form the ectoderm (*ect*). The rudiments of the mid-gut epithelium are formed by the inward immigration of blastoderm cells, a discoid swelling being thus produced at each of the two ends of the middle plate but outside its limits. These rudiments later are covered by the ectoderm, excepting that in the case of the anterior rudiment a small circular area (*mge. a*) remains uncovered which later constitutes the floor of the stomodaeal invagination (Fig. 282, *mge*). During these changes the median dorsal area of the blastoderm, composed of thin flat cells, also becomes depressed and is overgrown by the dorsal margins of the lateral plates (Fig. 279). Meanwhile the cells of

this dorsal strip become aggregated in the cephalodorsal region of the egg to form a more or less discoidal mass, the "cephalodorsal body." This body appears to be nothing more than a thickened anterior end of the dorsal strip. It later degenerates in the yolk.

FIG. 281.—*Apis*. Cross sections of successive stages. (*do*) Primary dorsal organ. (*ect*) Ectoderm. (*il*) Inner layer. (*mge*) Mid-gut epithelium. (*neurg*) Neural groove. (*ser*) Serosa. (In part from Snodgrass.)

Ectodermal tissue is formed from the lateral plates, mesoderm from the middle plate, and the mid-gut rudiments are interpreted by some writers as the entoderm. During the formation of the germ layers both the middle and the lateral plates show distinct evidence of body segmentation which appears to correspond to the definitive segmentation of the embryo.

The serosa is single-layered and is formed from the dorsal half of the blastoderm. It separates from the dorsal margins (Fig. 281A,*ser*) of the lateral plates and gradually grows over the ventral face (Fig. 281B,*ser*).

The separation does not take place along the entire margin of the lateral plates simultaneously but occurs first at the cephalic end of the egg as a cap-like fold which grows rapidly caudad. A similar but slighter fold is later formed at the caudal end of the egg. The two folds eventually meet and coalesce near the caudal pole of the egg. At first the serosa consists of the dorsal part of the blastoderm except for the median longitudinal strip, but by the widening of the serosal bands the cells of their inner margins creep up over the dorsal strip, and the latter becomes

FIG. 282.—*Apis*. Median sagittal sections through the anterior mid-gut epithelium rudiment. (ect) Ectoderm. (mes) Mesoderm. (mge) Mid-gut epithelium rudiment. (mge.a) Surface area of rudiment. (ser) Serosa. (From Nelson.)

submerged in the yolk (Fig. 280). Subsequently there is a fusion of the serosal bands along the dorsal mid-line of the egg, beginning first at the cephalic end. While the serosa is thus covering the dorsal side of the yolk, it starts also to cover the ventral side. The serosa together with the anterior end of the germ band then separates from the yolk. Soon afterward it separates from the yolk over the entire cephalic pole of the egg, rising up in the shape of a hemispherical cap. Next it severs its connection with the germ band around the anterior end of the latter and slides over it in the form of a hood, thus forming the cephalic fold (Fig. 283A). This separation of the serosa from the germ band

progresses caudad along its lateral margins, accompanied by the caudal extension of the cephalic fold over the ventral face of the germ band. When the cephalic fold has covered about one-half the ventral face of the embryo, a caudal serosal fold (Fig. 283B) formed like the head fold appears at the extreme caudal end of the germ band. The two folds now approach each other until they finally meet and fuse at the caudal end (Fig. 283C). At this time the serosa also separates from the yolk on the dorsal side of the egg and thus forms a complete envelope surrounding the embryo. The extension of the serosa over the surface is due principally, if not exclusively, to a mere extension or spreading out of the original cells present at an earlier stage. Just before hatching, the serosa is broken up by the movements of the young larva. In the literature dealing with the development of the bee the serosa is termed the "amnion." The latter, however, is wholly lacking.

Shortly after the appearance of the head fold of the serosa, segmentation of the embryo occurs. Twenty-one segments are found, including an anal segment, or telson. Appendages appear, on the antennal, gnathal, and three thoracic segments, but none is found on the abdomen. Prior to hatching, the antennal rudiments as well as those on the thorax are reduced to epidermal thickenings. In the honeybee, as with other insects, the second maxillae fuse to form the labium.

The nervous system forms in general as with insects of other orders. In the abdomen 11 pairs of ganglia develop, the last 3 pairs fusing into a single one late in embryonic life. The neuroblasts divide unequally and teloblastically, giving rise to several cells smaller than themselves. The

FIG. 283.—*Apis*. Diagram of three stages in the development of the serosa (*ser*) in lateral aspect. (From Nelson.)

last-mentioned cells divide equally, the products becoming differentiated to form the ganglion cells. The optic ganglia are not, however, produced by the agency of neuroblasts but are formed as simple infoldings of the ectoderm. Beginning at the anterior margin of the mandibular segment and extending to the last segment of the trunk is a narrow median strip of ectoderm, the median cord. In the intrasegmental region this contributes the central portions of the ganglia; in the intersegmental regions, it constitutes a series of thickenings of the epidermis. The supra-esophageal commissure is formed, at least in part, from the median ectoderm. The outer neurilemma is formed from cells that have the same origin as the ganglion cells and that migrate to the external surface of the brain and ventral cord. An inner neurilemma is lacking.

The tracheal system is formed from 11 pairs of invaginations of the lateral ectoderm. The first of these, situated on the second maxillary segment, by the formation of four diverticula produces the anterior ends

of the main tracheal trunks, including the anterior tracheal commissure and also the trachea supplying the head. The 10 pairs remaining are situated on the second and third thoracic and the first eight abdominal segments. These also form four diverticula each. The anterior and posterior diverticula become united along each side of the embryo to form the longitudinal tracheal trunks. The ventral diverticula fuse with those of the opposite side of the same segments to form the tracheal commissures. The dorsal diverticula form branches supplying the dorsal region of the larva. The openings of the tracheal invaginations remain as the spiracles.

The tentorium is formed from two pairs of ectodermal invaginations. The first pair of these is situated in front of the bases of the mandibles; the second, behind the bases of the first maxillae. The invaginations belonging to the first pair grow caudad and mesad; those belonging to the second pair, cephalad and mesad. All four meet in the median plane to form a structure having the form of an X, extending across the head capsule between the esophagus and the subesophageal ganglion. An invagination situated immediately caudad of the base of the mandibular rudiments produces the apodeme for the adductor muscle of the mandible.

The openings of the silk glands appear first just behind the bases of the second maxillae. As these appendages move toward each other and fuse to form the labium, the gland apertures also approach each other and unite into a common median orifice which is finally situated on the labium in the larva. The invaginations themselves lengthen to form long slender glandular tubes extending the length of the trunk.

The oenocytes, of which there are eight sets, are situated on the first eight abdominal segments in line with the openings of the tracheal invaginations. They are produced by immigration of cells from localized areas of the lateral ectoderm.

The mesoderm, soon after its formation, becomes differentiated laterally into two layers: an outer somatic and an inner splanchnic layer; along the ventral mid-line it remains single-layered. Separate coelomic sacs are not present, the somatic and splanchnic layers of each side being continuous longitudinally throughout the trunk. At the lateral margins of the mesoderm the two layers are continuous and in this region are composed of long columnar cells. The median single-layered section of the mesoderm breaks up into rounded blood cells. The somatic layer forms the trunk muscles, both longitudinal and oblique, the pericardial fat cells, and the dorsal diaphragm including the pericardial cells. The splanchnic layers sends off from its dorsal border a mesal layer which forms the muscular layer of the mid-gut. The remainder of this layer is principally concerned in the formation of the two main divisions of the fat body. This is exceptional, since in most insects the fat body

arises from the somatic layers. The heart is formed in the usual manner from the cardioblasts. A mass of mesoderm cells, forming the anterior end of the mesoderm and evidently belonging to the primary head segment, closely surrounds the stomodaeum at its appearance and later forms the muscular layer of the fore-gut. A similar mass at the posterior end of the embryo forms the muscular layer of the hind-gut.

The ovaries are derived from cells of the genital ridges. These ridges are formed from the dorsal portion of the splanchnic layer, in the fifth to the tenth abdominal segments, inclusive. This portion becomes detached from the remainder of the splanchnic layer. During the devel-

FIG. 284.—*Apis*. Sagittal section of anterior end. (*mge*) Anterior mid-gut rudiment. (*stom*) Stomodaeum. (*yc*) Yolk cell.

opment of the embryo the genital ridge gradually shortens, finally occupying a position in the seventh to the tenth segments inclusive. Meanwhile it loses its attachment to the dorsal splanchnic layer, at the same time receiving an investment of cells from the splanchnic mesoderm lying immediately ventrad of it. This investiture, composed of flat cells, contracts and adheres to the ventral border of the heart.

The mid-gut is formed from the anterior and posterior mesenteron rudiments. The discoid anterior rudiment becomes transferred from the ventral to the dorsal side of the cephalic pole of the egg by the lengthening of the embryo. At the same time it increases in superficial area, covering the cephalic end of the yolk like a cap. Its caudal margin now extends rapidly caudad over the dorsal surface of the yolk (Fig. 284, *mge*). Meanwhile the posterior mesenteron rudiment similarly transfers to the dorsal side of the caudal end of the egg. It now sends out a thin tongue-like process cephalad over the dorsal surface of

the yolk. The caudal extension of the anterior rudiment and the cephalic extension of the posterior rudiment (Fig. 285, *mge*) next meet on the dorsal surface of the yolk about one-third the length of the egg from

FIG. 285.—*Apis*. Sagittal sections. *A*, anterior, *B*, posterior ends. (*mge*) Mid-gut rudiments. (*proct*) Proctodaeum. (*stom*) Stomodaeum.

its cephalic pole. The epithelial strip thus formed extends rapidly ventrad over the sides of the yolk until the latter is completely enclosed, the two margins of the epithelium meeting and uniting along the ventral mid-line of the yolk a short time before hatching (Fig. 281C, *mge*). Both fore- and hind-guts are formed as usual by ectodermal invaginations (Fig. 285). The stomodaeal invagination is, however, not completely ectodermal, since its floor is formed by cells belonging to the anterior mesenteron rudiment, which is not covered by ectoderm. The hind-gut is exclusively ectodermal. The lumen of the stomodaeum becomes connected with that of the mid-gut shortly before hatching. A proventricular valve is also formed at this time by folding of the stomodaeal or esophageal wall. The lumen of the proctodaeum is at no time in connection with that of the mid-gut, both the cephalic end of the hind-gut and the caudal end of the mid-gut being blind. The four Malpighian tubules are formed as ectodermal invaginations which make their appearance prior to the formation of the proctodaeum, grouped around the point where the proctodaeum is to appear. Four separate invaginations have not

been observed, the pair situated on each side of the mid-line being connected by a shallow crescentic groove.

The primary yolk cells, which are derived from cleavage cells remaining within the yolk, multiply by mitosis, the mitotic figures being at first

similar to those of the cleavage cells. A little later, irregular mitotic figures are found. These are usually minute and have the appearance of being in some cases multipolar and in others unequal. Multinucleate cells soon become abundant, some of them being of large size. Degeneration of the nuclei of the yolk cells soon becomes frequent, such nuclei diminishing in size and finally becoming reduced to minute deep-staining spherules which leave the cell body and enter the yolk. Secondary yolk cells are formed by the immigration of nuclei from the blastoderm into the yolk. These soon are indistinguishable from the primary yolk cells. Yolk cells are found distributed through the yolk until shortly before hatching. They are frequently seen clustered under the epithelium of the mid-gut, during the time when the latter is engaged in covering the lateral faces of the yolk. Yolk cells and yolk disintegrate at the time of hatching, being presumably digested.

The total time normally required for the development of the egg is 76 hours. This is divided approximately as follows: cleavage, 14 to 16 hours; formation of the blastoderm, 14 to 16 hours; formation of mesoderm, rudiments of mesenteron, and embryonic envelope, 12 to 14 hours; remainder of development, including differentiation of tissues and organs, 32 to 34 hours. The earlier stages, including the formation of the germ layers, the serosa, etc., occupy considerably over one-half the time required for total development.

A detailed account of the embryology of the honeybee is to be found in a monograph by Nelson (1915).

References

- HYMENOPTERA: Bischoff (1928), Blochmann (1884, 1886), Brandt (1878), Carrière (1886), Gatenby (1918), Leiby (1926), Marchal (1897), Stuhlmann (1886), Whiting (1937). *Ageniaspis fuscicollis*; Silvestri (1906a, 1908b). *Anaphoidea luna*; Silvestri (1915). *Apanteles* sp.; Mukerji (1930). *A. glomeratus*; Grandori (1911), Hegner (1915). *A. thompsoni*; Vance (1931). *Apis mellifica*; Blochmann (1887, 1889), Bütschli (1870), Dickel (1901, 1902, 1904), Graber (1888b), Grassi (1884), Hegner (1915), Kowalewsky (1871), Nachtsheim (1913), Nelson (1912-1915), Petrunkevitch (1901, 1903), Schnetter (1934), Siebold (1856), Snodgrass (1925). *Azteca* sp.; Strindberg (1916b). *Banchus femoralis*; Bledowski and Krainska (1926). *Biorhiza aptera*; Weismann (1882). *Bombus* sp.; Weyer (1928). *B. terrestris*; Korschelt (1886). *Camponotus* sp.; Blochmann (1892), Strindberg (1913a), Weyer (1928). *C. herculeanus*; Hegner (1915). *C. ligniperda*; Hecht (1924), Reith (1931), Strindberg (1913b). *Cephus cinctus*; Smith (1938). *Chalicodoma muraria*; Carrière (1890), Carrière and Bürger (1897), Wheeler (1898). *Copidosoma* sp.; Hegner (1914), Howard (1919), Leiby (1929). *C. buyssoni*; Silvestri (1910). *C. gelechia*; Hegner (1915), Leiby (1922). *C. tortricis*; Howard (1925), Patterson (1915). *C. truncatellum*; Hegner (1915), Leiby (1922). *Dinocampus rutilis*; Jackson (1928). *Encarsia partenopea*; Silvestri (1915). *Encyrtus* sp.; Howard (1906). *E. aphidivorus*; Silvestri (1908b). *E. fuscicollis*; Bugnion (1891), Marchal (1898, 1899, 1904), Martin (1914). *E. mayri*; Silvestri (1915). *E. testaceipes*; Marchal (1904c). *E. variicornis*; Howard (1919). *Formica* sp.; Ganin (1869), Graber (1888b), Strindberg (1913a), Weyer

(1928). *F. rufa*; Strindberg (1913b). *Formicidae*; Blochmann (1884, 1886), Reith (1932b), Strindberg (1917b). *Glypta rufiscutellaris*; Crawford (1933). *Habrobracon* sp.; Gilmore and Whiting (1931), Whiting (1924, 1934), Whiting and Gilmore (1932). *H. juglandis*; Henschen (1929). *Inostemma* sp.; Marchal (1904a, 1906). *Lasius* sp.; Weyer (1928). *L. niger*; Henking (1890-1892), Tanquary (1913). *Leptothorax acervorum*; Strindberg (1915a). *Litomastix kriechebaumeri*; Ferrière (1926). *L. truncatellus*; Giard (1897), Silvestri (1906b, 1907). *Macrocentrus ancyliivorus*; Daniel (1932). *M. gifuensis*; Parker (1931). *Mesochorus splendidulus*; Kulajin (1892a). *Messor* sp.; Weyer (1928). *Microgaster connexus*; Gatenby (1919). *M. glomeratus*; Kulajin (1892a). *Myrmica* sp.; Ganin (1869). *M. rubra*; Janet (1899), Strindberg (1913a). *Nematus ventricosus*; Packard (1872). *Oicophylla* sp.; Weyer (1928). *Oophthora* sp.; Hegner (1911b). *O. semblidis*; Silvestri (1908b). *Ophioneuris* sp.; Ganin (1869). *Paracopidosomopsis floridanus*; Patterson (1917, 1918, 1921). *Platygaster* sp.; Ganin (1869), Marchal (1904a, 1906). *P. dryomyiae*; Silvestri (1916, 1921). *P. herricki*; Hill and Emery (1937), Kulajin (1897). *P. hiemalis*; Hill (1922), Leiby and Hill (1923). *P. instructor*; Kulajin (1890, 1892, 1894, 1897). *Polistes* sp.; Graber (1888b). *P. pallipes*; Marshall (1907), Marshall and Dernehl (1905). *Polyergus* sp.; Weyer (1928). *Polynema* sp.; Ganin (1869). *Polynotus minutus*; Bugnion (1905), Marchal (1903, 1904a). *Prospalta berlesi*; Silvestri (1908a, 1915). *Pteromalid*; deFilippi (1852). *Rodites rosae*; Henking (1890-1892), Weismann (1882). *Selandria cerasi*; Winchell (1865). *Smicra* sp.; Henneguy (1891, 1892). *Spathius clavatus*; Meissner (1855). *Synopeas rhanis*; Marchal (1904a, 1906). *Tapinoma erraticum*; Strindberg (1919b). *Teleas* sp.; Ganin (1869), Metschnikoff (1866b). *Tenthredo viridis*; Meissner (1855). *Tetramorium* sp.; Weyer (1928). *T. caespitum*; Strindberg (1915e). *Trachusa serratulae*; Strindberg (1914a). *Trichacis remulus*; Marchal (1904a, 1906). *Trichogramma* sp.; Howard (1937). *Vespa* sp.; Weyer (1928). *V. vulgaris*; Strindberg (1914a).

CHAPTER XIX

TRICHOPTERA AND LEPIDOPTERA

TRICHOPTERA

THE CADDIS FLY (*Neophylax concinnus*)

According to Patten (1884) the somewhat oval eggs of the caddis fly collected from the muddy bottom of a slow-running stream are laid in clumps and surrounded by a gelatinous mass. After a primary epithelium (blastoderm) of uniform thickness has been formed, the cells become long and columnar at one pole and correspondingly thinner at the other, the thickened area being the germ disk. Amniotic folds appear on all sides of the embryonic area, gradually extending until they

FIG. 286.—*Neophylax*. Sagittal section of germ band. (*am*) Amnion. (*ch*) Chorion. (*ser*) Serosa. (*yc*) Yolk cell.

meet nearly over the middle of the germ disk (Figs. 287, 288). The tail fold appears first and grows rapidly (Fig. 286). As development progresses, the amnion (Fig. 288) becomes thinner (Fig. 289), and the germ disk elongates until it extends over two-thirds of the circumference of the egg. Previous to this a gastrular furrow (Fig. 287, *gastr*) has formed, the lips of which close, cutting off from the surface a median longitudinal band of cells, which on spreading out forms the inner layer (Fig. 289, *il*). A gastrular tube, however, does not appear. The inner layer soon divides along the median longitudinal line, thus forming a pair of lateral mesodermic bands, each of which at the same time divides into segments or somites. No coelomic cavities are formed.

In the formation of the primary epithelium (blastoderm) no yolk cells remain behind in the yolk. Later, during the formation of the embryonic envelopes, amoeboid cells with large nuclei can be seen in the yolk which have migrated back from the blastoderm and have been gradually distributed through all parts of the yolk. These are the yolk,

FIG. 287.—*Neophylax*. Cross section of head region. (*am*) Amnion. (*ch*) Chorion. (*gastr*) Gastrula furrow. (*ser*) Serosa.

or entoderm cells (*yc*), which arise from any point in the blastoderm by delamination. This process may continue even after a part of the blastoderm has been converted into the ventral plate.

The procephalic lobes increase in thickness, and the embryo lengthens until head and tail almost come in contact with each other (Fig. 290, *ceph*). After the appearance of the proctodaeum the posterior end of the

FIG. 288.—*Neophylax*. Cross section of head region. (*am*) Amnion. (*ch*) Chorion. (*mes*) Mesoderm. (*ser*) Serosa.

body becomes bent forward on itself, marking the first step toward revolution of the embryo. At the stage when head and tail are in close proximity with each other, the rudiments of antennae, mouth parts, and legs appear.

The neural groove begins at the anterior end of the body and extends to the place where the proctodaeal invagination is to appear. Certain

ectoderm cells (neuroblasts) on each side of the groove divide and later give rise to the nerve cord. The compound eyes appear just before the revolution of the embryo on the surface of the procephalic lobes as round refractive areas, in which subsequently six dark-red pigment spots appear. At this period the ectoderm shows a thickened area in the region of the eyes, which ultimately becomes connected with the brain.

Tracheae are formed in all the postoral segments except the last two or three segments of the abdomen. The spinning and salivary glands are formed by ectodermic invaginations on the inner side of the second maxillae (labium) and the mandibles, respectively. The Mal-

pighian vessels arise as six separate evaginations of the blind end of the proctodaeum, a further increase in number being produced by budding from the first three pairs.

The mesoderm in a preceding stage had separated into segments, the lateral extremities of which were formed of two irregular layers of

FIG. 289.—*Neophylax*. Cross section through thorax before appendages appear. (am) Amnion. (ch) Chorion. (il) Inner layer. (ser) Serosa.

FIG. 290.—*Neophylax*. Lateral view of 12-day embryo. (am) Amnion. (an) Anus. (ant) Antenna. (ceph) Cephalic lobes. (ch) Chorion. (lb) Labium. (md) Mandible. (mx) Maxilla. (p 1) First thoracic leg.

cells with no definite body cavity present. Later the mesoderm increases in extent, and at the same time the cells composing it become less definitely and compactly arranged. The yolk becomes reduced in amount and gradually recedes from the ventral plate. Into the cavity thus formed amoeboid mesoderm cells migrate, giving rise to the blood corpuscles. As the yolk continues to withdraw from the ventral plate, the

mesoderm follows it by a rapid growth along its lateral margins. When the lateral margins come in contact with the yolk, they are reflected backward and inward toward the median line, thus forming, on either

FIG. 291.—*Neophylax*. Cross section of first abdominal segment. (*ect*) Ectoderm. (*n*) Connective of nerve cord. (*som. m*) Somatic mesoderm. (*splm*) Splanchnic mesoderm. (*yc*) Yolk cell migrating into the body cavity.

FIG. 292.—*Neophylax*. Sagittal section of embryo. (*an*) Anus. (*malp*) Malpighian tubules. (*mes*) Mesoderm. (*spg*) Spinning glands. (*yc*) Yolk cells.

side of the body, a mesodermic layer, bounding the yolk on the ventral side. By continued growth the margins finally meet each other (Fig. 291). The inner (splanchnic) layer of mesoderm extends over and encloses the yolk to form the muscle layer of the mid-gut. This occurs *before* the yolk (entoderm) cells have formed the epithelial lining. The

outer, or somatic, mesoderm becomes closely united to the ectoderm, extending dorsally to form the outer wall of the sides and the dorsum. Before the folds meet on the middorsal line, the amnion and serosa are ruptured.

The yolk or entoderm cells increase very rapidly both in number and in size before the dorsal closure. Before the splanchnic mesoderm has completely separated the yolk from the body cavity on the ventral side, some of the yolk cells migrate into the body cavity (Fig. 291, *yc*) where they arrange themselves irregularly along the sides of the body wall. At first the cells are arranged singly and indefinitely along the outer wall of the body (Fig. 292), but later, by increasing in numbers, they become arranged in distinct groups. These entoderm (yolk) cells are both more distinct and more numerous in the posterior part of the yolk sac, the epithelial lining of the stomach probably being formed first in the neighborhood of the proctodaeum and then extending forward to the stomodaeum. It is certain that the yolk cells (entoderm) do not form a continuous sac until some time after the formation of the mesodermic musculature of the yolk sac

FIG. 293.—*Neophylax*. Lateral view of right side after revolution. (*md*) Mandible. (*mx 2*) Labium. (*p 1*) First thoracic leg.

FIG. 294.—*Neophylax*. Cross section of advanced embryo. (*b. cv*) Body cavity. (*h*) Heart. (*som. m*) Somatic mesoderm. (*splm*) Splanchnic mesoderm. (*yc*) Yolk cells.

The last stage in the development of the embryo starts when the embryonic envelopes rupture. The process of the elimination of the envelopes is the same as with the dragonflies, the earwigs, and other insects, a secondary dorsal organ being produced which later sinks into the yolk and is absorbed. After the rupture of the membranes and during the changes that take place in the dorsal organ, the abdomen of the

embryo becomes folded more and more toward the ventral side, until the curvature of the embryo becomes completely reversed (Figs. 290, 293).

After the dorsal organ has passed into the yolk, the lips of the dorsad-growing mesoderm, which on either side unite the splanchnic and somatic layers, gradually envelop the yolk, and finally meet each other along the middle line of the dorsum. By the fusion of these two mesodermic lips a *solid cord* of cells is formed, occupying the median longitudinal line of the back indicating the first foundation of the heart (Fig. 294). The cord later acquires a lumen. This observation of Patten is at variance with what usually takes place in insects.

Strindberg (1915) in his account of *Sialis*, takes exception to Patten's interpretation as given above of the development of the mid-gut epithelium in *Neophylax*, expressing his belief that this layer of cells arises from anterior and posterior mesenteron rudiments as in *Sialis*. The subject is more fully discussed in Part I.

LEPIDOPTERA

THE YELLOW BEAR (*Diacrisia virginica* Fabr.)

Diacrisia virginica, which is widely distributed over the United States, is quite common in its range. Males are frequently taken at light; the females, more rarely. The spherical eggs which are laid in clumps upon the host plant hatch in about six days at normal autumn temperature. In captivity the moth lays her eggs in the evening of five or six successive days until several hundred are deposited.

About 40 minutes after deposition, the egg nucleus is to be seen in the anaphase stage of the first maturation division lying a little to one side of the upper pole of the egg and embedded in a mass of the peripheral cytoplasm (Fig. 295*B*). At this time, elimination of chromatin takes place in the form of an equatorial disk, the amount eliminated being variable, leaving a constant amount in the daughter cells. This process agrees with Seiler's account (1914) for *Lymantria dispar* and *Orgyia antiqua*.

The chromosomes are oval, more or less uniform in size, estimated to average 0.5 micron in length, thus resembling those of *Lymantria dispar* as figured by Seiler (1914). The axis of the spindle is perpendicular to the surface of the egg. The sperm (Fig. 295*B*) at this time is located apparently directly under the upper pole about 90 microns from the egg surface. It has the form of a thick, straight rod, in an island of cytoplasm. In the next two hours the second maturation division takes place, and the female pronucleus migrates inward and fuses with the sperm. The first polar body does not divide completely, though a spindle is formed and an irregular division of chromosomes occurs. The second polar body lies in contact with the first.

Since segmentation of the nucleus begins before it reaches the center of the egg, the cleavage cells are located in the upper half of the egg at the fourth hour after deposition. Segmentation beginning in the third hour now goes on rapidly, and by the eighth hour the cleavage cells, dividing mitotically, have nearly reached the surface, a few remaining behind in the yolk to form the yolk cells. Of the cells penetrating the periplasm to form the blastoderm, the cells destined to form the serosa reach the surface a little earlier than those which are to form the embryonic rudiment. At this time no sharply marked cell walls can be distinguished. The actively dividing cells soon cover the entire surface,

FIG. 295.—*Diacrisia*. A, fragment of blastoderm as seen from within at junction of germ band (*gb*) and serosa (*ser*). B, section of egg at the time of first maturation division. (*nu*) Nucleus. (*sp*) Sperm. (*y*) Yolk.

and by the tenth hour the blastoderm is completed with cell walls distinctly marked. The axis of the spindle of the dividing cells is invariably parallel to the surface of the egg.

After they reach the surface, the cells at the micropylar end and at the lower pole of the egg no longer divide, are larger than the others, and have two to four nuclei in each; the cells around the sides of the egg in active mitosis are uninucleate. The former will form the serosa; the latter, the germ band. It should be noted that Ganin (1869), Hatschek (1877), and others long ago figured this condition for the Lepidoptera. Harold (1815) also recognized and figured the serosa, although he did not understand its significance. Kowalewsky (1871) stated that the cells that form the germ band in *Pterophorus* are smaller and flatter than those which form the serosa. Woodworth (1889) likewise noted that in *Eu Vanessa* the transition between the germ band and the serosa is quite abrupt. A surface view at the junction of germ band and serosa shows

a striking difference, the cells of the former being in active mitotic division, whereas the latter, binucleate and quadrinucleate, have ceased dividing (Fig. 295A). The germ band, when thus first formed, lies

FIG. 296.—*Diacrisia*. Germ band (*gb*) 10 hours old. (*ser*) Serosa.

wrapped around the equator of the yolk, in length nearly equal to the circumference of the egg, the head and tail ends being separated by a narrow isthmus of serosa cells. The band is about one-third as wide as it is long (Fig. 296). Though most of the cells of the germ band are actively dividing, the divisions are not synchronous. The serosa cells and those of the germ band are still about equal in thickness. At this stage the serosa is dumbbell-shaped and occupies rather less area than the germ band. With its edges now lapping over the margin of the germ band the serosa gradually spreads, until by the sixteenth hour the germ band and yolk are entirely covered. The increase in the area of

FIG. 297.—*Diacrisia*. Embryos free from yolk and envelopes, as seen from the yolk side. A, 30-hour; B, 35-hour; C, 42-hour; D, 54-hour embryo.

the serosa is accomplished by a spreading and thinning of the membrane and not by cell proliferation. So far there is no trace of an amnion. The completed serosa, at this stage thinner than the germ band, exhibits

at intervals swollen places which mark the position of the nuclei. After completion of the serosa, the edge of the germ band becomes slightly reflexed; the edge later (Figs. 298, 299A) thins out, expands, and finally, at 28 to 30 hours, completely covers the whole ventral face of the embryo as a very thin membranous amnion marked here and there with swollen places which indicate the position of the nuclei.

While the amnion is forming, the embryonic rudiment increases in size through active mitosis, forming a cup-like disk with inturned edges (Figs. 297A,B) penetrating the yolk. The cephalic and caudal ends of the rudiment close over the dorsal (yolk) side, forming an anterior

FIG. 298.—*Diacrisia*. 20-hour embryo. (am) Amnion. (emb) Embryo. (ser) Serosa. (y) Yolk. (ysp) Yolk spherule.

two-lobed and a posterior simple pouch. About this time the yolk material lying immediately beneath the surface forms yolk spherules, each enclosing one or, less commonly, two or more yolk cells (Fig. 298). In the course of the next few hours the entire yolk is reduced to large yolk spherules, each with one or more yolk cells. The nuclei of these cells are distinctly larger than those of the germ band though smaller than the nuclei of the serosa at this time. Each spherule is surrounded by a delicate yolk membrane. The cephalic lobes are now quite distinct, the body acquiring in the course of the next 24 hours its greatest length (Fig. 297D). While the germ disk is elongating, a median strip 8 to 10 cells in width (Figs. 299B,C) sinks into it. This strip extends from the head lobe longitudinally to the tail, though at first it is not in evidence in either the head or the tail pouch, nor does it appear uniformly and simultaneously throughout its length. The growth of the lateral parts of the ectoderm toward the median line and their final fusion result in the median strip's becoming the inner layer (Figs. 299C,D). The sinking

in of the middle strip reduces the width of the embryo, except at the head and tail ends. As development progresses, and coincident with the

FIG. 299.—*Diacrisia*. A, amnion beginning to form. B, section through abdomen of 34-hour embryo. C, through anterior part of abdomen of 35-hour embryo. D, through neck region of 42-hour embryo. (am) Amnion. (ect) Ectoderm. (gb) Germ band. (il) Inner layer. (ser) Serosa.

beginning of segmentation of the ectoderm (Fig. 297C), the inner layer also assumes a more segmental character. Its cells at the intervals between the segments do not multiply so rapidly as in the segments

FIG. 300.—*Diacrisia*. A, section through head of 42-hour embryo. B, through head of 44-hour embryo. (am) Amnion. (ect) Ectoderm. (gastr) Gastrula furrow. (il) Inner layer.

themselves where they form irregular layers (Fig. 302). The mass of inner-layer cells at the anterior extremity is larger both in width and

depth than elsewhere. At no time and at no part of the germ band is there the slightest resemblance to the formation of a gastrular tube. Neither is there a proliferation at this time along the middle line, as described by Eastham for *Pieris*.

FIG. 301.—*Diacrisia*. Section through head at stomodaeum (*stom*). (*am*) Amnion.

At 42 hours (Fig. 297C) the two anteriorly directed cephalic pouches so prominent in earlier stages (Figs. 297A,B) are still present, though they have become smaller and shallower. Just posterior to their dividing wall may be seen a mass of cells of the inner layer which in the middle is

FIG. 302.—*Diacrisia*. Longitudinal section (slightly oblique frontal) of 48-hour embryo. (*ab* 1-10) Abdominal segments 1 to 10. (*am*) Amnion. (*lb*) Labium. (*md*) Mandible. (*mx*) Maxilla. (*stom*) Stomodaeum. (*th*) Thoracic segments.

four or five cells thick (Fig. 300A). Posteriorly, it is continued as a median band a number of cells in width. Two hours later there is anterior to this mass in the head an inner layer one cell in thickness. Neither stomodaeum nor proctodaeum is as yet in evidence. At this

time the gastrula furrow has closed anteriorly (Fig. 300B) but is not yet obliterated posteriorly by the union of the edges of the ectoderm. The caudal pouch (telson) at this stage has become smaller though more elongated and tubular, and into it the lower layer extends, apparently without a break.

Until now the inner layer has consisted of a longitudinal band of cells, distinctly enlarged at the anterior extremity and to a lesser degree at the posterior end. We may conceive of this layer as composed of two lateral strips which are to form the mesoderm, a middle strand, and an anterior and a posterior cell mass. These two cell masses in *Diacrisia* are regarded as the anterior and posterior extremities of the middle strand, which later break down completely, the liberated cells being absorbed in the yolk.

Segmentation of the body begins soon after the fortieth hour, and soon thereafter the gnathal segments of the head become well marked; the protocephalon includes the labrum, which is not yet bilobed, the mouth, and the antennae. At this time the antennae are still postoral in position. The stomodaeum, at the fifty-fifth hour, is feebly indicated, and opposite it is found the anterior cell mass, though there is as yet no trace of the proctodaeum. Paired swellings appear on the head, the thorax, and to a lesser extent on the abdomen, marking the beginning of antennae, mouth parts, and thoracic and abdominal legs. As the appendages lengthen, a lumen is formed in them. With formation of the neural groove the cells along the median line (the middle strand) are loosened and set free in the body cavity. The mesodermal strips are now separated by the neural groove in the posterior part of the head, in the thorax, and in the abdomen except at the apex. There is as yet no trace of coelomic sacs, though the lateral margins of the mesoderm are in places dorsally reflexed, the margin thus appearing two-layered for a depth of two or three cells. Toward the caudal end in the last two or three segments is found the posterior cell mass several layers deep and with no longitudinal median interruption. Neither is there any interruption at this stage that can be interpreted as a division between the lateral mesoderm and the posterior cell mass.

In the part of the head in front of the stomodaeal invagination below the ectoderm a single layer of loosely connected cells may be observed extending into the cephalic lobes. A little more caudad in the region of the stomodaeal invagination is the anterior cell mass several layers deep. It is not separated or differentiated from the cells immediately posterior to it. In the region of the mandibles and maxillae the mesoderm extends as a single layer into the evaginations. The mandibles and maxillae are now fully as long as they are broad. Two or three hours later the anterior cell mass becomes somewhat reduced in size by cells

set free opposite the point of the stomodaeal invagination (Fig. 301). By the time the embryo is 52 hours old, the anterior cell mass has been forced away anteriorly and laterally from the apex of the invagination, and caudad of it the subesophageal body (Fig. 303*B*, *suboesb*) is developed. In the more generalized Orthoptera this body originates as a paired structure, but in *Diacrisia* it is vaguely bilobed.

FIG. 303.—*Diacrisia*. Median longitudinal section of 52-hour embryo. *A*, proctodaeum (*proct*). *B*, cephalic end. (*am*) Amnion. (*coel*) Coelomic cavity. (*stom*) Stomodaeum. (*suboesb*) Subesophageal body.

The preoral region is lined with a single layer of cells. The tip of the stomodaeal invagination at 57 hours has become quite thin (Fig. 304*B*); the labrum (*lr*) is well developed; and the neuroblasts (*neur*), characterized by their larger size, lie below an irregular layer of mesoderm in the cephalic lobes. At 59 to 60 hours the coelomic sacs, though quite small, have reached their fullest development in head segments four to

FIG. 304.—*Diacrisia*. *A*, cross section of abdomen of 52-hour embryo. *B*, cross section of head at 57 hours. (*am*) Amnion. (*coel*) Coelomic cavity. (*lim. m*) Limiting membrane of the stomodaeum. (*lr*) Labrum. (*mes*) Mesoderm. (*neur*) Neuroblast. (*neurg*) Neural groove.

six (Fig. 305, *coel*) with a single pair in the preoral region. At this time also the mouth parts have distinctly elongated, though their segmentation is not yet evident (Fig. 305*B*).

Meanwhile segmentation of thorax and abdomen, which began after 40 hours, has distinctly progressed. At 48 hours (Fig. 302) the mesoderm clearly shows a segmental character. The neural groove is deep

and conspicuous, extending from the first gnathal head segment to the last abdominal segment. On each side of the neural groove the neuroblasts are already distinct in each segment. Of these there are from two to four pairs in transverse section of the intermediate body segments (Fig. 304A), though they are not so regularly arranged as described by Wheeler (1889) for the Orthoptera. At 50 hours, daughter cells may be found in mitotic division and more or less continuous longitudinally. Laterad and dorsad is the mesoderm, which in the intermediate abdominal segments now shows well-developed coelomic sacs. Since the inner layer at the beginning consisted of a single layer of cells and not of a gastrula tube, the coelomic sacs are formed by a folding back of the lateral margin in each segment (Fig. 304A, *coel*). These sacs, though never large, have reached their fullest development at 60 hours and are

FIG. 305.—*Diacrisia*. A, cross section of head between mandibles and maxillae of 60-hour embryo. B, through maxillary segment of 64-hour embryo. (*am*) Amnion. (*coel*) Coelomic cavity. (*mes*) Mesoderm. (*mx*) Maxilla. (*neur*) Neuroblast. (*neurg*) Neural groove.

apparent in the protocephalic region, in the gnathal and thoracic segments, and in the abdominal segments, with the exception of those toward the posterior extremity adjacent to the proctodaeum. The thoracic and abdominal legs are at this stage conspicuous evaginations of the body wall and are filled with yolk.

The caudal pouch, so conspicuous and distinctive at 30 hours, becomes smaller and more tubular as the embryo lengthens. At 48 hours, the tubular part at the caudal end of the embryo measures about 60 microns in length to the point where it opens to the yolk cavity on the dorsal side. Except on the middorsal line, it is lined with mesoderm. At this time, very near the tip of the caudal pouch on its dorsal (yolk) side, the proctodaeal invagination appears. A few hours later the blind end of the proctodaeum becomes free from mesodermal cells, but proliferating mid-gut epithelial cells appear in the tip (Fig. 303A). With the increase in depth of the proctodaeum the dorsal side of the caudal pouch shortens (Fig. 303A). Between the proctodaeum and its envelope (the caudal pouch) there are two layers of mesoderm, which, however, at this stage

do not completely cover the dorsal side, except toward the caudal end. The blind end of the proctodaeum, as noted above, is now entirely free from mesoderm, though a few free cells remain near it. At 54 hours the proctodaeum is about twice as deep as it is wide and shows the first indication of the Malpighian tubes. Embryos at 59 hours show no indications of the formation of a mid-gut epithelium, though soon thereafter rudiments appear.

The anterior rudiments are first visible at the posterolateral angles of the stomodaeal membrane; the posterior mesenteron rudiments, at the anterolateral angles of the proctodaeum near the origin of the Malpighian tubes. By the sixty-fourth hour these rudiments have elongated ribbon-like, so that the tips of the anterior pair growing backward have nearly reached the tips of the posterior pair growing forward. Cells in mitotic division are to be seen near the tips of these rudiments as well as more remote from the tip. These ribbon-like strands of the mid-gut epithelium are at first but a few cells in width (Fig. 307, *mge*). In structure their cells do not differ from those of the stomodaeal membrane, nor is there any indication of an interruption in the continuity of the tissues. This condition is similar to that described by Schwartze (1899) for the lepidopterous genus *Lasiocampa* and by Toyama (1902) for the silkworm (*Bombyx*) as well as by a number of workers for species of other orders and has given rise to the view that the epithelial layer of the mid-gut arises from the ectoderm.

The cephalic ends of the lateral parts of the inner layer give rise to the mesoderm of the protocephalon; the lateral mesodermal parts, to the muscles of the esophagus; and the median part, which originally lay where the stomodaeum arises, is in part liberated as isolated cells and in part pushed down by the stomodaeal invagination to form the sub-esophageal body (Fig. 303B, *suboesb*). This body has been interpreted as endodermal by Hirschler *et al.*, although Wiesmann (1926) regards it as mesodermal. In *Diacrisia* this structure is purely embryonic, as it is no longer to be identified after the end of the fourth day. The cells that lie in the caudal pouch surrounding the proctodaeum give rise to the muscles of the hind intestine.

As has already been stated, the stomodaeum is feebly indicated at 45 hours, and 2 or 3 hours later the proctodaeum becomes evident. The latter grows rather more rapidly, so that at 52 hours it is larger than the stomodaeum (Fig. 303). The lumen of the stomodaeum becomes slender, and the membrane forming the blind end quite thin. At 65 hours it is about 0.10 mm. in length, projecting inward nearly at right angles to the axis of the body (Fig. 306B). Dorsally and laterally it is surrounded by the mesoderm from which the muscle layers are developed, ventrally by the unpaired subesophageal body (*suboesb*). At this stage

FIG. 306.—*Diacrisia*. Proctodaeum (A) and stomodaeum (B) of 65-hour embryo. (am) Amnion. (lr) Labrum. (mcs) Mesoderm. (proct) Proctodaeum. (stom) Stomodaeum. (suboesb) Subesophageal body.

FIG. 307.—*Diacrisia*. Cross section of head of 65-hour embryo. A, through mandibular segment. B, through labial segment. (am) Amnion; (i) inner, (o) outer. (amf) Amniotic fold. (ect) Ectoderm. (gl) Hypostigmatic gland. (lb) Base of labium. (md) Base of mandible. (mes) Mesoderm. (mge) Strand of mid-gut epithelium. (nc) Ventral nerve cord. (neurg) Neural groove. (silkg) Silk-gland invagination. (splm) Splanchnic mesoderm. (suboesb) Subesophageal body. (y) Yolk.

FIG. 308.—*Diacrisia*. A, section through neck region. B, through mesothorax of 65-hour embryo. (am) Amnion. (mge) Mid-gut epithelial strand. (p) Leg. (silkg) Silk gland. (splm) Splanchnic mesoderm. (tr) Trachea. (tr. i) Tracheal invagination. (trich) Trichogen cell.

the proctodaeum (Fig. 306A) is as long as the stomodaeum but with larger lumen. The Malpighian tubes arise at its tip, three on each side; and as they develop, they extend parallel and caudad for about three-fourths of its length. Though originating from a pair of invaginations in the same manner as described by Schwartz (1899) for *Lasiocampa*, the short basal stem is not evident in *Diacrisia*. The splanchnic, or visceral, layers of the mesoderm from which the muscles of the mid-gut are formed are at this time visible as two longitudinal bands of cells extending from the labial head segment caudad to the origin of the Malpighian tubes (Figs. 307B, 308, *splm*). The mid-gut epithelial strands lie dorsad of the splanchnic mesodermal strands.

At 82 hours the closing membrane of the stomodaeum has spread out cup-shaped (Fig. 310). The continuity of this membrane with the mid-

FIG. 309.—*Diacrisia*. Parasagittal section of stomodaeum of 77-hour embryo. (*lim. m*) Limiting membrane. (*mge*) Mid-gut epithelial ribbon. (*suboesb*) Subesophageal body. (*y*) Yolk.

FIG. 310.—*Diacrisia*. Sagittal section of 82-hour embryo. (*abd*) Rudiment of proleg of third abdominal segment. (*am*) Amnion. (*amf*) Amniotic fold. (*lr*) Labrum. (*p*) Thoracic legs. (*proct*) Proctodaeum, obliquely cut. (*stom*) Stomodaeum. (*suboesb*) Subesophageal body. (*y*) Yolk.

gut epithelial strands is clearly indicated from the sixty-fifth hour onward (Fig. 309). Although at 60 hours not yet apparent, at 65 the proctodaeum shows the six longitudinal folds so characteristic in many groups

of insects (Fig. 311). The splanchnic layer of the mesoderm and the mid-gut epithelial strands soon broaden, growing around the yolk. The

FIG. 311.—*Diacrisia*. Cross section through posterior end of 82-hour embryo. (*am*) Inner fold of amnion. (*bl*) Blood cells. (*f*) Fat body. (*malp*) Malpighian tubules. (*nc*) Nerve cord. (*proct*) Proctodaeum. (*tr*) Tracheal invagination. (*trich*) Trichogen cell. (*y*) Yolk.

two ribbons of the mid-gut epithelium fuse ventrad of the yolk (Fig. 312, *mge*); at 84 hours and a little later the strips of mesoderm also fuse.

FIG. 312.—*Diacrisia*. Cross section of abdomen of 84-hour embryo. (*am*) Amnion. (*bl*) Blood cells. (*g*) Gonad. (*malp*) Malpighian tubules. (*mge*) Mid-gut epithelium. (*nc*) Nerve cord. (*oen*) Oenocytes. (*splm*) Splanchnic mesoderm. (*trich*) Trichogen cell.

Shortly after the embryo rotates on its longitudinal axis, both these layers have met and fused on the dorsal side. The fat body developing

from the somatic mesoderm is composed of cells that are nearly as large as the oenocytes but differ in being vacuolate. It is not until the fourth day that fat and muscle cells are sharply differentiated, the latter becoming striate a few hours before emergence of the larva.

Toward the end of the third day the gonads are well advanced, the genital ridges being formed laterally on the splanchnic mesoderm. In the 84-hour-old embryo, they lie in the fifth abdominal segment (Fig. 312,g).

The neural furrow is well indicated at 45 hours. Three hours later neuroblasts are distinctly differentiated from adjacent cells of ectoderm in head and body segments. In its earlier stages the head exclusive of the gnathal region is not segmented. The supraesophageal ganglion formed by delamination from the ectoderm of the cephalic lobes at 65 hours shows by the presence of its neuropile a distinct tritocerebrum, which is further identified by its commissure. The deutocerebrum is obscured by the great development of the protocerebrum. Before the end of the third day the divisions of the subesophageal ganglion, as well as the ganglia of the thorax and abdomen, are well developed. As development proceeds, the nerve cord separates from the adjoining ectoderm. At 65 hours it is already quite free except along the median furrow where ectoderm and cord merge. Six hours later the edges of the ectoderm have fused along the middle line. The simple eyes, of which five pairs develop, arise from clusters of moderately large ectodermal cells, which appear early in the fifth day.

Shortly before the mid-gut epithelium begins to develop, apodemes appear in the head. The first, near the base of each mandible, is a deep tubular invagination extending caudad, forming one of the anterior arms of the tentorium. Two other shallower invaginations for the attachment of the mandibular muscles appear in this head segment. A larger apodeme on the side of the maxilla extending back into the labial head segment forms one of the posterior arms of the tentorium. In the second maxillary segment there are two pairs of invaginations: the inner pair becomes the silk glands; the outer pair develops into the so-called "hypostigmatic gland" of Toyama (1902). The invaginations for the silk glands (Fig. 307B,silk g) are found just laterad of the neural groove in the labial segment. By the sixty-fifth hour they extend back as simple, single-layered tubes to opposite the second pair of thoracic legs; by the eighty-fourth hour they extend beyond the seventh abdominal segment.

The "hypostigmatic gland" develops as an invagination near the root of the second maxilla (labium). At 65 hours, the invaginated cells are larger than those adjacent; the entire invagination is spherical in form and gland-like in appearance (Fig. 307B,gl), with the mouth of the invagination directed cephalad. During the course of the next 10 hours

the structure has migrated mesad and slightly caudad, coming to lie in front of the prothoracic legs, and has lost its attachment with the surface. Later, its cells can no longer be distinguished from those of the adjacent mesoderm. It seems probable that it is the rudimentary cervical gland which is so highly developed in the caterpillars of *Schizura concinna*, *Dicranura vinula*, and other notodontids, though vestigial in many other lepidopterous larvae. In the silkworm, according to Toyama, it persists in the larva as branched glands in the first thoracic segment.

In lepidopterous larvae the first thoracic segment bears a distinct spiracle, and in some cases a vestigial one may be demonstrated between segments two and three. In the embryo at 65 hours on the anterior margins of thoracic segments two and three the invaginations for the tracheae have advanced sufficiently to permit the recognition of a short anterior and a posterior branch. Their walls are single-layered and indistinguishable from the adjacent ectoderm (Fig. 308*B*, *tr. i*). There is no indication of a tracheal invagination on the prothorax. Invaginations for the abdominal tracheae are equally advanced at this stage, located on the anterior part of segments one to eight, the last one being the largest. The ninth and tenth segments, as well as the telson, are not provided with tracheal invaginations. By the seventy-seventh hour the most anterior spiracle has migrated on to the prothorax; the second one is no longer apparent.

The oenocytes, of ectodermal origin and associated with the tracheal invaginations, lie in clusters ventrad of the spiracles. In the 84-hour stage they resemble the fat cells in size but are not vacuolate; consequently, they stain more deeply. They are conspicuous in the newly hatched larva.

The trichogen cells are by far the largest and most conspicuous ectodermal cells in the embryo. They cannot well be confused with the oenocytes, being larger and more dorsad in position. At 59 hours they are not yet differentiated, but at 65 hours they may be found in both thoracic and abdominal segments (Fig. 308*B*, *trich*). They are so large that they extend far below the level of the neighboring ectodermal cells. In some sections, as in the one figured, they are cut tangentially, so that they appear to be located among the underlying mesodermal cells. The seta develops shortly before hatching.

Shortly after the beginning of body segmentation, the rudiments of the appendages appear. At 45 hours the mouth parts and the thoracic legs are as long as broad, with the lumen distinctly marked. At 65 hours, mouth parts and thoracic legs show distinct segmentation. Twelve hours later, the thoracic legs are three-segmented; the maxillae and labium, two-segmented. The labrum, at first simple, in the 65-hour-old embryo becomes bilobed. The future abdominal prolegs, which at

42 hours are not distinguishable from the rudiments on abdominal segments one, two, seven, eight, and nine, soon develop rapidly, while the rudiments on the segments mentioned become reduced.

The mid-gut epithelial strands fuse on the longitudinal mid-ventral line at 84 hours, but dorsally the edges are still far apart (Fig. 312, *mge*). The middle portion of the dorsal body wall is likewise still open (umbilical passage), although at the ends the amniotic folds have already closed over the dorsum (Fig. 310). Five hours later the edges of the amniotic folds, which at 82 hours (Fig. 310, *amf*) were still far apart, have fused, completing the dorsal wall (Fig. 311).

The cardioblasts arise on the lateral margins of the somatic mesoderm. At about 92 hours they are to be seen in cross section as a small group of cells arranged crescent-like with the convex side directed laterad and blood cells lying between the horns. Posteriorly, in the region of the hind intestine, the horns of the crescentic group of cardioblasts have fused to complete the heart. Two or three hours later, the heart and aorta are also completed anteriorly; the edges of the splanchnic mesodermal layer likewise meet dorsally, completing the mid-gut. Blood cells are abundant in the heart. Communication between the mid-gut and the stomodaeum and proctodaeum is established at this time by the disappearance of the stomodaeal and proctodaeal membranes. The closure of the dorsal wall of the mid-gut at 94 to 95 hours results in the inclusion of yolk. From about the thirtieth hour, when the embryo begins to sink into the yolk, until the rupture of the amnion a few hours before emergence of the larva, the embryo is immersed, the peripheral yolk being about the thickness of the diameter of one yolk spherule during the greater part of this time. This peripheral yolk which is present at the time of the rupture of the amnion is soon consumed by the young larva a few hours before the rupture of the chorion. At first, after the completion of the dorsal wall of the mid-gut, there are still yolk cells to be found, both in the peripheral yolk and in that contained in the alimentary canal, but later both yolk masses are liquefied, and the cells are no longer present. No yolk is to be found in the esophagus or in the hind intestine.

When the dorsal body wall is closed, the embryo rotates about its longitudinal axis until the ventral surface is directed toward the center of the egg. The rotation is about half completed at 89 hours. In the 82-hour stage the amniotic fold has already extended beyond the tips of the stomodaeum and proctodaeum. In Fig. 310 the proctodaeum has been cut somewhat obliquely, owing to the slightly spiral position of the embryo in the egg. A cross section through the proctodaeum of an embryo of the same age is shown in Fig. 311, indicating how the inner fold of the amnion forms a provisional dorsal wall—a condition also to

be found among certain Coleoptera. This dorsal wall later becomes somewhat wrinkled at the posterior end of the embryo before its replacement by the ectoderm. After the closure of the umbilical passage and the dorsal wall of the mid-gut and the breaking down of the stomodaeal membrane, the esophagus telescopes a short distance into the mid-gut, forming the esophageal valve. Some time after 112 hours, the outer remaining part of the amnion is ruptured, and the larva begins feeding upon it and upon the yolk material which is still present between the amnion and serosa. At 132 hours, or five and one-half days after the deposition of the egg, the larva, having wholly consumed the remaining yolk and the serosa, liberates itself by rupturing the vitelline membrane and the chorion.

References

TRICHOPTERA: *Mystacides* sp.; Graber (1888b). *M. nigra*; Weismann (1864). *Neophylax* sp.; Graber (1888b). *N. concinnus*; Patten (1884). *Phryganea* sp.; Brandt (1878), Melnikoff (1869), Zaddach (1854).

LEPIDOPTERA: Bott (1924), Herold (1815), Hirschler (1907b,c), Hollande (1930), Meissner (1855), Pictet (1906), Schwangart (1905), Stuhlmann (1886). *Abraxas grossulariata*; Doncaster (1914). *Antheraea peryi*; Saito (1934). *Attacus cynthia*; Schwartz (1899). *A. mylitta*; Selvatico (1881). *Bombyx mori*; Acqua (1932), Bataillon and Tchou (1928, 1931, 1933), Beer (1932), Bugini (1931, 1932), Della Corte (1925), Dohrn (1876), Foa (1924, 1937), Ganin (1869), Goldschmidt and Katsuki (1928), Graber (1888b, 1890b), Grandori (1914-1932), Henking (1888a, 1890b, 1891b, 1892), Hibbard (1932), Ikeda (1906), Jucci (1926, 1934), Masera (1935), Niceta (1930), Plagniol (1886), Rizzi (1912), Selvatico (1881), Strindberg (1915b), Takahashi (1911), Tangl (1909), Tichomiroff (1879, 1882, 1885), Tirelli (1934, 1935, 1939), Tokunaga (1929), Tonon (1925), Toyama (1902), Umeya (1937), Vaney and Conte (1911), Verson (1909), Wong and Li (1934), Zanini (1930). *Bombyx quercus*; Herold (1839). *Botys hyalinialis*; Jeffrey (1887), Osborn (1885). *Carpocapsa pomonella*; Wiesmann (1935). *Catocala nupta*; Hirschler (1906). *Chaerocampa elpenor*; Friedmann (1934). *Colias hecla*; Klots (1935). *Cossus* sp.; Bessels (1867). *Diacrisia virginica*; Johannsen (1928, 1929), Richards (1932). *D. latipennis*; Richards (1932). *Dilina tilae*; Vaternahm (1918). *Endromis* sp.; Schwangart (1904). *E. vericolor*; Schwangart (1907). *Ephestia kühniella*; Drummond (1936), Schl (1931). *Estigmene acraea*, *E. congrua*; Richards (1932). *Eudemis naevana*; Huie (1918). *Euprepria lubricipeda*; Meissner (1855). *Euproctis chrysorrhoea*; Hatschek (1877), Schwartz (1899). *Euwanessa antiopa*; Woodworth (1889). *Galleria mellonella*; Tchang (1929). *Gastropacha* sp.; Bessels (1867), Graber (1888b, 1890). *G. quercifolia*; Graber (1888a). *G. pini*; Kowalewsky (1871). *Isia isabella*; Richards (1932). *Lasiocampa fasciatella*; Schwartz (1899). *Leucoma salicis*; Henking (1888a, 1890b, 1891b, 1892). *Liparis* sp.; Bessels (1867). *L. salicis*; Meissner (1855). *Nyssia florentina*; Grandori (1932). *Odonestis potatoria*; Friedmann (1934). *Orgyia antiqua*; Christensen (1937). *Pieris* sp.; Brandt (1878), Graber (1888b, 1891a). *P. brassicae*; Grandori (1925), Henking (1888a, 1890a), Henson (1932), Herold (1839), Pieta (1935, 1936), Schwartz (1899). *P. crataegi*; Brandt (1880). *P. rapae*; Eastham (1927, 1930). *Pontia* sp.; Bessels (1867). *Papilio* sp.; Goossens (1885). *Phragmatobia fuliginosa*; Seiler (1924). *Plodia interpunctella*; Müller (1938). *Porthesia chrysorrhoea*, *P. auriflua*; Schwartz (1899). *Porthetria dispar*; Goldschmidt (1917, 1931),

Hertwig, (1923), Platner (1888). *Psyche helix*; Siebold (1856). *Pterophorus* sp.; Graber (1888b). *P. pentadactylus*; Kowalewsky (1871). *Saturnia pyri*; Mariani (1837), Selvatico (1881). *Selenia* sp.; Harrison (1933). *Solenobia clathrella*, *S. lichenella*; Siebold (1856). *S. triquetrella*; Lautenschlager (1932). *Sphinx* sp.; Bessels (1867), Graber (1888b, 1891a). *S. ocellata*; Herold (1815). *S. populi*; Kowalewsky (1871). *Thyridopteryx* sp.; Bruce (1885, 1886). *Tortrix viridana*; Gasow (1925). *Vanessa urticae*; Waldeyer (1870). *Zeuzera* sp.; Bessels (1867). *Zygaena* sp.; Graber (1890b, 1891a), Schwangart (1904).

Prodenia eridania; Gross and Howland (1940).

CHAPTER XX

SIPHONAPTERA AND DIPTERA

SIPHONAPTERA

THE FLEAS

Except for a few brief papers dealing with the embryology of the fleas of the dog, cat, and hedgehog but little work had been done on this group of insects until the appearance of the work of Kessel (1939) which is an extended account of the development of the cat flea (*Ctenocephalides felis*), the rat flea (*Nosopsyllus fasciatus*), and the wood-rat flea (*Hystri-chopsylla dippei*). The following abstract, based upon Kessel's work, applies to the three species just mentioned unless otherwise stated.

The eggs of these fleas are regularly prolate-spheroidal in shape and when first deposited are glistening white. The sculpturing of the chorion is least distinct on that of the cat flea. Micropylar openings are found on both poles of the egg. Although the large number of micropylar openings suggests polyspermy, it was not observed by Kessel.

Early cleavage stages are synchronous. After the sixth division the cleavage cells definitely begin their migration to the egg surface. Relatively few cleavage cells remain behind in the yolk as vitellophags, or trophonuclei. After the seventh cleavage, or the 128-cell stage, the nuclei reach the periplasm, the mitotic spindles in this division being parallel to the egg surface. Further repeated divisions of the cells in the periphery result in the completion of the blastoderm. In flea eggs the primary vitellophags (trophonuclei) are augmented by the immigration of cells (secondary trophonuclei) from the periphery back into the yolk, where they lose their cell boundaries and become incorporated into the cytoplasmic syncytium which ramifies through the yolk and where they appear indistinguishable from those of the primary group.

In the fleas a variable number of cleavage nuclei pass into the posterior periplasm and constrict off from the body of the egg surrounded by cytoplasm, to become the first germ cells. This occurs following the seventh cleavage stage. Before the walls of the blastoderm cells appear, the germ cells migrate back into the body of the egg. The oösome, or the so-called "germ-line determinant," is lacking in the eggs of the fleas. Nevertheless the germ cells are distinguishable from other early cells of the embryo by their larger size, their more prominent nuclei, and the usual clearness of their cytoplasm. With the appearance of the

mesenteron rudiment, the germ cells come to lie on the inner surface of the rudiment. When the posterior portion of the germ band is involuted into the yolk, the germ cells, together with the rudiment, are carried along, later to be incorporated into the gonads.

After the blastoderm has formed, the cells are equally distributed over the surface of the egg. Soon there occurs a concentration of cells toward the ventral mid-line and polar surfaces, forming a ventral thickening, the cells of the median dorsal region becoming somewhat flattened, apparently as the result of lateral tension exerted upon them. Although at first there is no sharp line of demarcation between the thinned dorsal area and the thickened ventral blastoderm, along the mid-line near the anterior and posterior extremities of the thickened area rather abrupt swellings soon become evident. These are the first indications of the so-called "mesenteron rudiments," which at a subsequent stage will form the mid-gut epithelium. They represent the first transformations of the single-layered blastula to a multiple laminated condition.

The amnion and serosa are formed in the normal manner. At first the posterior amnioserosal indentation is identical with that of the anterior fold. The caudal end of the developing embryo extends over on the dorsal side, extending deep into the yolk and carrying with it the amnioserosal fold in a manner similar to, but in lesser degree than, those of the odonate and hemipteran embryos. There is a fusion of the amnioserosal folds on the third day of the embryonic period, whereby amnion and serosa are completely separated, the former covering the ventral face of the embryo, the latter the entire egg. Later the caudal end of the embryo with the amnion still intact comes to lie at the surface, with head and tail ends nearly touching.

Early on the fourth day the serosa ruptures ventrally and is drawn dorsally to form an indistinct clump of cells which lie for a short time on the dorsal surface of the yolk. This clump of serosal cells is homologous with the secondary dorsal organ but lacks the tubular structure characteristic of this organ. Like a similar structure in *Chironomus*, it is absorbed in yolk. After the rupture of the serosa the amnion is said to become completely detached from the embryo, forming a complete envelope enclosing the egg contents for a time, when it, too, ruptures along the ventral line and contracts dorsally to be absorbed in the yolk just before the dorsal closure of the embryo. The remains of the amnion before its absorption are called by Kessel the "third dorsal organ" and correspond to the degenerating provisional dorsal wall of those insects in which the secondary dorsal organ assumes a tubular form.

With the development of the embryonic envelopes the gastrulation process also takes place. At an early stage in the anterior third of the germ band, including a brief section between the anterior mesenteron

rudiment already mentioned, and the anterior amnioserosal fold there is a simple emigration of cells from the blastoderm without the formation of a perceptible groove. No proliferation of cells takes place but merely a sinking in of the cells located at the mid-line. In the region adjacent to the anterior rudiment the transition from the cells of the inner layer to those of the rudiment is difficult to make out. Posteriorly the migration of cells appears to become more regular. At the beginning of the second third of the germ band there is a gradual transition from this method of inner-layer formation to that in which the migration of cells is combined with the formation of a shallow groove whose sides are destined to form the inner layer. The sides of the groove approximate but never form a tube in this region. At a point somewhat ventral to the posterior pole of the egg, the groove deepens abruptly, and its sides widen out below the surface layer, after which the lips of the groove approach each other to fuse and form a tube with a distinct lumen. In the relatively short region at the posterior end of the embryo, between the posterior mesenteron rudiment and the tubular section, a simple groove is again produced, and finally in the terminal section the inner-layer formation is like that of the anterior third of the embryo. As has already been stated, the mesenteron rudiments of the flea originate from near the anterior and posterior ends of the germ band, before the formation of the inner layer is evident.

True segmentation of the germ band in the flea takes place the third day of development when the germ layers are completely differentiated and revolution has taken place. The procephalic lobes become divided into three segmental regions, of which the most anterior develops into a bilobed prominence, the anlage of the labrum; the second, into the antennal segment; and the third, into the intercalary segment. The protocormic region gives rise to 17 segments plus an additional incomplete one which is to be regarded as the telson. The three procephalic and the three gnathal segments soon fuse to form the syncephalon of the developing larva. Of the remaining segments the first three form the future thorax. The small eleventh abdominal segment is soon carried inward by the invagination of the proctodaeum, telescoping into the tenth. In the later stages of development the embryo greatly elongates and retains its curled position until the time of hatching after the sixth day of development.

The fore-gut and the hind-gut arise as ectodermal invaginations, the former ultimately reaching about one-fourth the length of the egg. The point at which the embryonic band sinks inward into the yolk is almost immediately over the position of the posterior mesenteron rudiment and therefore somewhat anterior to the posterior extremity of the germ band. This is also the point at which the proctodaeum pushed inward so that

the first part of the resulting invagination to form appears to belong to both the proctodaeum and the amniotic cavity and has consequently been termed the "amnioproctodaeal cavity," following Lassmann (1936). Since this first portion of the cavity of the invagination is bounded on both sides by the embryonic rudiment, it is definitely the lumen of the proctodaeum. Later a portion of the extraembryonic blastoderm is drawn into the yolk to form the internal section of the amnion. That part of the cavity which is bounded on one side by the amnion is the only portion of the entire invagination that becomes the amniotic cavity alone. Stomodaeum and proctodaeum appear simultaneously; the former is nearly straight; the latter soon becomes coiled and in some stages is curved somewhat laterally to the mid-line. The Malpighian tubes arise as diverticula of the blind end of the proctodaeum and are four in number, their blind ends remaining free in the haemocoel.

The mid-gut lining is derived from the two entodermal rudiments that have already been described. With the shrinkage of the yolk and the invagination of the stomodaeum and proctodaeum, the two entodermal rudiments are carried into the interior of the embryo. From each rudiment is proliferated a pair of tongue-like processes which grow toward each other, fuse, and widen gradually, until they form a closed tube enclosing the yolk, in the same manner as has been described for a number of other insects. The dorsal closure of the tube is delayed until the mass of cells composing the ruptured amnion has sunk into the yolk. The breaking down of the cells that form the blind ends of the stomodaeum and proctodaeum establishes the continuity of the alimentary canal.

The development of the nervous system of the flea offers nothing particularly striking. Soon after the differentiation of the inner layer, the neural groove appears along the entire mid-ventral line of the germ band, even before the first manifestations of the cephalic appendages. Instead of originating by invagination, the neural groove appears to be produced by two longitudinal thickenings of ectoderm, one on each side of the mid-line of the germ band, the median unthickened portion becoming the groove. The protocerebral and deutocerebral ganglia form anterior, the tritocerebral ganglion posterior, to the stomodaeum, the last mentioned later moving forward to fuse with the first to form the definitive brain. A coalescence of the ganglia of the three gnathal segments forms the subesophageal ganglion. Of the 10 abdominal ganglia the last 3 fuse to form one definitive ganglion.

The most novel thing in connection with the development of the mesoderm of the flea is the presence of coelomic sacs, these being absent in the embryos of the nemocerous Diptera, the nearest relatives of the Siphonaptera. The mesoderm forms as a complete layer the full width of the germ band. This later thickens on the extreme lateral margins

and divides into metameres. In most of the somites formed by this process, there is developed a pair of coelomic cavities, each cavity bounded by thick walls, similar to that described by Heider (1889) for *Hydrophilus*. These sacs do not communicate with each other. The number of pairs occurring in the fleas appears to be 16, the most anterior lying in the deutocerebral segment. There is no indication of their presence in the preantennal or in the intercalary segment. Of the remaining pairs occurring in the flea they are located in the first 15 segments posterior to the stomodaeal invagination.

The definitive body cavity of fleas is chiefly a secondary one in that it is derived for the most part from the epineural sinus, as in other insects, rather than from the cavities of the coelomic sacs. As the yolk reduces in size, a space is left constituting the epineural sinus. As the yolk shrinks, it withdraws from the germ band, first along the mid-ventral region, so that the resulting cavity lies immediately above the nerve cord. Later, the epineural sinus extends laterally and dorsally on both sides until finally, with the dorsal closure of the embryo, it entirely surrounds the mesenteron which has formed in the meantime about the remaining yolk. The cavities of the relatively small coelomic sacs are added to the epineural sinus. The splanchnic walls of these sacs break through, bringing their respective lumina into communication with the extensive epineural sinus, thereby establishing the definitive body cavity.

Of the other mesodermal structures, the development of the muscles, fat, haemocytes, and circulatory system offers little that differs from that of other insects. From their positions, it appears that the pericardial fat cells come from the somatic layer, whereas the perivisceral ones are derived from the splanchnic mesoderm adjacent to the developing enteric muscles. The gonads are prominent embryonic organs. They are produced by the formation of a splanchnic mesoderm sheath about the germ cells which have separated into two groups and migrated laterally and anteriorly during the development of the embryo and come to lie in abdominal segments four to six.

The invaginations of the tracheal system make their first appearance about the time the coelomic sacs arise and while the neural groove is still open. The invaginations themselves deepen, branch, and anastomose to form the complex respiratory system of the larva. The definitive number of spiracles found in the fully developed embryo is 10 pairs. All of them arise in their definitive position except the first which originates on the mesothorax and migrates forward to its larval position during embryonic development. The oenocytes arise from the lateral ectoderm of the anterior region of the abdomen, and metastigmatic invaginations are differentiated. At first resembling other ectodermal cells, they soon increase in size and assume their characteristic appearance.

Hatching occurs after six days of development under controlled temperature and humidity conditions. After swallowing the amniotic fluid, the young larva escapes from the egg through a slit in the shell.

The type of development of the hedgehog flea resembles that of other fleas although Strindberg (1917) failed to find the early development of the germ cells at the posterior end of the egg. It is possible that Strindberg overlooked the germ cells, since Kessel found them in the species studied by him; and Packard (1872) states that at a very early stage before the completion of the blastoderm, four distinct "polar cells" (germ cells) are found at the posterior pole of the egg of *Pulex canis* (*Ctenocephalides canis*). Likewise in the plague flea (*Xenopsylla cheopis*) germ cells are clearly evident before the completion of the blastoderm, as shown by the work of Cameron (1940) whose slides also distinctly show the presence of yolk cells at this stage. Balbiani (1875) found a group of micropylar openings at each end of the egg of *P. felis*, a condition that Cameron also found in *X. cheopis*.

DIPTERA

THE MOURNING GNAT (*Sciara coprophila*)

At an early age the nucleus is at the center of the fertilized egg lying in the yolk. A layer of cytoplasm, the periplasm, which is much thicker at the poles, surrounds the deutoplasm. At the posterior pole in the periplasm lies a saucer-shaped granular plate, the oösome, or germinal cytoplasm.

The fusion nucleus is no sooner formed after the union of the male and female pronuclei than it divides. The resultant daughter nuclei move apart, and a second division takes place, four nuclei being formed. As this process continues regularly through four divisions, or until there are 16 nuclei in all, each nucleus surrounded by a mass of cytoplasm moves toward the periphery of the egg (Fig. 313).

At the fifth division, according to Du Bois, two of the cleavage nuclei penetrate the oösome and become differentiated as the germ cells. They apparently absorb the granular material of the disk (Fig. 315) and become greatly enlarged and altered in appearance. They continue their migration through the periplasm that surrounds the oösome until they lie outside in contact with the vitelline membrane where they divide until there are from 22 to 28, forming a lumpy protuberance at the posterior end of the egg.

While the two nuclei are passing through the oösome, the other nuclei in migrating toward the periphery continue to multiply, arranging themselves in the periplasm in a single layer forming a blastoderm around the yolk (Figs. 313, 314). Cell walls form around them on the outside, but

on the inside the cell wall has not been completed. After they reach the periplasm, some of the nuclei migrate back into the yolk where they become the yolk cells, or vitelophags, as indicated by Du Bois (1932).

Before the inner cell walls of the

FIG. 313.—*Sciara*. Section of developing blastoderm, four hours old. (cc) Cleavage cells. (gc) Germ cells. (y) Yolk.

FIG. 314.—*Sciara*. Cross section of developing blastoderm four and one-half hours old. (cc) Cleavage cells. (y) Yolk.

blastodermal cells are formed, the germ cells migrate inward, passing separately between the blastodermal cells (Fig. 313). They lie just inside

FIG. 315.—*Sciara*. Longitudinal section of posterior pole of egg. (gc) Germ cells. (os) Oösome.

the blastoderm at the posterior end of the egg. At about the tenth hour, when the germ cells and the vitelophags have completed their inward

migration, the inner walls of the blastoderm cells form, and the blastoderm is complete (Fig. 316).

Between the twelfth and the thirteenth hours the ventral wall of the blastoderm thickens, forming the ventral plate. A groove now appears on the ventral side, marking off a triangular section. The broader side of the triangle lies toward the anterior pole of the egg; the blunt apex reaches nearly to the posterior end. The triangle will form the embryo, the broad end becoming the head, the apex forming the tail.

FIG. 316.—*Sciara*. Longitudinal section of 12-hour blastoderm (*bld*). (*gc*) Germ cells. (*y*) Yolk cells.

FIG. 317.—*Sciara*. Longitudinal section at 15 hours. (*am*) Amnion. (*am.cav*) Amniotic cavity. (*do*) Primary dorsal organ. (*gb*) Germ band. (*gc*) Germ cells. (*ser*) Serosa.

In a live egg the transverse crease marking the anterior limit of the future embryo appears first. Within fifteen minutes the blastodermal cells lying anterior to the crease fold over the embryo and grow toward the posterior end of the egg. They thus form the anterior amniotic fold. Although this fold can at first be seen only in the anterior end, it is growing at the same time over the lateral edges of the embryo which is invaginating into the yolk (Fig. 318). The fold forms last of all over the posterior extremity. The area of the embryo left uncovered by the amniotic fold on the ventral side (Fig. 317) constantly grows smaller until by the fifteenth hour the embryo is covered over entirely and lies inside, protected by the two envelopes.

While the inner layer, which is to be described later, is forming, the embryo lengthens rapidly. The head end reaches the anterior pole of the egg at the twentieth hour and extends to the dorsal side where it develops into two hollow lobes. The posterior extremity in the meantime pushes under the germ cells and grows into a spiral around the germ cells on the dorsal side. It reaches its extreme length at the twenty-fifth hour (Fig. 321). The lengthening of the posterior extremity in *Sciara* and in *Musca* corresponds to the rotation of the embryo of some other insects. There is no rotation about the longitudinal axis in *Sciara* at any time.

As the embryo lengthens, the amnion breaks on the ventral side. The anterior portion of the amnion disappears before the twenty-seventh

FIG. 318.—*Sciara*. Cross section of 15-hour germ band. (am) Amnion. (amf) Amniotic fold. (ect) Ectoderm. (il) Inner layer. (ser) Serosa. (y) Yolk.

hour, probably being absorbed in the yolk. The posterior end of the amnion remains until about the fiftieth hour. During this time it shortens, and at its inner end where it attaches to the posterior extremity of the embryo it becomes thick. As the posterior end of the embryo uncoils, the thickened amnion increases in size, and shortly before the fiftieth hour it completely disappears probably being absorbed in the yolk.

The serosa at the time the head invaginates is very thick, especially in the anterior end of the egg. It thins out during the next three hours into a membrane with many nodules on its inner surface, indicating the location of the nuclei (Fig. 317). The primary dorsal organ (*do*), which appears at an early stage before the amniotic folds have closed over the ventral side, is a thick saucer-shaped group of cells on the dorsal side that projects into the yolk. It reaches its greatest size at the fifteenth hour and from then on decreases, until shortly after the thirtieth hour it

disappears altogether. The serosa continues unbroken throughout the development of the embryo until the ninety-second hour, when the larva breaks through its protective coverings and emerges from the egg. The nodules indicating the position of the nuclei mentioned above are large at first, but they gradually flatten down into mere oval thickenings in the

FIG. 319.—*Sciara*. Cross section of germ band. (am) Amnion. (ect) Ectoderm. (il) Inner layer.

serosa membrane. Figures 317 and 318 show them just after the serosa is formed. Figure 326 shows them at an advanced stage of development at the eighty-fourth hour. At no time does the serosa form simply part of the dorsal body wall. It is completed at an early hour and remains a separate and distinct membrane until ruptured in the process of hatching.

Soon after the fifteenth hour a depression appears on the ventral side that is caused by a layer of cells, U-shaped in cross section, pushing into the yolk along the mid-longitudinal line (Fig. 318). The depression extends the full length of the embryo, although it does not appear simultaneously throughout its extent (Fig. 321). The lateral portions of the embryo separated by the groove come together and fuse, obliterating the groove and pinching off the U-shaped ridge of cells, which then forms an imperfect gastrular tube, the lumen of which is never very distinct except at the ends (Fig. 318). The lumen soon disappears, leaving a mass of cells lying in an irregular elongate heap along the median line on the inside (Fig. 319).

The heap soon flattens out into a plate of columnar cells nearly as wide as the embryo itself (Fig. 322).

FIG. 320.—*Sciara*. Cross section of germ band at caudal end. (am) Amnion. (ect) Ectoderm. (gc) Germ cells. (il) Inner layer.

The entoderm that will form the epithelial lining of the mid-gut will develop from two masses of cells, which form the two ends of the inner layer. These are not connected by a middle entodermal strand. The remainder of the inner layer lying between the entodermal masses will become the mesoderm. This is similar to the development of the entoderm and mesoderm in *Musca*, as described by Escherich (1900) and Graber (1889).

Segmentation begins at the twenty-fifth hour. This process starts first at the cephalic end, the head segments forming and deepening long

FIG. 321.—*Sciara*. Longitudinal section of embryo at 34 hours. (*am*) Amnion. (*ect*) Ectoderm. (*gc*) Germ cells. (*il*) Inner layer. (*y*) Yolk.

FIG. 322.—*Sciara*. Cross section of coiled embryo at 34 hours (amnion omitted). (*ect*) Ectoderm. (*gc*) Germ cells. (*il*) Inner layer. (*y*) Yolk.

before the tail shows any signs of metameric formation. At the anterior pole one of the segmental folds continues to deepen and soon can be identified as the stomodaeum. At the thirty-sixth hour, mandibular, maxillary, and labial segments can be distinguished, with the stomodaeum between the mandibles appearing much deeper than the segmental grooves.

At the time that segmentation begins, a second longitudinal depression, the neural groove, forms on the ventral side. A ridge of cells pushes inward against the lower layer, separating it into two parts except for the two entodermal cell masses at the ends which are left intact. These terminal masses are the mesenteron rudiments which will later form the mid-gut.

At the fiftieth hour the cells lining the neural groove may be seen in cross section as two parallel vertical rows of neuroblasts formed in the neural ridge. They soon are modified as the ridge widens out and show the presence of ganglia before the sixty-fifth hour. The ganglia become distinct with the appearance of the neuropile. The ectoderm separates from the nerve cord at the same time. The neuropile of the brain appears before that of the ganglia of the nerve cord, and at the eightieth hour the circumesophageal commissure is distinct.

At the time segmentation begins, the stomodaeum appears as a shallow depression in the ectoderm in the anterior region of the embryo. At first this depression is no deeper than those formed by the process of segmentation, but it soon becomes a deep tube closed at its inner end.

FIG. 323.—*Sciara*. Cross section of 50-hour embryo. (*mes*) Mesoderm. (*mge*) Mid-gut epithelial ribbons. (*neurug*) Neural groove.

In the meantime the inner layer, during the process of segmentation, divides into transverse masses of cells that lie in close contact with the segmentally divided ectoderm. One of these cell masses of the inner layer, no different in appearance from the others, lies around the base of the stomodaeum. It corresponds to the anterior mesenteron rudiment in the muscoidean Diptera but is not pushed into the yolk on the end of the invaginating stomodaeum.

The cells of the anterior mesenteron rudiment, multiplying rapidly, grow over the end of the stomodaeum and send out posteriorly two slender ribbons into the yolk. These are the branches of the anterior mesenteron rudiment that will form the anterior end of the mid-gut. These branches develop from the ventral side of the mesenteron rudiment and are only a few cells in width. They lie at the sides and above the neural ridge, in close contact with the mesoderm (Figs. 323, 324, *mge*).

The proctodaeum is not discernible until nearly the fiftieth hour, when the posterior end of the embryo loses practically all its curl by shortening and lies again on the dorsal side. The formation of the pos-

terior mesenteron ribbons that grow cephalad from the posterior enteron rudiment at the end of the proctodaeum is similar to the formation of the anterior pair already described. The two pairs of ribbons meet and fuse

FIG. 324.—*Sciara*. Cross section of 60-hour embryo. Differentiation of somatic (*som. m*) and splanchnic (*splm*) mesoderm. (*ect*) Ectoderm. (*mge*) Mid-gut epithelial ribbons. (*nc*) Nerve cord.

at the fiftieth hour to form two narrow strands of mid-gut epithelium connecting the stomodaeum and proctodaeum.

These strands now grow broader until they meet and join along the mid-ventral line to form a shallow trough in which the yolk rests. The

FIG. 325.—*Sciara*. Cross section of 85-hour embryo. (*ect*) Ectoderm. (*ggl*) Ganglion. (*mge*) Mid-gut epithelium. (*som. m*) Somatic mesoderm. (*splm*) Splanchnic mesoderm. (*y*) Yolk.

cells at the outer edges of the trough continue to divide so that the trough increases in depth until at the ninetieth hour it has grown completely around the yolk and the edges have fused on the dorsal side to form a tube, the mid-gut. The closure of the dorsal wall of the mid-gut occurs

about two hours before the edges of the ectoderm grow together and fuse along the dorsal mid-longitudinal line.

At 56 hours outgrowths that are the first evidence of the developing Malpighian tubules appear at the end of the proctodaeum. They develop into elongate slender tubules that can be seen distinctly in the later stages of the embryo. About 10 hours later the proctodaeum bends sharply in the form of a letter S. This bend soon forms a complete loop. The proctodaeum twists so that it can no longer be cut longitudinally in a verticle plane through the center of the egg. At 90 hours the loop is completed.

At the eightieth hour the mesenteron is still composed of a long shallow trough holding the yolk. Ten hours later the mid-gut is completed. Two gastric coeca form as outgrowths of the mid-gut wall at its anterior end. At this time the esophageal valve is forming. It develops from the inner end of the stomodaeum as an invagination into the mid-gut. As the stomodaeum lengthens, the membrane closing its inner end enlarges into a loose sack hanging down into the yolk (Fig. 326, *lim. m*). Sections cut at successive stages after the stomodaeum pushes into the mid-gut show that it greatly increases in length and resembles as to position the peritrophic membrane of the larva. Studies have been made indicating a definite relationship between the stomodaeal membrane and the peritrophic membrane (Gambrell, 1933).

Longitudinal sections taken just after the beginning of segmentation and the invagination of the neural ridge show masses of mesodermal cells lying in the segmentation cavities on both sides of the neural ridge. These are more than one layer thick in contrast to the single inner layer from which they were derived.

Shortly after the fiftieth hour a constriction appears in the mesoderm that divides it into two parts, an ental and an ectal part, as shown in Fig. 324 at the 60-hour stage. The ental part lying next to the mesen-

FIG. 326.—*Sciara*. Longitudinal section of 85-hour embryo. (*ect*) Ectoderm. (*ggl*) Ganglion. (*lim. m*) Limiting membrane. (*mge*) Mid-gut epithelium. (*proct*) Proctodaeum. (*ser*) Serosa. (*stom*) Anterior (*a*) and posterior (*p*) ends of stomodaeum. (*suboesg*) Subesophageal ganglion.

teron ribbons is the splanchnic mesoderm (*splm*), the ectal part in contact with the ectoderm is the somatic mesoderm (*som. m*).

The division of the mesoderm into splanchnic and somatic layers takes place over a considerable period of time. The constriction is not evident at 50 hours (Fig. 323). At 60 hours it is very plainly seen (Fig. 324), but not until after the eightieth hour is the separation completed. Figure 325 shows the mesenteron ribbons (*mge*) at this time considerably widened and nearly meeting on the ventral side over the nerve cord. The development of the gonads, fat body, and heart offers no unusual features. The definitive dorsal body wall is completed at the ninety-second hour.

BLOWFLIES (*Calliphora erythrocephala* L. and *vomitioria* L.)

The eggs of the members of the genus *Calliphora* are readily obtained by placing a dead bird or mammal out of doors. In a short time the female flies will begin deposition. The eggs will be found in small clumps, especially around the mouth or anus of the cadaver. The total number deposited by a single female is variable and may reach several hundred. The time of development is variable, ranging from 6 to 48 hours depending on temperature.

Immediately after deposition the egg shows the cleavage nucleus and perhaps its first cleavage stage in the anterior one-third. It has at this time an outer layer of formative periplasm, with scanty protoplasm in the yolk. The cleavage nuclei migrate to the periphery with the *centrosome* in front (peripheral), but the centrosome is lateral when division takes place. After some irregularity in distribution of the cleavage nuclei they later arrange themselves at a regular distance from the center and simultaneously migrate to the periphery which they reach at nearly the same time. The oösome may be seen in early stages of the egg near the posterior pole where the periplasm has thickened (Fig. 327*A, os*) during development. Until the cleavage nuclei have nearly reached the periphery they all look alike, but those which pass into the oösome assume a rounded appearance. The oösome breaks up into as many parts as there are cells in contact with it, a part surrounding each cell in the form of a finely granular peripheral crescentic body (Fig. 327*B*). While the other cleavage nuclei form the blastoderm, the germ cells become differentiated and may be readily recognized as such for a long time. They become visible externally, bulging beyond the surface. Contrary to Graber's statement, the same is true for *Lucilia*, though here they are less protruding. At the stage when the first germ cells free themselves and assume a rounded appearance, there are 15 or more cells present. As development goes on, they increase in number.

On the approach of the cleavage nuclei at the posterior end, the original peripheral formative protoplasm thickens but becomes thinner again

when the cleavage nuclei enter this layer. It then becomes thicker when the nuclei reach the surface. The closing in of the blastoderm under the

FIG. 327.—*Calliphora erythrocephala*. A-C, Successive stages. D, longitudinal section. (bld) Blastoderm. (cc) Cleavage cell nucleus. (gc) Germ cells. (os) Oosome. (pr) Periplasm. (pr. i) Inner periplasm. (y) Yolk. (yc) Yolk cell.

germ cells is not complete, but there is formed here a funnel-shaped invagination, from the margin of which a migration of nuclei begins into the egg mass where they become yolk cells (Fig. 327C).

This migration has been noted by Voeltzkow (1889), Metschnikoff (1866), Will (1888), and Lassman (1937), though Graber controverted it. In other respects Graber's account is correct as regards the migration of other lateral blastoderm cells into the interior. It seems probable that some of the yolk cells come from cleavage nuclei that had remained behind, as Blochmann, Graber, and Kowalewsky have already noted, but the majority of yolk cells arise from the return migration of blastoderm cells, though only after the cells of the periphery are closely crowded. Those which remain behind do not do so *a priori* but turn back when they have nearly reached the surface. In *Calliphora* only one to three such cells come from the cleavage cells that had remained behind, but in *Lucilia* they are more numerous. This relation is therefore variable in the Muscoidea. The usual view of the function of the yolk cells is that they are concerned in the breaking down of the yolk substance to render it available for the blastoderm. Noack (1901), however, believed that these cells, in the muscids at least, by their pseudopod-like processes are for the mechanical purpose of yolk support, perhaps in addition to their other use.

The cleavage nuclei reach the surface simultaneously, but the germ cells remain separated from the periphery by yolk. Later a second layer of cytoplasm (*pr. i*) is said to be formed under the blastoderm and is separated from it by a thin layer of yolk substance. Noack, however, states that this is only in part true. The distribution is not irregular, as Graber has stated, but is as shown in the accompanying figure (Fig. 327D). Dorsally it is very thin, but it is thicker ventrally and not developed posteriorly.

Absorption of nutriment by the blastoderm does not begin until the blastoderm cells extend (in depth) in contact with the yolk. The yolk elements absorbed by the cells do not appear to differ from the other yolk elements. After a time the lower blastoderm cell wall is formed so that the yolk no longer is in direct contact with the protoplasm of the cell.

It should be stated that the cells of the developing embryo are columnar, whereas the undifferentiated cells of the original blastoderm on the dorsal side are quite flat. Since the latter, though they change but little in character, function as an envelope, they have been designated as the serosa by some writers, Graber among others. The differentiation of the germ band consists rather of a thinning of the dorsal and lateral sides of the blastoderm than of a thickening on the ventral side.

A surface examination of the developing egg shows that early in the formation of the embryo two transverse furrows develop which extend around the egg and divide it into three divisions, the middle section between the furrows on the ventral side where the middle plate later forms, being again divided by five lines into six divisions of about equal

width (Figs. 328A,B). The anterior piece is again divided by a curved furrow into two parts. Laterally the five ventral lines are bounded by a longitudinal line on each side. These lateral lines mark the edges of the lower layer, or middle plate.

The five lines are not furrows but represent differences in thickness of the inner protoplasmic layer showing through. Later, as development progresses, they become furrows. The germ band continues around the

FIG. 328.—*Calliphora erythrocephala*. A, lateral; B, ventral; C, lateral ventral; D, dorsal aspect. Successive stages. A, formation of germ band. B, development of median plate. C, closure of mesodermal tube. D, postmesenteron rudiment invaginated into the yolk. (ent) Entoderm. (fr) Furrow. (gb) Germ band; (a) anterior; (m) median; (p) posterior. (gc) Germ cells.

egg at both poles and is not restricted to the mid-ventral section, as Voeltzkow believed. The middle section of the germ band now begins to sink below the level of the surface, and the cells of the band become quite deep. The middle section of the band is sharply limited posteriorly by the posterior furrow, anteriorly by the converging fold. From this it is seen that the entire band is composed of an anterior, a middle, and an end piece. The middle section now forms a depressed area from which the mesoderm is formed; from the anterior and posterior parts the mid-gut epithelial rudiments are to develop. It was formerly believed that the middle section of the germ band between the anterior and posterior transverse furrows constituted the entire lower layer. However, as has

FIG. 329.—A–C, *Calliphora vomitoria*. D, *Lucilia caesar*. Section A taken at level of *x* in B. Section C at level of *z*. Section D at level of *q*. (*ect*) Ectoderm. (*ent*) Entoderm. (*fr*) Oblique head furrow. (*gc*) Germ cells. (*mes*) Mesoderm. (*yc*) Yolk cell. Sections A and B of Fig. 335 are taken at the levels of *k* and *u*.

already been stated, this part gives rise only to the mesoderm which by the deepening of the longitudinal ventral furrow later forms a tube (Figs. 328C, 329A).

Escherich (1900) especially emphasized the point that the mesoderm near the anterior end of the embryo originates below the ectoderm as lateral diverticula of the gastral furrow (Fig. 329C), thus conforming with the mode of development exemplified by the Chaetognatha (*Sagitta*) (Fig. 40), except that in the muscid it is restricted to the posterior extremity of the very short anterior mid-gut rudiment, the middle strand being absent.

The tube is first completed at the anterior and posterior ends. Anteriorly the invagination is complicated by the appearance of diverticula (Figs. 329B,C, 330). During this time, because of the growth of the embryo and the lengthening of the tubular mesoderm, the posterior mesenteron rudiment together with the germ cells is pushed over on the dorsal side (Figs. 329B,D). The transverse lines now deepen and extend around the egg. With the elongation of the tubular mesoderm these transverse furrows become displaced so that they occupy a more or less oblique position (Fig. 328D). This is the only indication of rotation that is observable in the embryo of the muscids. The anterior converging folds now elongate still more as well as coming closer together, with the result that the anterior end of the germ band is more sharply defined.

The original posterior transverse furrow which is now carried by the dorsad-growing posterior section of the germ band becomes more longitudinal in position, so that eventually it becomes a longitudinal furrow (Fig. 328D). The transverse lines which originally were found only on the ventral side now become more evident on the dorsal side and finally disappear on the ventral side entirely. When the posterior transverse furrow assumes a longitudinal position, the two branches come closer together and then fuse (Fig. 328D). Meanwhile just in front of this, *i.e.*, dorsad, a transverse invagination, the amniotic fold, appears, the first ectodermal invagination (Figs. 331A,B).

FIG. 330.—*Calliphora vomitoria*. Frontal section same age as Fig. 329. (*ect*) Ectoderm. (*ent*) Entoderm. (*fr*) Oblique head furrow as in Fig. 328A. (*fr.h*) Horizontal head furrow. (*mes*) Mesoderm.

The mesodermal tube continues to elongate, its caudal end being drawn more and more into the interior, thus becoming more and more angulated until at the time when the tube is at its maximum length the two limbs of the tube lie parallel with each other.

Before the union of the mesenteron ribbons on the ventral side, clefts form laterally in the mesoderm, in which, at an earlier period, the lumen had been obliterated. This is the first indication of the definitive haemo-

FIG. 331.—*Calliphora erythrocephala*. A, sagittal section of anterior end. B, sagittal section of posterior end. (am) Amnion. (am. cav) Amniotic cavity. (ect) Ectoderm. (ent) Entoderm. (mes) Mesoderm. (proct) Proctodaeum. (stom) Stomodaeum.

coele (body cavity) and of the separation of the mesoderm into the splanchnic and somatic layer. Somewhat later the somatic layer differentiates into numerous somatic muscles. The differentiation of the muscles of the mid-gut into transverse and longitudinal fibers occurs in a very late stage of the embryo or possibly even during postembryonic development in the Muscoidea, as is the case also in some other insects.

Before the time when head and tail ends lie closest together, the proctodaeal invagination appears at right angles to the amniotic cavity and parallel to the longitudinal axis of the egg. Some of the early

writers confused the amniotic cavity with the proctodaeum, giving rise to erroneous interpretations. As development continues, the caudal end pushes still farther forward; the proctodaeum deepens; and from near its extremity, dorsal and ventral diverticula, the beginnings of the Malpighian tubules, appear. The posterior mesenteron rudiment is closely fused with the apex of the proctodaeum. At this time the head and tail end of the embryo lie rather close together, a condition that, however, does not last long (Fig. 331A). Then the shortening of the embryo

FIG. 332.—*Calliphora erythrocephala*. Sagittal sections of two stages, A and B. (ect) Ectoderm. (ent) Entoderm. (ggl) Nerve ganglion. (malp) Rudiment of Malpighian tubule. (mes) Mesoderm. (proct) Proctodaeum. (stom) Stomodaeum. (y) Yolk.

begins and continues until the anal end again lies at the posterior end of the egg (Figs. 332A,B).

When the germ band has reached its greatest length, the transverse amniotic invagination marks the caudal extremity as seen from the dorsal surface (Fig. 333). At this time the vestiges of six pairs of stigmal ectodermic invaginations are also in evidence, the first stigmata apparently belonging to the mesothorax. Anteriorly in dorsal aspect the two head lobes are visible. At this stage distinct segmentation may be seen on the ventral side.

The salivary glands according to Graber (1889) first show as paired ectodermal invaginations between the third and fourth head segments or

possibly on the fourth segment. The esophageal valve is formed in the usual way by the invagination of the smaller esophagus into the larger mid-gut.

FIG. 333.—*Calliphora vomitoria*. Dorsal aspect. (am) Amniotic invagination. (hl) Head lobes. (st) Stigmata.

At this time, also, scattered large oval or round neuroblasts separate from the inner walls of the ectoderm of the head lobes. Ventrally on each side of the neural groove are the neuroblasts which are to develop into the ventral nerve cord (Fig. 334). The segmentally arranged neuroblasts at this stage are present in nearly the entire length of the embryo. As development progresses, the cord separates from the outer ectoderm, and connectives and commissures are established. The brain and the subesophageal ganglia appear more or less simultaneously with the ventral nerve cord. The nerve cord, until the last third of the developmental period, extends nearly to the caudal end of the body, but at hatching it scarcely reaches the middle. The extreme cephalization found in the mature larva takes place after hatching.

As has been stated, the posterior mesenteron rudiment, *i.e.*, the caudal end of the lower layer, is distinctly differentiated from the middle section, or mesoderm portion, of the lower layer from the beginning. With the increasing length of the mesoderm, the mesenteron rudiment together with the germ cells is pushed around on the dorsal side. Later at least some of the germ cells (*gc*), which until this time are found at the surface of the enteron rudiment (Fig. 329*B*), pass through the rudiment into the interior (Fig. 329*D*). At this period the portion of mesoderm and the mesenteron rudiment which lie on the dorsal side of the egg have sunk beneath the surface.

When the embryo has attained its greatest length, the stomodaeal invagination is first indicated impinging upon the anterior mesenteron rudiment. Escherich (1900) especially emphasizes the fact that the rudiment is distinctly differentiated before the invagination appears.

FIG. 334.—*Lucilia caesar*. Cross section of posterior region. (ent) Entoderm. (mes) Mesoderm. (neur) Neuroblast. (neur) Neural groove. (proct) Proctodaeum.

The rudiment by this time has become cleft at the free end into two branches which are in contact with a ribbon of mesoderm that is destined to form the muscle layers of the mid-gut. Later the mesenteron rudiments elongate, and the stomodaeal invagination deepens (Fig. 332A).

FIG. 335.—*Calliphora vomitoria*. Section *A* is taken at the level of *k* of Fig. 329; *B* at the level of *u*. (*ect*) Ectoderm. (*ent*) Entoderm. (*mes*) Mesoderm.

Posteriorly at this time the posterior mesenteron rudiment is divided apically into two branches in the same manner as the anterior rudiment. With the shortening of the embryo the proctodaeal opening comes to lie near the posterior end of the egg, with the result that the posterior mesenteron rudiment has its apex directed anteriorly (Fig. 332B). Subsequently the elongation of the paired branches, or ribbons, of the two rudiments meet and then widen until their edges fuse, forming the mid-gut epithelium, a tube enclosing the yolk except for a small portion of the yolk which remains in the head region. The yolk cells take no part in the formation of the mid-gut epithelium.

Escherich (1900) and Noack (1901) both maintain that the anterior and posterior mid-gut rudiments represent the entoderm. Escherich, in common

FIG. 336.—*Calliphora vomitoria*. Section taken slightly above the level of *x* in Fig. 329. (*ent*) Entoderm. (*mes*) Mesoderm.

with a number of other investigators, considered the longitudinal ventral furrow as a much elongated gastrula furrow at the extremities still preserving its original condition, the invaginated part formed exclusively of entoderm (Fig. 335A, *ent*). At the anterior end but slightly farther back lateral mesodermic diverticula appear (Fig. 335B, *mes*), and a

little farther back still there is no longer any evidence of entoderm, the two mesodermic diverticula appearing as a flattened tube. At the extreme posterior end the mesoderm is again lacking. It will be observed that the anterior section (Fig. 335A) indicates simple gastrulation with only the ectodermic wall and an inner entodermic lining, whereas the section shown in Fig. 335B indicates the formation of the mesodermic diverticula in a manner similar to that of the chaetognath *Sagitta* (Fig. 40). In the middle region, where the entoderm is lacking, the flattened mesodermic tube is evident. This theory of the formation of the muscid embryo by the process of gastrulation analogous to that of *Sagitta*, because of its plausibility, has had a number of adherents.

References

- MECOPTERA: *Panorpa*; Brandt (1878).
- SIPHONAPTERA: *Ctenocephalides felis*; Kessel (1939). See also *Pulex. Hystrichopsylla dippiei*; Kessel (1939). *Nosopsyllus fasciatus*; Kessel (1939). *Phthirus pubis*; Grimm (1870). *Pulex canis*; Packard (1872), Weismann (1863). *P. erinacei*; Strindberg (1917a). *P. felis*; Balbiani (1875). *P. serratipes*; Tichomirowa (1890b). *Xenopsylla cheopis*; Cameron (1940).
- DIPTERA: Carrière (1886), Heymons (1893b), Ravetta (1931), Rostrand (1927), Stuhlmann (1886), Townsend (1934). *Anopheles* sp.; Christophers (1911), Hinman (1932). *A. maculipennis*; Nicholson (1921). *Calliphora*; see also *Musca*. *C. erythrocephala*; Noack (1901), Parker (1922), Pauli (1927), Strasburger (1933, 1934). *C. vomitoria*; Blochmann (1887), Escherich (1900, 1901), Graber (1888b, 1889b), Henking (1888-1892), Herold (1839), Korschelt (1886), Tangl (1909), Verhain (1921), Voeltzkow (1888, 1889), Waldeyer (1870), Weismann (1863). *Cecidomyiidae*; Graber (1888b). *Chironomidae*; Branch (1931), Brandt (1878), Sebess v. Zilah (1932). *Chironomus* sp.; Craven (1909), Graber (1888b), Grimm (1870), Hasper (1910, 1911), Jaworowsky (1880), Kölliker (1843), Kupffer (1866), Ritter (1890), Robin (1862), Sachtleben (1918), Weismann (1864, 1882). *C. confinis*; Hasper (1911). *C. dorsalis*; Miall and Hammond (1900). *C. grimmii*; Schneider (1885). *C. riparius*; Hasper (1911). *C. zonatus*; Kölliker. *Compsilura cincinnata*; Hegner (1915). *Crataerhina pallida*; Hardenburg (1929). *Culex* sp.; Nath (1925). *Culicidae*; Hinman (1932). *Drosophila* sp. and *D. melanogaster*; Bodenstein (1938, 1939), Child and Howland (1933), Dobzhansky (1931), Ephrussi (1925), Geigy (1926, 1927, 1931), Hanson and Heys (1938), Henshaw (1934), Howland (1932), Huettner (1923, 1924, 1927, 1935), Morgan (1914), Poulson (1937), Rabionowitz (1937), Smith (1935), Sonnenblick (1934), Strasburger (1935), Sturtevant (1929), Wolff and Ras (1934), Woskressensky (1928). *Lipotena cervi*; Hardenburg (1929). *Lucilia* sp.; Escherich (1902), Graber (1888b). *L. caesar*; Escherich (1900), Graber (1889b). *L. illustris* (= *silvestris*); Noack (1901). *Melophagus ovinus*; Hardenburg (1929), Lassmann (1936), Leuckart (1858a), Pratt (1897, 1901). *Miasor* sp.; Leuckart (1858b), Metschnikoff (1865, 1866b), Pagenstecker (1864), Wagner (1865). *M. americana*; Hegner (1912, 1914, 1915), Huettner (1934). *M. metraloas*; Gabritschewsky (1928, 1930), Hanin (1865), Kahle (1908), Meinert (1864), Siebold (1864). *Musca* (see also *Calliphora*); Bruce (1887), Bütschli (1888), Escherich (1900, 1901), Graber (1888b), Kowalewsky (1886), Weismann (1891b). *M. domestica*; Husain (1927), Pauli (1927), Reith (1925), Verhain (1921). *Muscids*; Schmidt (1889). *Oligarces* sp. Harris (1924). *O. paradoxus*; Ulrich (1936). *Ophyra cadaverina*; Tangl (1909). *Phormia regina*;

Auten (1934), Noack (1901), Schaefer (1938). *Phytophaga destructor*; Metcalfe (1935). *Rhabdophaga saliciperda*; Sen (1939). *Sciara coprophila*; Butt (1934), DuBois (1932), Metz (1938), Schmuck and Metz (1932). *Simulium* sp.; Graber (1888b), Melnikoff (1869), Metschnikoff (1866b). *S. canescens*; Klliker (1843). *S. pictipes*; Gambrell (1933). *Stenopteryx hirundinis*; Hardenburg (1929). *Tanypus*; Hasper (1911), Robin (1862). *Tanytarsus boiemicus*; Johannsen (1937), Zavrel (1926). *T. dissimilis*; Johannsen (1910, 1911, 1937). *T. grimmi*; Schneider (1885).

CHAPTER XXI

MYRIAPODA

CHILOPODA, THE CENTIPEDES

Scolopendra cingulata and *dalmatica*

The Egg Cleavage and Blastoderm Formation.—The eggs of these two European centipedes are laid during June in the earth at a depth of 3 to 8 cm. in clumps of 15 to 20 or more, the female remaining curled around the mass until the young begin feeding. The short ovoid egg averages 3 mm. in length and has a thin but brittle chorion. Although the egg

FIG. 337.—*Scolopendra*. Median section after intravittelline differentiation of the cleavage cells. (ic) Intercalary cells. (cc) Cleavage cells. (Adapted from Heymons.)

contains a protoplasmic reticulum, the meshes of which contain the food yolk, a periplasm is apparently lacking. Shortly after fertilization some cleavage nuclei surrounded by a layer of cytoplasm appear in the yolk. Meanwhile the egg yolk undergoes a pyramidal cleavage (Fig. 337) with the polygonal bases at the egg surface (Fig. 338). A few cleavage cells which Heymons (1901) designates as intercalary cells (*i. c*) are found on the bounding surfaces of the yolk pyramids, and in the central part of the egg are a number of cleavage cells designated as "pyramid cells" (Fig. 337, *c. c*). The intercalary cells mitotically divide and migrate toward the periphery, where further cell division takes place, the blastoderm thus arising from isolated cell groups that have developed from the outward

migrating intercalary cells. At one point on the ventral egg surface cell division is more active, giving rise to a small nearly circular germ disk. This is in evidence even before the formation of the blastoderm in *S. dalmatica*, but in *S. cingulata* the blastoderm forms first, the isolated cell groups eventually becoming contiguous by single cells wandering into the intervening spaces.

FIG. 338.—*Scolopendra cingulata*. (*emb*) Embryonic rudiment. (*cp*) Cumulus primitivus (early rudiment). (*yp*) Yolk pyramid (macromere). (Adapted from Heymons.)

Germ Layers.—The germ disk by rapid mitotic division soon becomes several layers thick (Fig. 339), in structure resembling the *cumulus primitivus* in spiders, the yolk masses immediately below being broken up. A few cells set free from the inner surface wander into the yolk, forming yolk cells, which are found not only on the dividing surfaces of

FIG. 339.—*Scolopendra cingulata*. Section through early rudiment. (*blast*) Blastoderm. (*cp*) Cumulus primitivus (early rudiment). (*ent*) Entoderm cell. (Adapted from Heymons.)

the yolk pyramids but also in the peripheral part of the pyramids. A few degenerating cells, the paracytes, may also be observed. Later yolk cells are also gradually given off from the inner surface of the blastoderm.

The formation of the entoderm takes place in the same manner as that of the yolk cells. Cells are set free from numerous points of the inner

ventral surface of the egg which become lodged on the yolk surface. At first they are indistinguishable from the yolk cells. Soon more cells are liberated from the cumulus primitivus and from its vicinity. These represent mesoderm or mesenchyme cells. Yolk cells and entoderm cells probably arise chiefly from the ventral side of the egg. The relatively few cells liberated from the inner dorsal side of the egg are probably mainly or exclusively mesenchyme (mesoderm) cells.

The germ disk represents the posterior part of the future germ band. The heap of cells (Fig. 339) that at first developed on the inner side of the

FIG. 340.—*Scolopendra cingulata*. Cross sections A, B, successive stages. (bl) Blood cell. (dm) Membrana dorsalis. (ent) Entoderm cell. (mes) Mesoderm. (vm) Membrana ventralis. (y) Yolk. (yc) Yolk cell. (Adapted from Heymons.)

germ disk becomes dispersed, migrating forward as two lateral mesoderm bands of cells. Meanwhile the ectodermal layer, except on the median line which is now but one cell layer in thickness, gives rise to additional ectodermal cells by radial cell division and mesodermal cells by tangential division (delamination), the latter not encroaching on the median line (Fig. 340A). The occasional isolated cells found on the median line below the ectoderm are doubtless undifferentiated entoderm and mesenchyme cells, but the cells that are later found between the two lateral mesoderm bands appear to develop into blood cells. The entoderm cells, in contrast to the mesoderm cells, become somewhat flattened and attach themselves to the yolk surface (Fig. 340B). A median longitudinal furrow or invagination is not formed in the germ band.

Segmentation of the Germ Band and Appearance of Appendages.—

When the germ disk has somewhat lengthened until it is about twice as long as the broadened anterior half and before the cephalic end is sharply differentiated from the blastoderm in front, the first indication of mesodermic segmentation becomes apparent by the formation of three segments some distance from the posterior end of the disk. At this time the mouth may be seen as a slight depression at the anterior end. In this region the mesoderm is lacking on the median line. With the increasing length of the embryonic rudiment, which we may now call the "germ

FIG. 341.—*Scolopendra cingulata*. A, germ band. B, lateral aspect, later stage than that of Fig. 342. (ant) Antenna. (dm) Membrana dorsalis. (lr) Labrum. (md) Mandible. (mpd) Maxilliped. (mx) Maxilla. (p) Leg. (pren) Preantenna. (prz) Proliferation zone. (ster) Sternite. (tel) Telson. (ter) Tergite. (vm) Membrana ventralis. (Adapted from Heymons.)

band," more segments appear, and the anal opening becomes visible close to the posterior end.

In front of the crescent-shaped oral invagination the clypeus develops as an unpaired lobe, and at some distance posterior to this invagination the rudiments of the antennae appear. Between the posterior margin of the antennal segment and the anterior margin of the mandibular segment the intercalary segment is apparent, though it does not develop so fully as the other metameres, nor will it bear appendages. Two maxillary, one maxillipedal, 21 rump, and a relatively large, cordate telson, or anus-bearing segment, make up the remainder of the body.

Upon completion of the segmentation the lateral segmented mesoderm bands become more widely separated (Fig. 341A), rendering the one-layered middle ectodermal strip (*membrana ventralis*) more conspicuous. Meanwhile the anlagen of the appendages appear. The lateral part of the segment will develop into the tergite, the mesal part into the sternite (Fig. 341A, *ter*, *ster*).

The appendages now begin to lengthen; the antennae (*ant*) become preoral in position; the unpaired labrum (*lr*) develops as a lobe on the clypeal margin and overhangs the mouth. A prominence in front of each antenna that is pushed forward by the anterior migration of the antenna also elongates to become the preantenna (Fig. 341A, *pren*).

FIG. 342.—*Scolopendra cingulata*. Formation of yolk furrow. (*ant*) Antenna. (*cly*) Clypeus. (*dm*) Membrana dorsalis. (*lr*) Labrum. (*p*) Leg. (*pren*) Preantenna. (*prz*) Proliferation zone. (*tel*) Telson. (*ter*) Tergite. (*vm*) Membrana ventralis. (Adapted from Heymons.)

Bending of the Germ Band.—

When the segmentation of the germ band has been completed and the rudiments of the appendages are well established, the right and left halves of the germ band separate more and more (Fig. 341A) from each other except at the two extremities. Each half bends sharply at about the ninth and tenth segments to such an extent that the anterior and posterior sternal parts face each other (Fig. 342). The *membrana ventralis* (*vm*) stretches,

and the head and tail approach each other until they meet (Fig. 341B, side view). The stretching of the *membrana ventralis* is accompanied by the formation of a deep transverse furrow through it, cutting deeply into the yolk which finally divides it, except for a dorsal bridge, into two parts. Figure 343 is a diagrammatic representation of a section taken at right angles to the furrow of the *membrana ventralis* when the crests of the furrow from each side have met inside, completely dividing the yolk. The halves of the germ band, in contact only at head and tail (Fig. 341B), lie separated from each other by the yolk, connected dorsally by the *membrana dorsalis* (blastoderm) and ventrally by the *membrana ventralis* (Figs. 343, 344).

Development of Body Wall and Appendages.—As has already been stated, the rudiments of the appendages develop in a row near the center of each lateral strip, the lateral portion of the strip to form the tergites; the mesal portion, the sternites. As development progresses, the anlagen

of tergites and sternites widen, encroaching upon the *membrana dorsalis* and *ventralis* (Fig. 344, *ter*, *ster*), enveloping the yolk (*y*). The germ band now being more sharply defined may be designated as the embryo. A

FIG. 343.—*Scolopendra cingulata*. Cross section of young embryo soon after flexure of germ band. (*coel*) Coelome. (*dm*) Membrana dorsalis. (*mge*) Mid-gut epithelium. (*p*) Leg. (*sin*) Lateral blood sinus (schizocoel). (*ster*) Anlage of lateral sternite. (*ter*) Anlage of lateral tergite. (*vm*) Membrana ventralis. (*y*) Yolk. (Adapted from Heymons.)

FIG. 344.—*Scolopendra*. Cross section. (*dm*) Membrana dorsalis. (*ggl*) Rudiment of ganglion before mesad migration. (*p*) Leg. (*ster*) Sternite. (*ter*) Tergite. (*vm*) Membrana ventralis. (*y*) Yolk. (Adapted from Heymons.)

FIG. 345.—*Scolopendra*. Cross section of stage later than that of Fig. 344. (*ggl*) Ganglia after mesad migration. Other designations as in Fig. 344. (Adapted from Heymons.)

distinct but thin and colorless cuticula forms over the body wall. On the lateral margin of the second maxilla a sclerotized egg tooth is developed by means of which the very brittle chorion is broken into equal parts, one hemisphere in part covering the anterior, the other the posterior half of the

embryo. The body is visible between the two halves. The embryo now undergoes its first molt, after which it assumes a horseshoe form, the head not quite touching the tail, the dorsal side directed outwardly, the body nearly cylindrical although somewhat thicker in the middle owing to the presence of the greater quantity of yolk. At this time the further development of the appendages and of the internal organs, later to be described, is taking place. A second molt then occurs with an increase in length but a decrease in diameter of the embryo, whose middle section is still more or less circular but with the anterior and posterior ends of the body already assuming their definitive flattened (depressed) form. This stage is still under the care of the mother whose body encircles the brood. The stage that is intermediate between the strictly embryonic and the free-living has been designated by Latzel as the "fetal stage." The young colorless fetus is helpless, nearly motionless, at most capable of creeping slowly over the body of the mother, and still dependent upon the yolk within it for sustenance. After a third molt the free-living centipede assumes its definitive shape and leaves its mother to forage for itself, the reproductive organs maturing during the succeeding instars.

Before the first molt has taken place, an epithelial thickening will be observed along the ventral margin of the anlagen of the sternites (Fig. 344, *ggl*). From this thickening an inwardly and medially directed proliferation of ganglion cells occurs. As development proceeds, the sternites of each segment are formed from the two lateral anlagen and from the *membrana ventralis*, the ganglion masses being carried mesad to unite into a single strand (Fig. 345). The contraction of the *membrana ventralis* causes its flat cells to become closely crowded, rounded cells. The tergites likewise are composed of three parts: the two lateral parts, anlagen of the tergites, and the median *membrana dorsalis*, the lines of demarcation of the three parts becoming obliterated. This obliteration, however, is a transitory condition, since later, before the first molt, a suture appears on each side of both tergite and sternite, the middle dorsal section owing its origin largely to the *membrana dorsalis*, the ventral to the *membrana ventralis*. In addition to the longitudinal sutures, a transverse suture is formed close to the anterior margin of each tergite; this suture, in general, outwardly marks the location of the dorsal longitudinal muscle insertions. Likewise before the first molt the tracheal invaginations are formed just above the base of the rudimentary appendages, where the integument will remain soft and flexible to form the pleural membrane (a derivative of the tergum).

Meanwhile at the anterior end the primitive preoral acron is joined by the forward migrating postoral preantennal and antennal segments. The unpaired clypeus is derived from the acron, the clypeus bearing the unpaired labrum on its anterior margin. The acron lacks a coelomic sac.

The preantennal and the antennal segments each have a pair of appendages, although the former with its appendages is evanescent, present only in the embryo. The clypeus and labrum soon occupy a ventral position; the dorsal part of the acron together with that part of the *membrana dorsalis* which belongs to the gnathal or jaw segments fuse into a plate known as the *lamina cephalica*. The remaining postoral segments of the head are the intercalary, the mandibular, and the first and the second maxillary segments, each with distinct coelomic sacs and, with the exception of the intercalary segment, with appendages also. The intercalary segment is apparent in the embryo only. The hypopharynx is developed from the sternite of the mandibular segment alone, the sternite of the first maxillary playing no part in its formation. The appendages that will develop on the first segment behind the head are the prehensile maxillipeds joined to a broad sternocoxal plate. Following the maxilliped segment are 21 rump segments, each bearing a pair of leg rudiments. The telson, bearing the anus, first develops in the form of a horseshoe but later becomes transversely oval. The coelomic sacs are lacking in it. Between it and the last leg-bearing segment is an interpolated segment which later divides transversely, forming the twenty-second and twenty-third rump or the twenty-ninth and thirtieth postoral segments which Heymons calls the "pregenital" and "genital" segments, respectively. Though small, they are typical metameres, each with a pair of coelomic sacs.

Derivatives of the Mesoderm.—The early differentiation and segmentation of the mesoderm have already been mentioned. The mesoderm lies in the form of two lateral bands with segmental swellings, inside which (toward the yolk) is the entoderm in the form of a sheet of flattened cells (Fig. 340A, *ent*), which lies not only in the region of the germ band but, in contrast to the mesoderm (*mes*), extends between blastoderm (Fig. 340B, *dm*) and yolk. Soon the greater number of mesoderm cells (*mes*) take on a cubical cylindrical form and attach themselves to the ectoderm; others, more flattened, lie near the entoderm, the former later forming the somatic, the latter the visceral wall. At first closely in contact with each other, these mesoderm cells later separate, leaving a cleft between them, the coelomic cavity. Six pairs of these sacs are developed in the head, a pair in the maxilliped segment, and a pair in each rump segment; only acron and telson lack them. At first the sacs are lenticular; but as soon as the buds of the appendages (*p*) appear, the somatic layer follows the evagination whereby the lumen of the sac increases in size (Fig. 346, *coel*), that of the antennae being largest. The coelomic sac of the preantennal segment likewise is large and sends forward a flat process into the preoral region (Fig. 347, *pren*). The coelomic cavity of the intercalary segment (*int*) is small and evanescent. Mesoderm not used in the formation of

the coelomic sacs at the anterior end surrounds the stomodaeal invagination and at first even covers its blind end. Some mesoderm also pushes into the labrum and into the clypeal region. In a similar manner at the posterior end residual mesoderm covers the proctodaeal invagination. In

FIG. 346.—*Scolopendra cingulata*. Cross section of rump segment. (coel) Coelomic sac. (dm) Membrana dorsalis. (ent) Entoderm cell. (p) Leg. (sin) Sinus. (splm) Splanchnic mesoderm. (ster) Sternite. (ter) Tergite. (vm) Membrana ventralis. (yc) Yolk cell. (Adapted from Heymons.)

addition to the median masses of mesoderm, isolated mesenchyme cells may be found along the median line.

After the rudiments of the appendages appear, each coelomic sac may be regarded as composed of three parts: the middle part whose cavity extends into the developing appendage, a mesad projecting flattened part with a cleft-like cavity lying under the anlage of the sternite, and a similar lateral part lying under the anlage of the tergite. Figure 346 represents

FIG. 347.—*Scolopendra cingulata*. Parasagittal section through head. Coelomic sacs of antennal (ant), intercalary (int), mandibular (md), first and second maxillary (mx), and preantennal (pren) segments. (bl) Blood cells. (ent) Entoderm. (Adapted from Heymons.)

a cross section, before the flexure of the germ band, showing these features. It will of course be understood that the definitive position in the rump segments of the middle part having the rudiment of the appendage will be lateral, the part under the anlage of the sternite will be ventral, and the part under the anlage of the tergite will be dorsal. In the early stages of

development these three parts of each of the coelomic sacs are not distinctly separated from each other, the visceral wall of each forming a common cover for all of them. Some cells of this visceral wall become free later to attach themselves to the entoderm epithelium (Fig. 348, *ent*)

FIG. 348.—*Scolopendra cingulata*. Cross section, left half. (*cbl*) Cardioblasts. (*coel*) Coelome. (*ent*) Entoderm cell. (*f*) Fat body. (*g.coel*) Genital coelome. (*mus*) Muscle. (*mst*) Middle strand. (*nc*) Nerve cord. (*splm*) Splanchnic mesoderm. (*st*) Stigmata. (*ster*) Sternite. (*yc*) Yolk cell. (Adapted from Heymons.)

where they multiply and form a thin cellular layer, the anlage of the mid-gut muscle layer (Fig. 348, *splm*). Dorsal and ventral longitudinal muscles arise by proliferation of cells from the somatic wall of the coelomic sacs of the rump segments, the dorsal above, the ventral below the rudiments of the appendages (Fig. 348, *mus*). In a similar manner the mesoderm which lines the appendages is the scene of proliferations and

small evaginations for the formation of the muscles of mouth parts and legs (Fig. 348, *mus*).

About the time that the flexure of the embryo occurs the yolk sac separates from the body wall at each lateroventral angle (Fig. 343, *sin*) forming a lateral blood sinus, which represents the first anlage of the definitive body cavity or schizocoel. The blood cells in the cavity come from mesoderm cells which some time before were observed on the median line between the coelomic sacs. At this time the coelomic sacs are located in a restricted space in and at the base of the appendages (Figs. 343, 346). Later the blood sinus becomes narrower but extends much further toward the dorsal side (Fig. 348). With the extension of the blood sinus the coelomic sac pushes dorsally and ventrally (*coel* 1, *coel* 2). At the same time the widely separated nerve ganglia move toward the ventral median line. The middle section of the coelomic sac no longer exists as such, having been wholly converted into leg muscles, dorsoventral muscle strands (Fig. 348, *mus*), fat (*f*), and mid-gut peritoneum. The dorsal and ventral stretching of the sac results in the lumen's becoming reduced and in the walls' becoming thin, the cells assuming a spindle-like character. At the dorsal junction of the visceral and somatic layers of the dorsolateral limb of the sac are the cardioblasts (*cbl*) which are destined to form the heart muscles. The dorsal limbs of the coelomic sacs near the cardioblasts, including their metameric arrangement and the septa between the coelomic cavities, are well preserved, although the ventral limbs of the sacs are in varying stages of modification. This dorsal portion may be designated as the genital region, for in it the germ cells will later be harbored. The splanchnic mesoderm has grown around the yolk (Fig. 348, *splm*) as a thin-walled sac, whose growth is independent of and more rapid than the dorsal and ventral growth of the coelomic sacs (Fig. 348, *coel*).

The cardioblasts (*cbl*), which are readily distinguishable from adjacent mesoderm cells by their larger size and their oval nuclei, form a longitudinal strand of cells extending from the eighth to the twenty-eighth metamere. In the anterior part from the antennal to the maxilliped segments, smaller, less sharply differentiated cells, which Heymons calls "vasoblasts," will form the aorta. The dorsal growth of the dorsal limb of the coelomic sac (*coel* 1) carries with it the crescent-shaped cardioblasts, which, meeting those from the opposite side, unite to form the heart, the space left between the horns of the crescents forming the lumen. The lumen of the heart is therefore not a part of the coelomic cavity. The heart itself is composed of two layers: the inner layer of transverse muscle fibers derived from the cardioblasts, the outer layer of longitudinal fibers derived from the smaller adjacent mesoderm cells. The heart valves are also derived from the cardioblasts and are approximately segmental in

position. In a manner similar to the formation of the aorta, the ventral blood vessel (epineural vessel) is formed; *i.e.*, mesally the ventral margins of the coelomic sacs unite, leaving a small canal between them. Thus the slender tubular blood vessel composed of contractile fibers is formed. The lateral transverse vessels, intersegmental in position, arise independently by the meeting of two adjacent coelomic sacs of the same side in the same manner as the formation of but not as evaginations from the epineural vessel.

The dorsal growth of the dorsal limb (Fig. 348, *coel* 1) of the coelomic sac which has carried the cardioblasts (*cbl*) into their definitive position

FIG. 349.—*Scolopendra*. Cross section (schematic). (*alm*) Heart wing muscle. (*dl*) Dorsal ligament. (*dr*) Dorsal nerve. (*ep*) Epidermis. (*f*) Fat. (*g.coel*) Genital coelome. (*h*) Heart. (*lm*) Longitudinal splanchnic muscle. (*mge*) Midgut epithelium. (*mus*) Muscle. (*pm*) Paricardial membrane. (*splm*) Splanchnic mesoderm. (*tp*) Tunica peritonealis. (*xl*) Transverse splanchnic muscle.

has brought the mediiodorsal parts of the sacs of the two sides into contact with each other in the form of a pair of contiguous flat tubes (Fig. 349, *g.coel*), constituting the genital anlagen. The somatic (dorsal) wall of this anlage is continued laterally in the somatic wall of the original coelomic sac, from which later cells are given off for the formation of the thin paricardial membrane (Fig. 349, *pm*). This membrane is split near the heart into two lamellae, the lower one fusing with the heart wall, the upper (dorsal) one continuing on the side of the heart and attaching itself to the dorsal body wall (Fig. 349), forming a dorsal ligament (*dl*). The visceral wall of the coelomic sac will form the muscles and the very thin peritoneum of the gut (Fig. 349, *tp*, *xl*, *lm*). Only a small part of the cells of the lateral somatic wall of the coelomic sac enters into the formation of the paricardial membrane; the remainder will give rise to the wing heart muscles (Fig. 349, *alm*). The wing heart muscles (*alm*) and the paricardial membrane (*pm*) together form the pericardial septum. Dorsad of this septum is the pericardial chamber in which the dorsal

longitudinal muscles (*mus*) are found. The intersegmentally arranged transverse ventral body muscles are developed from the somatic layer of the ventral limb of the coelomic sacs.

From the somatic walls of the coelomic sacs the fat bodies develop in the form of a narrow strand at the sides of the body (Fig. 348). This strand spreads out to occupy the greater share of the body cavity when the yolk has become reduced. "Fat-body" cells are also found in the space at the sides of the heart which later is bounded by the two lamellae of the pericardial membrane (Fig. 349, *pm*). These cells have sometimes been called "pericardial cells" and are of mesodermic origin.

Derivatives of the Ectoderm.—Ectodermal spiracular invaginations are in evidence soon after flexure of the germ band at the time when the anlagen of ectodermal glands and hypodermal invaginations for muscle attachments make their appearance. Nine pairs are developed in all,

FIG. 350.—*Scolopendra cingulata*. Cross section of a left leg. (*coel*) Coelomic sac. (*ggv*) Ganglionic pit. (*p*) Leg.

belonging to rump segments 3, 5, 8, 10, 12, 14, 16, 18, and 20. From the simple spiracular invaginations (Fig. 348, *st*) tubular branches arise which later develop as the primary tracheal trunks. At first one may distinguish an anteriorly and a posteriorly directed branch and a third somewhat smaller one which passes ventrad to the appendage. Later a number of tracheae are added so that finally a tuft of them arises from the bottom of the spiracular pocket. The first and last pairs of spiracular pockets send strong branches into head and tail end, respectively. Taenidial thickenings are first in evidence in the fetus.

The ventral nerve cord arises as a pair of widely separated longitudinal ectodermal thickenings several cell layers deep before the first molt has taken place (Fig. 344, *ggl*). Some of the superficial cells in this thickening sink more deeply into the epidermis (Fig. 350, *ggv*). Here a small shallow depression is formed which is located in the middle of each rump segment ventrad of the rudiment of the appendage. Heymons designated this depression as the "ganglion pit," since it represents the developmental center of the ganglion cells which line the pit. Mesad of and contiguous to the ganglion pits some superficial cells migrate more

deeply into the multilayered ectoderm to become the middle-strand nerve cells (Fig. 351, *mst*). (This section is taken tangent to the pit which therefore does not show.) The middle-strand nerve cells later form a band that connects with the *membrana ventralis* (Fig. 348, *mst*). The overgrowth of the ganglia by the epidermis, their separation from it, and the subsequent contraction of the middle-strand nerve-cell band result in bringing the right and left ganglion toward the median line where they

FIG. 351.—*Scolopendra cingulata*. Cross section of trunk, left half. (*mes*) Mesoderm. (*mst*) Median strand. (*p*) Leg. (*vm*) Membrana ventralis. (Adapted from Heymons.)

later fuse into a single ganglion (Figs. 348, 352, *ggv*, *mst*). Certain cells in contact with the ganglion cells laterally, which were drawn in with them, develop into the neurilemma. Before the median fusion of the ganglia, the neuropilar fibers form a continuous longitudinal strand without neuroglia cells. After the first molt and after fusion of the ganglia, neuroglia cells, probably originating from the middle cell strand, are interspersed. Thus the connectives arise. With the fusion of the

FIG. 352.—*Scolopendra dalmatica*. Cross section of anlage of a rump ganglion. (*bl*) Blood cell. (*coel*) Coelome. (*ep*) Epidermis. (*ggv*) Ganglion pit. (*mst*) Median strand. (*mus*) Muscle. (*n*) Nerve. (*neur. p*) Neuropile. (*sin*) Sinus. (*vbl*) Vasoblasts. (*vm*) Membrana ventralis. (Adapted from Heymons.)

ganglia along the median line the middle strand is enclosed, while fibers passing transversely from each ganglion unite with the fibers of the neuropile to form the commissures. These, however, are not sharply differentiated in *Scolopendra*. From the mesoderm a peritoneum is developed covering the entire nerve cord. Lateral nerves develop early from each ganglion, becoming elongated when the ganglia migrate toward the center line. The nerve cord, exclusive of the subesophageal ganglion, consists of

24 pairs of ganglia, the first belonging to the maxilliped segment, 21 to the rump segments, the last 2 to the pregenital and genital segments. The last two pairs of ganglia later fuse in one. Ganglia are not developed in the telson.

The supra-esophageal ganglion, or brain, is here considered as composed of three parts: the forebrain, or procerebrum (or protocerebrum in the broader sense); the midbrain, or deutocerebrum; and the hindbrain, or tritocerebrum. The procerebrum again may be divided into a preoral part which includes the archicerebrum, the *lamina dorsalis cerebri*, the frontal lobes, and the optic lobes; and a postoral part which includes the protocerebrum (in the strict sense) and belongs to the preantennal segment. The three ganglia of which the subesophageal ganglionic mass is composed develop in the same way as those of the rump segments, except that they form a compact body.

FIG. 353.—*Scolopendra cingulata*. Cross section of preoral part of germ band. (*arch*) Archicerebrum. (*ep*) Epidermis. (*mbp*) Median brain pit. (*mes*) Mesoderm. (*pp*) Proliferation pit. (*yc*) Yolk cell. (Adapted from Heymons.)

The development of the brain is more complicated than that of the subesophageal ganglion, four distinct anlagen entering into its composition. These are (1) an unpaired preoral anlage in the acron, the archicerebrum; (2) two pairs of preoral anlagen, the *lamina dorsalis cerebri* and the frontal lobes including the optic lobes; (3) a metameric pair of postoral ganglia in the preantennal segment, in the antennal segment, and in the intercalary segment (protocerebrum, deutocerebrum, and tritocerebrum); and (4) an unpaired preoral part of the visceral nervous system, the frontal ganglion. To the statement that the preantennal and antennal ganglia represent postoral somites Snodgrass (1938) offers the objection that it is not substantiated by external evidence of segmentation in the corresponding cephalic region of the embryo. The median archicerebrum (*arch*) is formed first, before there is any indication of the segmental ganglionic thickenings. Its anlage is formed in and restricted to the clypeal region, developing from ectodermal cells by delamination (Fig. 353, *arch*). Before delamination takes place, a shallow invagination (Fig. 353, *mbp*), or depression, is formed on each side of the archicerebrum, mesad and distinctly in front of the base of the preantennae.

These depressions are termed by Heymons the "median brain pits" and are analogous to the ganglion pits of the rump segments. Cells from these pits which later will join the archicerebrum take part in the formation of the dorsal cortex (*lamina dorsalis cerebri*) of the protocerebrum. About the time that the median brain pits begin producing ganglion cells, another brain pit ("lateral brain pit") is formed laterad of the first and in front of the preantennae. These will give rise to ganglion cells for the frontal lobes and probably also for the small optic lobes which lie on the lateral margins of the frontal lobes, the last mentioned but feebly marked in *Scolopendra*. Brain pits are also developed laterally on the preantennal, antennal, and intercalary segments. The ganglia-anlagen originating from these three pairs of pits are serially connected with the anlagen of the ganglia of the gnathal and rump segments. Even when the brain-pit capsules have become detached from the epidermis, they still continue to function in giving off ganglion cells. Later the archicerebrum and the adjacent ganglionic masses fuse so that their limits are no longer sharply marked. The ganglia of the preantennal segment form the broad connection between procerebrum and the deutocerebrum. Several nerves arise at the junction of procerebrum and deutocerebrum of which two, somewhat larger than the others, may be the preantennal nerves. The ganglia of the antennal segment form the large deutocerebral lobes, which originally were placed behind the procerebrum but later migrate forward. The ganglia of the intercalary segment form the halves of the tritocerebrum, lying ventrad of the deutocerebrum and later merge with this without sharply marked limits.

Scolopendra as well as some related chilopods lack well-defined transverse commissures. In fact the subesophageal commissure is completely wanting. In the brain there is a broad transverse neuropile mass which bridges the esophagus, but isolated commissures are not well-differentiated.

The visceral, or stomatogastric, nervous system becomes apparent shortly after flexure of the germ band. On the dorsal walls of the stomodaeum at the base of the labrum, differentiation of ectodermal cells takes place. These cells become free to form the frontal ganglion. When the ganglia of the intercalary segment are crowded dorsad by the developing head, these cells are pushed against and unite with the frontal ganglion. It is then no longer possible to say what part belongs to the tritocerebral lobes and what part to the frontal ganglion. The whole is now a united mass (Fig. 354, *fg*) whose median section certainly is derived from the frontal ganglion and which has been designated as the stomatogastric bridge. This bridge lies just dorsad of the esophagus and is closely united with the underside of the forebrain. Between bridge and forebrain is a foramen (Fig. 354) through which the aorta (*ao*), two

muscles, and a dorsal and ventral trachea pass. The recurrent nerve arising from the posterior end of the bridge owes its origin to ganglion cells which developed from the median dorsal wall of the stomodaeum where it remains under the muscle layer. At the time the cardioblasts meet on the middorsal line, small cells are liberated from the ectoderm immediately above the heart to form a nerve that later attaches itself to the heart (Fig. 349, *dr*). This nerve is formed independent of either the central nervous or the visceral systems.

The Tömösvarý sense organs connected with the brain and located in the head have been described for *Scolopendra*, *Glomeris*, *Lithobius*, and

FIG. 354.—*Scolopendra cingulata*. Cross section of foetal head. (*ao*) Aorta. (*fg*) Neuropile of frontal ganglion. (*ggl*) Ganglion cells. (*md*) Mandible. (*mus*) Muscle. (*neur. pl*) Neuropile of deutocerebrum. (*neur. p2*) Neuropile of frontal lobe. (*op. n*) Optic nerve. (*töm*) Tömösvarý organ. (*töm. n*) Tömösvarý nerve. (Adapted from Heymons.)

other myriapod genera. In *Scolopendra* the organ is closely associated with the development of the frontal lobes of the forebrain. Near the frontal lobes, which owe their origin to the lateral brain pits, there is an inward migration of some cells that closely resemble those of the frontal lobes and that remain attached to the epidermis for a time. These cells represent the anlage of the Tömösvarý organ. As development proceeds, the organ loses its connection with the surface but retains its connection with the frontal lobe by means of a string of cells. This string becomes the Tömösvarý nerve which joins the brain at the junction of the optic and frontal lobes (Fig. 354, *töm. n*). The function of these organs is unknown.

The anlagen of the four pairs of eyes (stemmata) appear dorsad and somewhat behind the insertion of the antennae. At the place where they are to be formed the nuclei of the epidermal cells assume a basal position and lie in a single plane. The cells around the margin of each eye merge gradually into the adjacent epidermal cells.

Below the base of the cells that are to form the retinal and the nerve-fiber cells (Fig. 355, *rt*) flattened cells (*en. c*) appear from which the envelope cells will arise. The delicate radiating plasma processes (*rbd*) of the retinal cells develop into the visual rods. The cells that are mingled with the plasma-process bearing retinal cells now draw down in contact with the eye-envelope cells and become fusiform nerve fibers. Thus the undifferentiated cells marked "*rt*" in Fig. 355 differentiate into retinal and nerve-fiber cells. The optic nerve appears to originate from a prominence (*op. n*) at the proximal end of the eye anlage, the nerve therefore growing inward to meet the optic lobe rather than growing outward from it. The optic lobe and the eye recede from each other,

FIG. 355.—*Scolopendra cingulata*. Section through anlage of eye. (*bl*) Blood cell. (*bsm*) Basement membrane. (*cut*) Cuticula. (*ect*) Ectoderm. (*en. c*) Envelope cell. (*gglc*) Ganglion cell. (*lt*) Lentigene cell. (*op. n*) Proximal end of optic nerve. (*pr. gglc*) Proliferation center of optic ganglion. (*rbd*) Rhabdome. (*rt*) Retinal cell. (Adapted from Heymons.)

but the connection between them remains. When the embryo enters the so-called "fetal stage," having shed the chorion and thrown off the embryonic cuticula, the first pigment granules may be seen. Soon the corneagene (lentigene) cells, which surround the periphery of the eye (*lt*), grow over the eye surface and proceed to secrete a delicate cuticula, which is continuous with that of the adjacent body wall. The subsequent development of the eye is postembryonic and may be briefly described as follows: Fig. 356 represents the eye of an adult centipede. Before a molt takes place, the corneagene cells (*lt*), which normally form iris-like under the cornea, close up the "pupil" by cell division and then secrete a new cuticular lens, after which the central cells apparently degenerate to be developed again by the peripheral corneagene cells just preceding another molt. By this process the cornea is constructed. The retinal cells consist of an elongate cone-like inwardly directed part (visual rod) and a nucleated outwardly directed part. The visual rod

represents the light-sensitive part; the basal portion of the retinal cells, the connection with the optic-nerve neurons surrounding the eye bulb.

The Dorsal Organ.—About the time that the germ band flexes, a crescent-shaped thickening appears in the ectodermal *membrana dorsalis*

FIG. 356.—*Scolopendra dalmatica*. Section of eye of adult. (cut) Cuticula. (ect) Ectoderm. (lt) Lentigene cells. (op. n) Optic nerve. (rbd) Rhabdome. (Adapted from Heymons.)

FIG. 357.—*Scolopendra dalmatica*. Cross section. (bl) Blood cell. (cbl) Cardioblast. (ent) Entoderm. (g. coel) Genital coelome. (h) Heart. (splm) Splanchnic mesoderm. (Adapted from Heymons.)

a short distance in front of the head, the concave side proximad. This is the dorsal organ made up of several layers of cells. After a time the cells of the organ, except for the outmost layer, begin to degenerate. Numerous entodermal cells gather below it, and they, together with an occasional yolk cell, without doubt absorb the degeneration products.

The organ is in all probability homologous with the dorsal organ of the apterygotes. Its function is problematical.

The Reproductive Organs.—The dorsal extensions of the coelomic sacs remain intact as a pair of contiguous, flattened, longitudinally chambered genital tubes below the heart (Fig. 357, *g. coel*). More room is provided for the development of the parts lying above by the reduction in the diameter of the mid-gut because of the diminution of the yolk within, the genital tubes becoming circular in cross section (Fig. 358, *g. coel*). As development proceeds, single cells with larger nuclei and more abundant cytoplasm may be observed in the genital anlagen, or gonads. These cells are germ cells as well as cells that will be future follicular epithelium.

FIG. 358.—*Scolopendra cingulata*. Cross section of late embryo. (*bl*) Blood cell. (*ent*) Entoderm. (*ep*) Epidermis. (*g.coel*) Genital coelome. (*n*) Dorsal nerve. (*pc*) Pericardial cell (pericardial fat cells not yet distinguishable from these). (*pm*) Pericardial membrane. (*spltm*) Splanchnic mesoderm. (*y*) Yolk. (Adapted from Heymons.)

It is a characteristic that, with those insects in which germ cells are recognizable at an early stage, they form as a mass at the posterior end of the egg or of the germ band and then wander or are pushed forward into the middle or anterior abdominal region where they undergo further development. In *Scolopendra*, at the posterior end of the germ disk, a mass of cells likewise appears, which, though not yet recognizably differentiated, later migrate forward to be eventually enclosed in the epithelial layer of the coelomic sacs. These cells then find a place especially on the ventral and mesal walls of the genital tubes. The mesal walls of the two contiguous tubes as well as the division walls of the longitudinally placed chambers break down, resulting in the formation of a single elongated median gonad, which is outwardly clothed with a muscular layer and inwardly lined with regularly arranged, genital epithelial cells.

At an earlier stage in both pregenital and genital segments, as in the rump segments, the coelomic sacs in large part lie in the evaginations of the rudiments of the appendages. Later they are drawn more and more into the body cavity where one may distinguish their thickened somatic and the much thinner visceral walls. Muscles develop from the somatic walls, while the visceral wall divides the coelomic sac from the large, now yolk-free body cavity of the pregenital and genital segments. The large coelomic sacs of these segments are contiguous on the middorsal line (Fig. 359), but ventrally they reach only the margin of the nerve cord. After the separation of the muscle anlagen the somatic walls have also become thin. At the lower ends of the sacs four diverticula (Fig. 359, *amp*) are given off: two for the pregenital and two for the genital segment.

FIG. 359.—*Scolopendra cingulata*. Cross section of genital segment. (*amp*) Genital ampulla. (*g. coel*) Genital coelome. (*ggl*) Ganglion. (*h*) Heart. (*mus*) Muscle. (*pm*) Pericardial membrane. (Adapted from Heymons.)

These diverticula, which we may call “genital ampullae,” are the remains of the coelomic cavities that extended into the rudimentary appendages of the corresponding segments. The breaking down of the walls between the two sacs on each side and then of the median wall gives rise to a single large thin-walled sac, or genital sinus. The single dorsal genital sinus is produced ventrally into two sac-like shanks which are in communication with the ampullae. The wall between the genital sinus and the tubular gonad now also breaks down, establishing continuity. The genital sinus with its shanks then becomes more constricted and inconspicuous, the latter becoming tubular canals (ducts) connecting dorsally with the gonad and ventrally ending in the ampullae. Toward the end of the embryonic period the caudal end of the gonad (genital tube) passes over on the right side of the alimentary canal finally to assume a ventral position. In consequence of this shift of position the ducts noted above are much affected. The right duct remains relatively large and thick

to become the definitive genital duct. The left duct, on the other hand, is stretched over the dorsal side of the alimentary canal, forming a slender transverse arch.

The connection between the mesodermal and ectodermal parts of the reproductive organs is established during postembryonic life. After the rupture of the chorion the pregenital and the genital segments telescope more or less into the preceding rump segments of the young fetus. The sternite of the twenty-third segment (genital segment) becomes modified into two small lateral processes which may be called the "genital lobes." The two-lobed genital sternite in the female is fully telescoped into the body so that between it and the sternite of the twenty-second segment (pregenital segment) a deep chamber, or pocket, is formed which Heymons designated as the "genital atrium." It is lined with the ectodermal conjunctiva of the two sternites. In the male a similar invagination occurs, but here the lobes of the genital sternite are longer and more slender and not wholly retracted into the atrium. Consequently the atrium is smaller. Furthermore, in the male a small median invagination is formed between the lobes of the genital sternite which will develop into the ejaculatory duct. At this time, also, two pairs of ectodermal glands are formed in both sexes. In the female the anterior pair of gland rudiments retracted into the atrium will form the receptacula seminis (spermatheca); the posterior pair which opens between the lobes of the genital sternite will form the accessory glands. Homologous glands are also developed in the male.

A free communication between the mesodermal genital ducts and the atrium is not established until the free-living stage is reached. In the female the two ampullae of the twenty-third segment (genital segment), which mark the extremities of the two future genital ducts (left one non-functional) and which lie in contact with the blind anterior end of the atrium, fuse below the alimentary canal into a single chamber, and soon thereafter the union of atrium and ampullae takes place. The ampullae of the pregenital segment at this time gradually contract, shorten, and soon are no longer apparent. Finally a cuticula lines the entire atrium and covers the lobes of the genital sternite.

In the male the development follows a similar course, except that the posterior pair of ampullae, instead of uniting with the atrium, fuse with each other and then unite with the invagination which is to form the ejaculatory duct. As with the female, the left primary genital duct becomes nonfunctional; but whereas in the female it becomes a slender duct, in the male it is more or less distended, sac-like. This sac has formerly been considered the seminal vesicle, but Heymons states that it does not contain spermatozoa. The paired lobes derived from the twenty-third sternite doubtless represent the intromittent organ.

The Alimentary Canal.—The origin of the entodermal cells has already been mentioned. They form a thin layer on the ventral side of the egg immediately outside the yolk (Figs. 340A, 346, *ent*). This layer spreads, apparently by a process of stretching, over the entire yolk as a thin-walled sac before the formation of the individual coelomic sacs. The yolk cells (trophocytes, or vitellogophs) are similar to entoderm cells in physiological and morphological characters, the nuclei being usually larger, often irregular in shape, with one or more nucleoli. The yolk

FIG. 360.—*Scolopendra cingulata*. Sagittal section of the stomodaeum. (*br*) Brain. (*fg*) Anlage of frontal ganglion. (*lr*) Labrum. (*mus*) Muscle. (*rn*) Recurrent nerve. (*sin*) Sinus. (Adapted from Heymons.)

cells in the egg center break down by the time segmentation of the germ band is completed, and soon thereafter the yolk pyramids also disintegrate, the yolk being reduced to a homogeneous mass by the time the lateral halves of the germ band separate from each other (Fig. 341A). By this time or soon afterward the yolk cells become more uniformly distributed through the yolk (Fig. 348) and are then characterized by their much larger nuclei, preliminary to their degeneration. The entodermal cells, which now form a sac-like layer around the yolk, take over the function of reducing the yolk. Meanwhile the stomodaeum and procodaeum have formed as simple sac-like invaginations (Fig. 360), the former arising shortly before the latter. The dorsal wall of the stomo-

daeum (Fig. 360) will give rise to the stomatogastric nervous system, hence is thicker than the ventral wall. The mesoderm (*mus*) of the stomodaeum arises in large part from cells that were present in the median line in the region of the mouth, that of the proctodaeum from the mesoderm cells of the telson. The coelomic sacs apparently do not contribute to the formation of muscles of either stomodaeum or proctodaeum. The ectodermal cellular layer at the blind ends of both invaginations by this time has become very thin (Fig. 361, *lm*). Two diverticulae are formed at the blind end of the proctodaeum which represent the anlagen of the Malpighian tubules. Although the entoderm (Fig. 361) elsewhere forms a layer of flattened cells, in the periphery of the blind end of the proctodaeum they are more or less columnar. In the first embryonic stage,

FIG. 361.—*Scolopendra cingulata*. Sagittal section of proctodaeum. (*bl*) Blood cell. (*ent*) Entoderm. (*lm*) Limiting membrane of proctodaeum. (*mus*) Muscle layer. (*tel*) Telson. (Adapted from Heymons.)

before the first molt, both stomodaeum and proctodaeum as well as the two Malpighian tubules become elongated. At this time also the entodermal cells begin to feed on the adjacent yolk, thereby changing in shape from flattened cells into deep, vacuolated cells (Figs. 357, 358, *ent*) in which fat and yolk droplets may be detected. The absorption of yolk is apparently correlated with the rapid growth of the embryo at this stage. After the first molt the yolk cells still remaining in the yolk begin to disappear. The rupture of the blind ends of stomodaeum and proctodaeum and the formation of an intima take place during the post-embryonic period. During this period also the sac-like mid-gut becomes materially constricted, a condition brought about by the elimination of numerous cells of the entodermal epithelium into the lumen of the gut.

As outlined above, the first developmental period extends from the time of cleavage to the formation of the germ layers. The second includes the time of segmentation until the first appearance of the rudi-

ments of the appendages. The third period may be divided into three parts: (1) the truly embryonic, until the first ecdysis and the rupture of the chorion; (2) the first fetal or first postembryonic stage, ending in the second ecdysis; and (3) the second fetal or transition stage, when the body elongates and possesses spontaneous movement. In the fourth, or adolescent, period there are several molts, ending with the maturing of the sex organs.

In essential features the structure and development of the heart of *Lithobius forficatus* as described by Biegel (1922) resemble that of *Scolopendra*. The aorta, however, is not differentiated, and the aortic arches are lacking. In place of them a large head blood sinus functions. Lateral transverse vessels likewise are replaced by a segmentally arranged system of blood lacunae. Above the heart is a small dorsal heart sinus. Instead of the asymmetrically ending genital duct, in *Lithobius forficatus* both right and left ducts are functional.

FIG. 362.—*Platyrrhacus amauros*. Germ disk before flexure. (a) Anus. (ant) Antenna. (md) Mandible. (mx) Maxilla. (prz) Proliferation zone. (From Pflugfelder.)

DIPLOPODA, THE MILLEPEDES

Platyrrhacus amauros Attems

This species is found in the decaying wood of the coco palm and other plants on the island of Amboina (Moluccas). The eggs, which are laid in loose clumps of 60 to 80 in mulch, measure about 1 mm. in diameter, are rich in yolk, and hatch in about 19 days. According to Pflugfelder (1932), the cleavage nuclei surrounded by a thin layer of cytoplasm and more or less connected with each other by cytoplasmic strands migrate to the periphery where they undergo further division to form a blastoderm of flattened cells. A few yolk cells remain behind in the yolk. More active division of the cells on the future ventral half of the egg causes crowding and consequent deepening of the individual cells. The area of deep cells is elliptical in outline and constitutes the germ band, or disk.

A primary division of the disk gives rise to a head and a tail region between which there is an unsegmented middle section. Shortly following this, further segmentation, first of the head and thorax and finally of the abdomen, takes place. The germ disk (Fig. 362) now consists of protocerebral and deutocerebral segments still united on the lateral

margins, antennal, mandibular, maxillary, postmaxillary (second maxillary), and three double thoracic segments. Pflugfelder (1932) suggests that the clypeus anlage may represent the preantennal segment, since it later contains a coelomic sac. The preoral part is double, as indicated by the presence of two pairs of coelomic sacs, but the division does not extend to the lateral margins. Likewise, each thoracic segment is double, as indicated by the presence of two pairs of coelomic sacs, although there is but one pair of legs.

FIG. 363.—*Platyrhacus amauros*. Longitudinal section of gut. (ent) Entoderm cell. (lu) Lumen of gut. (mes) Mesoderm. (stom) Stomodaeum. (y) Yolk. (From Pflugfelder.)

At the time when segmentation of the body begins, it will be observed that active proliferation of cells takes place at the point where the future stomodaeum will form. These are the entoderm cells. Cells liberated here migrate toward the posterior pole. The cells at the seat of proliferation become fewer and leave an opening at the surface that projects itself into the proliferating cell mass to form a lumen (Fig. 363, *lu*). The migrating cells are at first fusiform, then acquire large nuclei with large nucleoli and relatively little chromatin material. Their plasma develops long anastomosing processes which may entangle yolk globules, which, however, are not found in the lumen. Gastrulation thus proceeds from a polar migration accompanied by an invagination. After a certain time when migrations of the entoderm cells cease, invaginations of the ectoderm at the anterior and posterior poles occur, establishing the stomodaeum and proctodaeum. The lengthening of these parts crowds the entoderm

cells together. These cells then arrange themselves in epithelial fashion and become enlarged and vacuolated (Fig. 364, *ent*). The musculature of the gut is derived from the mesoderm which surrounds the base of the

FIG. 364.—*Platyrhacus amauros*. Longitudinal section at junction between fore- and mid-gut. (*ect*) Ectoderm. (*ent*) Entoderm. (*mes 1*, *mes 2*) Outer and inner mesoderm layers. (From Pflugfelder.)

stomodaeal invagination (Fig. 363, *mes*). With the lengthening of the invagination the mesoderm is carried further inward (Fig. 364, *mes*), forming a provisional connection between fore- and mid-gut. This connection of mesoderm divides into two lamellae which give rise to an outer longitudinal muscle-fiber layer and an inner circular muscle-fiber layer (Fig. 364, *mes 1* and *mes 2*).

At the time when segmentation takes place, cell proliferation begins at the incisures; the cells wander out of the blastoderm and gather in loose mesenchyme masses on the segments.

These masses become more compact and form the mesodermic coelomic sacs (Fig. 365, *mes*). This process of mesoderm formation begins with the clypeus, where a coelomic sac is formed, and proceeds both forward and backward corresponding to the body segmentation, with coelomic sacs forming in the preoral region

FIG. 365.—*Platyrhacus amauros*. Longitudinal section of thoracic "double segment." (*mes*) Mesoderm. (*mes. c*) Center of mesoderm proliferation. (*v*) Vitellophag. (From Pflugfelder.)

and in the mandibular, maxillary, postmaxillary, and the following segments. As appendages appear, the sacs push into these evaginations, forming outwardly a close union with the ectoderm. The walls of the

sacs will form muscles for the most part, but part of the inner walls assumes a mesenchyme character.

The anlagen of proto- and deutocerebrum arise from cells on the sides of the preoral segment which by active radial division form cup-like

FIG. 366.—*Platyrrhacus amauros*. Longitudinal section of the brain. (*bsm*) Basement membrane. (*deut*) Deutocerebrum. (*nf*) Nerve fibrillae. (*prot*) Protocerebrum. (From Pflugfelder.)

FIG. 367.—*Platyrrhacus amauros*. Longitudinal section of germ band after flexure. (*ch*) Chorion. (*cly*) Clypeus. (*deut*) Deutocerebrum. (*ggl 1,4*) Ganglion of segments 1, 4. (*ggl.mx 1, mx 2*) Ganglia of maxillary segments. (*md*) Mandible. (*mes*) Mesoderm. (*mesc*) Proliferation zone of mesoderm. (*mx*) Maxillae. (*prot*) Protocerebrum. (*prz*) Proliferation zone. (*tel*) Telson. (From Pflugfelder.)

structures (Figs. 366, 367, *deut*, *prot*) whose bases later join. Cells adjacent to the deeply infolded basal membrane (*bsm*) then form the nerve fibrillae (Fig. 366, *nf*). The cup-like depressions disappear during

the molt at the beginning of the second postembryonic developmental period. Consequently the two pairs of ganglia by the constriction of the necks of the depression lose their connection with the ectoderm of the future body wall. The nerve connection between antennae and deutocerebrum is early established. Pflugfelder (1932) states that he made no observations on the origin of the tritocerebrum, a part that is poorly developed in the Myriapoda generally. The ganglia of the ventral nerve cord arise in the same manner as the brain lobes with the formation of cup-like invaginations of the ectoderm which are later cut off from the surface. Of these there is a pair for the antennal, mandibular, maxillary, and postmaxillary segments and two pairs for each of the following segments.

FIG. 368.—*Platyrrhacus amauros*. Germ band in surface view after flexure. (ant) Antenna. (cly) Clypeus. (tel) Telson. (From Pflugfelder.)

Blastokinesis, or flexure of the embryo during development, occurs by the folding in of the embryo into the yolk, the bend occurring at about the second maxillary segment leaving only clypeus and telson exposed at the surface (Fig. 368).

With blastokinesis modifications in certain structures are mechanically brought about. The postmaxillary segment (second maxillary) is relatively small, and earlier writers maintained that the appendages were lacking. Pflugfelder has shown that the appendages, though small, are present. They are closer together than the appendages of the maxillae so that when blastokinesis takes place the former are pushed between the latter, where they later fuse into a single structure, the gnathochilarium. The sternite of the second maxillary segment forms the gula (hypostoma of Latzel); the tergite forms the collum, which accordingly is a part of the head although not fused with the preceding parts.

Before the rupture of the chorion the embryo molts, although the skin still remains around it. This molt may be regarded as the beginning of the postembryonic period, since it is accompanied by an increase in the number of abdominal appendages, despite the fact that the chorion has not yet been shed.

Julus terrestris Leach

Heathcote (1886) states that in *Julus terrestris* the yolk forms early into yolk spherules which are present up to a very late stage of develop-

ment. Cleavage nuclei appear at the surface of the egg and by further division form a blastoderm of flattened cells. Thus cleavage is purely superficial. Connected with the blastoderm cells by protoplasmic processes are cells that have remained behind in the yolk. Of these, some will form the somatic and splanchnic mesoderm; others will form the mid-gut epithelium; and still others, after the mid-gut epithelium is formed, give rise to other mesoderm cells to form various muscles and the circulatory system. The amoeboid-like cells which are to enter into formation of the mesoderm approach the future ventral surface of the egg where they gather to form a longitudinal strip along the mid-ventral line. Here they become more compact with rounded nuclei. These cells by subsequent division together with cells derived from the ectoderm ectad of them soon form a longitudinal strip several layers in thickness. This strip later spreads out and becomes segmented. The somites are solid at first, but later a cavity appears in them. Early on the ninth day the stomodaeal invagination is evident, with the proctodaeum appearing soon after. The entoderm cells are still scattered within the yolk, but they gradually become collected on the median line just entad of the mesoderm. The stomodaeum and proctodaeum become more deeply invaginated, extending a considerable distance into the yolk; and at the same time the entoderm cells, loosely connected, begin to form the mid-gut epithelium, arranging themselves around a central lumen. At the end of the ninth day the embryo is long and oval in shape; the mesoderm is divided into eight segments, the first of which will form the future head; and the mid-gut epithelium is almost fully formed.

The tenth day brings about the completion of the ectodermal segmentation, the formation of the nervous system, and the formation of the ventral flexure, the mesodermal somites acquiring cavities with the embryo assuming its definitive shape. The ventral flexure is first formed by a deepening of the transverse furrow which forms the division between the seventh and eighth segments (Fig. 369); the head and tail ends nearly touch. The eighth segment is considerably longer than any of the others except the head. Even on the eleventh and twelfth days, the tissues of this segment are still imperfectly differentiated. At a later period of development the anal segment is constricted off from the eighth segment, and from its anterior part the future segments formed in later life are developed. Just before the first appearance of the ventral flexure when the body segments are fully formed, the embryo develops a cuticular envelope over the whole surface which separates from the body.

Of the nervous system the bilobed cerebral parts are formed first, followed by nerve cords which develop progressively backward. The cords are at first widely separated but connected by a thin median por-

tion. Later they closely approach each other and are completely separated from the ectoderm. On the eleventh day a second molt occurs.

Within the yolk, which still is present in great quantity in the body cavity, there are present a number of cells remaining over after the formation of the mesodermic median layer and the mid-gut epithelium. These cells eventually give rise to the circulatory system and to the muscles of the segments. The Malpighian tubules grow out of the proctodaeum on the twelfth day. Later on in the day the animal hatches with only the rudiments of its appendages present.

FIG. 369.—*Julius terrestris*. Longitudinal section of 11-day-old embryo. (*br*) Brain. (*ent*) Entoderm. (*ggl*) Ganglion. (*mes*) Mesoderm. (*n*) Nerve. (*stom*) Stomodaeum. (From Heathcote.)

Polydesmus abchasius Attems

The little oval egg of this species, which is scarcely 0.3 mm. long, was collected in the Black Sea region of the Caucasus. The egg undergoes total, equal cleavage (Fig. 370), as is the case with the species of the genera *Julus* (*Schizophyllum*), *Strongyloma*, and *Polydesmus* (*Polyxenus*) observed by Metschnikoff (1874). In the earlier stages of segmentation, as described by Lignau (1911), some cleavage cells return into the yolk, so that when there are about 50 peripheral blastomeres there are from 4 to 7 in the yolk. Hereupon, by reason of the migration of the nucleated protoplasmic masses which are forced to the periphery, the segmented structure of the egg is no longer evident. Here by further division they

soon cover the entire surface. Cells remaining within the yolk multiply until up to 275 may be observed. These are the vitellophags. This behavior is contrary to the observations of Silvestri (1898) on *Pachyiulus*, where but few vitellophags remain in the yolk.

On the fifth day of incubation the germ disk develops on the ventral side of the egg in the form of paired sets of thickenings connected by a longitudinal median swelling. An inner layer divided on the median line then forms. Next there may be observed a two-lobed head, three intermediate segments, and a diffuse tailpiece which passes over the posterior pole. At first the germ disk gradually merges into the dorsal, thinner part of the blastoderm, but later it becomes sharply delimited. At the point where the median thickening joins the head segment a thicker area is evident. Here a slight depression forms which later becomes the stomodaeum. The germ disk now elongates into a germ band, which at its period of greatest elongation passes three-fourths around the greater diameter of the egg. The germ band also increases in width. The number of segments then increases, the new metameres first appearing by division of the head segment to form the antennal segment. This is followed by the formation of maxillary, postmaxillary, and three rump segments, each bearing later a pair of leg rudiments. Although Lignau states that the part known as the "collar" is the tergite of the first rump segment, Pflugfelder (1932), Heymons, and Silvestri maintain that it represents the tergite of the postmaxillary (labial) segment.

Both the older and more recent workers are in agreement that the mid-gut epithelium arises from a loosely formed strand of cells, first solid but later with a lumen, extending through (not surrounding) the yolk. Cholodkowsky (1895) states that this strand arises from anterior and posterior entoderm rudiments which elongate and later fuse in the middle. Lignau, however, says that the strand originates from an anterior entoderm rudiment which elongates, pushes posteriorly in contact with the blastoderm, and later separates from it. The ectodermal, stomodaeal, and proctodaeal invaginations later unite with the entodermal strand, then contract, straightening the line and thereby drawing the thus completed alimentary canal into the yolk lying dorsad of it.

FIG. 370.—*Polydesmus abchasius*. Lateral aspect of an egg containing about fifty peripheral blastomeres. (From Lignau.)

REMARKS ON DIPLOPODA IN GENERAL

Silvestri (1898) and Robinson (1907) maintain that the postantennal or premandibular intercalary segment is present in the Diplopoda,

although opinions on this are divided. Pflugfelder (1932) failed to demonstrate it in *Platyrhacus*.

The first three rump segments, which correspond to the thorax of insects, each bear but a single pair of legs; in later (postembryonic) development the remaining rump segments have two pairs each. In *Platyrhacus*, however, Pflugfelder has shown that two pairs of coelomic sacs and two ganglia are formed in each of the first three segments, indicating their double nature despite their single pair of legs. The double segmentation may be a secondary adaptation.

During postembryonic development an invagination appears on each side of the fifth rump segment of the six-legged larva where the repugnatorial glands are to appear. Later, with the increase in number of segments, additional glands will arise, but a single pair only for each segment. They are lacking on the "thoracic segments."

The singular formation of the mid-gut epithelium as a strand of cells passing through, not surrounding, the yolk is a characteristic of the Diplopoda noted by both the earlier and later writers. The yolk lies in and fills the body cavity, so that the nervous system as well as the alimentary canal is surrounded by yolk.

The young animal on emerging from the chorion is a helpless six-legged creature, and only after another molt does it become active. In rare cases, as in *Polygonium germanicum*, there is present a fourth pair of legs, belonging to the first abdominal segment. In general, one or more pairs of legs are added with successive molts during adolescence.

SYMPHYLA, THE SYMPHYLIDS

Hanseniella sp.

Tiegs (1939) has found that in *Hanseniella*, a genus of the class Symphyla, the cleavage is total, as in Collembola and in some diplopods. By tangential division of the large yolk pyramids, an outer layer of small cells and an inner layer of very large cells arise, both rich in yolk. From the former the blastoderm develops. From the latter arises by further division the internal mass of yolk cells. These are not pure vitellophags, however, for from them the fat-body and the mid-gut epithelium develop.

An embryonic area forms by ventral thickening of the blastoderm. A precocious flexure then forms in the embryonic area, as in some diplopods, and thereby the germ band becomes defined. A dorsal organ is present, but embryonic membranes are lacking. The mesoderm arises by bilateral separation of cells from the germ band. Segmentation of the mesoderm into somites synchronizes roughly with external segmentation of the germ band. In the head there is no external sign of segmentation. Behind the labium are formed seven leg-bearing segments,

followed by a preanal segment, the appendages of which are the cerci. On the anal segment appendages are vestigial.

In the head, six pairs of coelomic sacs are formed, and in the abdomen each segment is provided with a single pair. The antennary and pre-antennary coelomic sacs together form the aorta. The coelomic sacs, from the mandibular segment backwards, grow through the yolk cells, enclosing part of these as mid-gut epithelium; they all furnish cardioblasts for the heart. The premandibular coelomic sac gives rise to a large excretory gland which degenerates at the time of eclosion; in association with it is a clump of nephrocytes, perhaps homologous with the sub-esophageal bodies of insects. The salivary gland is a remnant of the maxillary coelomic sac.

The genital tubes arise by concrescence of the vestiges of the coelomic sacs from the fourth abdominal to the preanal segments. Vestigial coelomoducts survive in the preanal segment until after eclosion.

The ganglia of the nervous system develop in association with "ventral organs" as in *Peripatus*. From the remnants of these organs the eversible sacs arise.

References

ONYCHOPHORA: (Included here for convenience) Bouvier (1905). *Euperipatus weldoni*: Evans (1902). *Peripatus* sp.; Balfour (1883), Ryder (1886a), Willey (1898). *P. capensis*; King (1926), Mosely (1874), Sedgwick (1885-1888). *P. edwardsi*; Kennel (1886). *P. imthurmi*; Sclater (1886). *P. novae-zealandica*; Sheldon (1887). *P. torquatus*; Kennel (1886).

CHILOPODA: Heymons (1898b); Verhoeff (1925). *Geophilus* sp.; Balbiani (1883), Leydig (1889), Metschnikoff (1874). *G. ferrugineus*; Zograf (1882, 1884). *G. proximus*; Zograf (1882, 1884). *Lithobius* sp.; Leydig (1889). *L. forficatus*; Biegel (1922). *Scolopendra* sp.; Heymons (1898a), Nath and Husain (1926). *S. cingulata*; Heymons (1901). *S. dalmatica*; Heymons (1901).

DIPLOPODA: Cholodkowsky (1895). *Craspedosoma* sp.; Stecker (1877). *Glomeris* sp.; Heymons (1897d), Stuhlman (1886). *Julus* sp.; Stecker (1877), Stuhlman (1886). *J. moreletti*; Metschnikoff (1874). *J. terrestris*; Heathcote (1886), Newport (1841). *Pachyiulus communis*; Silvestri (1898). *Platyrhacus amauros*; Pflugfelder (1932). *Polydesmus* sp.; Stecker (1877). *P. abchasius*; Lignau (1911, 1912). *P. complanatus*; Metschnikoff (1874). *Polyxenus lagurus*; Metschnikoff (1874). *Strongylosoma* sp.; Stecker (1877). *S. guerini*; Metschnikoff (1874).

PAUROPODA: *Pauropus amicus*; Harrison (1915).

SYMPHYLA: *Hanseniella* sp.; Tiegs (1939).

BIBLIOGRAPHY

- Articles that have not been examined by the writers are marked with an asterisk.
- *ACQUA, C.: Sulle diverse particolarità dello sviluppo dell' uovo di *Bombyx mori* sotto l'influenza di agenti bivoltenizzanti. *Boll. staz. sper. gelsicolt. Ascoli Piceno*. **11**: 142-143. 1932.
- AHRENS, W.: Die Entwicklung des "Corpus luteum" bei den Insekten. Nach Untersuchungen an *Termes redemanni*. *Zeitschr. mikrosk. anat. Forsch.* **37**: 467-500. 1935.
- *ASHBEL: *Carausius morosus* (Orth.), parallelism between gas exchanges and embryonic development. *Boll. soc. ital. bol. sper.* **6**: 663-669. 1931.
- AUTEN, M.: The early embryological development of *Phormia regina*. Diptera. *Ann. Entomol. Soc. Amer.* **27**: 481-506. 1934.
- AYERS, H.: On the development of *Oecanthus niveus* and its parasite, *Teleas*. *Mem. Boston Soc. Natural Hist.* **3**: 225-281. 1884.
- BADEN, V.: Embryology of the nervous system in the grasshopper, *Melanoplus differentialis*. *Jour. Morphology*. **60**: 159-190. 1936.
- : Origin and fate of the median cord in the grasshopper, *Melanoplus differentialis*. *Jour. Morphology*. **63**: 219-223. 1937.
- BAKER, A. C.: The practical significance of the revolution of the embryo in aphid eggs. *Science*. **54**: 133-135. 1921.
- BALBIANI, E. G.: Sur la reproduction et l'embryogénie des pucerons. *Compt. rend. hebd. d. séances d. l'acad. d. sci.* **62**: 1231-1234, 1285-1289, 1390-1394. 1866.
- : Mémoire sur la génération des aphides. *Ann. d. sci. naturelles*. **14** (5): 1-39, 2-36. 1870. **15** (5): 1-30, 1-63. 1870.
- : Sur l'embryogénie de la puce. *Compt. rend. hebd. d. séances d. l'acad. d. sci.* **81**: 901-904. 1875.
- : Sur la signification des cellules polaires des insectes. *Compt. rend. hebd. d. séances d. l'acad. d. sci.* **95**: 927-929. 1882.
- : Sur l'origine des cellules du follicule et du noyau vitellin de l'oeuf chez les géophiles. *Zool. Anz.* **6**: 658-662, 676-680. 1883.
- BALFOUR, F. M.: "A Treatise on Comparative Embryology." Macmillan, London. 1880 (reprinted 1885).
- : The anatomy and development of *Peripatus capensis*. *Quart. Jour. Micr. Sci.* **23**: 213-259. 1883.
- BARROIS, M. J.: Développement des podurelles. *Assoc. fr. pour l'avance d. sci. Compt. rend.* 7th session. **1878**: 778-779. 1879.
- BATILLON, E., and TCHOU SU: Maturation, fécondation et polyspermie chez l'oeuf de *Bombyx mori*. *Compt. rend. hebd. d. séances d. l'acad. d. sci.* **186**: 338-340. 1928.
- : Activation, élimination d'un globule polaire et polyvoltinisme chez le Bombyx du mûrier. *Compt. rend. hebd. d. séances d. l'acad. d. sci.* **193**: 380-383. 1931a.
- : Les trois types de mitoses caractéristiques du premier développement chez l'oeuf de Bombyx fécondé ou parthénogénésique. *Compt. rend. acad. sci. fr., Paris*. **193**: 415-417. 1931b.

- : Les processus cinétiques dans l'oeuf de Bombyx mori. (Fécondation normale; parthénogénèse; activation polyvoltinisante; dissociation expérimentale des rythmes.) *Arch. d. anat. micr.* **29**: 285–372. 1933.
- BEER, S.: Lo sviluppo delle ghiandole genitali nell'embrione e nella larva del filugello. I. L'embrione. *Boll. d. lab. d. zool. agr. e bach. d. reale ist. sup. agr. d. Milano.* **3**: 79–149. 1932.
- *BEKKER, E. G.: Origin of the abdominal appendages in Thysanura. *Proc. Congr. Zool. Anat. Histol. U.S.S.R., Leningrad.* **2**: 80–82. 1927.
- BERLESE, A.: "Gli Insetti." Vol 1. 1004 pp. Milano. 1909.
- BESSELS, E.: Studien über die Entwicklung der Sexualdrüsen bei den Lepidopteren. *Zeitschr. f. wiss. Zool.* **17**: 545–564. 1867.
- *BEZRUKOV, L.: Les oöthèques des Acridiens. *Bull. Siberian Entomol. Bur., Petrograd.* **2**: 25–37. 1923.
- BIEGEL, J. H.: Beiträge zur Morphologie und Entwicklungsgeschichte des Herzens bei Lithobius forficatus L. *Rev. suisse d. zool.* **29**: 427–480. 1922.
- BISCHOFF, H.: "Biologie der Hymenopteren." Pp. 1–598. Springer, Berlin. 1928.
- *BLEDOWSKI, R., and M. K. KRAINSKA: Entwicklung von Banchus femoralis. *Bibl. Univ. Lib. Polon.* **16**: 1926.
- BLOCHMANN, F.: Ueber eine Metamorphose der Kerne in den Ovarialeiern und über den Beginn der Blastodermbildung bei den Ameisen. *Verhandl. d. Naturhist.-Med. Ver., Heidelberg.* **3**: 243–247. 1886.
- *—: "Ueber die Reifung der Eier bei Ameisen und Wespen." Festschr. z. Feier d. 500-jährigen Bestehens d. Ruperto-Carola, dargebracht von d. Naturh. med. Verein z. Heidelberg. 143–172. 1884.
- : Ueber die Richtungskörper bei Insekteneiern. *Morph. Jahrb.* **12**: 544–574. 1887.
- : Ueber die Richtungskörper bei Insekteneiern. *Biol. Centr.* **7**: 108–111. 1887.
- : Ueber das regelmässige Vorkommen von bakterienähnlichen Gebilden in den Geweben und den Eiern verschiedener Insekten. *Zeitschr. f. Biol.* **24**: 1–15. 1888a.
- : Vorkommen bakterienähnlicher Körperchen in den Geweben und Eiern verschiedener Insekten. *Biol. Centr.* **7**: 600–608. 1888b.
- : Bemerkungen zu den Publicationen über die Richtungskörper bei parthenogenetisch sich entwickelnden Eiern. *Morph. Jahrb.* **13**: 654–663. 1888c.
- : Ueber die Zahl der Richtungskörper bei befruchteten und unbefruchteten Bienen-eiern. *Morph. Jahrb.* **15**: 85–96. 1889.
- : Ueber das Vorkommen von bakterienähnlichen Gebilden in den Geweben und Eiern verschiedener Insekten. *Centr. f. Bakt.* **11**: 234–240. 1892.
- BLUNCK, HANS: Die Entwicklung des Dytiscus marginalis L. vom Ei bis zur Imago. I. Th. Das Embryonalleben. *Zeitschr. f. wiss. Zool.* **111**: 76–151. 1914.
- BOBRETZKY, N.: Ueber die Bildung des Blastoderms und der Keimblätter bei den Insekten. *Zeitschr. f. wiss. Zool.* **31**: 195–215. 1878.
- BOCK, E.: Bildung und Differenzierung der Keimblätter bei Chrysopa perla. *Zeitschr. f. Morph. u. Oekol. Tiere.* **35**: 615–702. 1939.
- BODENSTEIN, D.: Untersuchungen zum Metamorphoseproblem. I. Kombinierte Schnürungs- und Transplantationsexperimente an Drosophila. *Arch. f. Entwickl. mech. Organ.* **137**: 474–505. 1938.
- : Investigations on the problem of metamorphosis. IV. Developmental relations of interspecific organ transplants in Drosophila. *Jour. Exptl. Zool.* 1939.

- BODINE, J. H.: Effect of temperature on rate of embryonic development of certain Orthoptera. *Jour. Exptl. Zool.* **42**: 91-109. 1925.
- : The effect of cyanide on the oxygen consumption of normal and blocked embryonic cells. *Jour. Cell. Comp. Physiol.* **4**: 397-404. 1934.
- and E. J. BOELL: Respiratory mechanism of blocked and normal embryonic cell. *Proc. Iowa Acad. Sci.* **41**: 313-314. 1934.
- : Peroxidases and cell activity in developing egg. *Proc. Soc. Exptl. Biol. Med.*, New York. **32**: 783-787. 1935.
- BOELL, E. J.: Respiratory quotients during embryonic development. *Jour. Cell. Comp. Physiol.* **6**: 369-385. 1935.
- BOTT, R.: Entwicklungsgeschichte unter besonderer Berücksichtigung der Verhältnisse bei den Lepidopteren. *Zeitschr. Intern. Entomol.* **18**: 161-164. 1924.
- BOUVIER, E. L.: Monographie des onychophores. *Ann. d. sci. naturelles zool.* **2**: 1-383. 1905.
- BRAEM, F.: Was ist ein Keimblatt? *Biol. Centr.* **15**: 427, 466, 491. 1895.
- BRANCH, H. E.: Identification of chironomid egg masses. II. *Trans. Kansas Acad. Sci.* **34**: 151-157. 1931.
- BRANDT, A.: Beiträge zur Entwicklungsgeschichte der Libelluliden und Hemipteren. *Mém. l'acad. imp. d. sci. d. St. Pétersburg.* 7th ser. **13**: 1-33. 1869.
- : Über das Ei und seine Bildungsstätte. 200 pp. W. Engelmann, Leipzig. 1878.
- : Commentare zur Keimbläsentheorie des Eis. I. Die Blastodermelemente und Dotterballen der Insekten. II. Das Keimbläschen als primäre Zelle. *Arch. Mikrosk. Anat.* **17**: 43-57, 551-574. 1879 (1880).
- BRASS, A.: Das Ovarium und die ersten Entwicklungsstadien des Eies der viviparen Aphiden. *Zeitschr. f. naturw.*, Halle. **55**: 339-375. 1882 (1883).
- BRAUER, A. Further notes on the oviposition of Bruchus and the orientation of the embryo in the egg during development. *Proc. Oklahoma Acad. Sci.* **5**: 74-76. 1925a.
- : Studies on the embryology of Bruchus quadrimaculatus Fabr. *Ann. Entomol. Soc. Amer.* **18**: 283-312. 1925b.
- and A. C. TAYLOR: Experiments to determine the presence, location and effects of an organization center in Bruchid (Coleoptera) eggs. *Anat. Record* 60. Supplement 61. 1934.
- : Experiments to determine the time and method of organization in Bruchid (Coleoptera) eggs. *Jour. Exptl. Zool.* **73**: 127-152. 1936.
- *BRAUNS, F.: Die Entstehung der Nährzelle und die Bedeutung derselben für das wachsende Ei bei Forficula auricularis. *Sitzb. natur. Ges. Rostock.* 4 N. F. Pp. 99-141.
- BRUCE, A. T.: Origin of the endoderm in Lepidoptera. *Johns Hopkins Univ. Circ.* **5** (43): 9. 1885.
- : Observations on the embryology of insects and arachnids. *Johns Hopkins Univ. Circ.* **5** (No. 49): 85. 1886. Summary: *Jour. Roy. Micr. Soc.* **6** (2): 590. 1886. Reprint: *Ann. Mag. Natural Hist.* **18** (5): 74-76. 1886.
- : "Observations on the Embryology of Insects and Arachnids." Pp. 1-31. Johns Hopkins University, Baltimore. 1887.
- BRUES, C. T.: A contribution to our knowledge of the Stylopidae. *Zool. Jahrb.* **18**: 241-270. 1903.
- and R. W. GLASER: A symbiotic fungus occurring in a fat-body of Pulvinaria innumerabilis. *Biol. Bull.* **40**: 299-324. 1921.
- BUCHNER, P.: "Tier und Pflanze in Symbiose." Pp. 1-900. Borntraeger, Berlin. 1930.

- BUGINI, F.: La partenogenesi naturale dimostrata nel filugello. *Boll. d. lab. d. zool. agr. e bach. d. reale ist. sup. agr. d. Milano.* **2**: 116-149. 1931.
- : Nuove osservazioni ed esperienze sulla partenogenesi naturale del filugello. *Boll. d. lab. d. zool. agr. e bach. d. reale ist. sup. agr. d. Milano.* **3**: 67-78. 1932.
- BUGNION, E.: Recherches sur le développement post embryonnaire l'anatomie et les moeurs de l'*Encyrtus fuscicollis*. *Rec. zool. suisse.* **5**: 435-534. 1891.
- : La polyembryonie et le déterminisme sexuel. *Arch. d. sci. phys. naturelle.* **20**: 699-702. 1905.
- : Etudes relatives à l'anatomie et à l'embryologie des vers luisants ou lampyrides. *Bull. biol. d. France d. Belg.* **56**: 1-53. 1922.
- : Mantis et empuses. *Mém. d. l. soc. vaudoise d. sci. naturelles.* **1**: 177-243. 1923.
- *BURMEISTER, H. C. C.: Beitrag zur Entwicklungsgeschichte der Ephemeriden. *D'Alton u. Burm. Zeitung Zool.* **1**: 109-112. 1848.
- BURNETT, W. I.: Researches on the development of viviparous aphids. *Amer. Jour. Sci. Arts.* **17** (11): 62-78. 1854.
- BÜTSCHLI, O.: Zur Entwicklungsgeschichte der Biene. *Zeitschr. f. wiss. Zool.* **20**: 519-564. 1870.
- : Bemerkungen über die Entwicklungsgeschichte von *Musca*. *Morph. Jahrb.* **14**: 170-174. 1888.
- BUTT, F. H.: Embryology of *Sciara*. *Ann. Entomol. Soc. Amer.* **27**: 565-579. 1934.
- : The origin of the peritrophic membrane in *Sciara* and the honey bee. *Psyche.* **41**: 51-56. 1934.
- : The early embryological development of the parthenogenetic alfalfa snout beetle, *Brachyrhinus ligustici* L. *Ann. Entomol. Soc. Amer.* **29**: 1-13. 1936.
- CALVERT, P. P.: see Tillyard (1917).
- CAMERON, D.: "The Embryological Development of the Asiatic Rat flea (*Xenopsylla cheopis*).". Abstracts of theses, Cornell University. (1939), 1940.
- CANTO, C. P.: Sobre la embriología del *Margarodes vitium* Giard. *Actes d. soc. sci. d. Chili.* **6**: 14-20. 1896.
- *CANZANELLI, A.: Contributo all' embriologia e biologia del tarlo de tabacco (*Lasio-derma serricorne*: Coleo.). *Boll. d. lab. d. zool. agr. e bach.*, Milano. **4**: 81-116. 1924.
- *———: *II Dermestes lardarius* L. *Boll. entomol. oss. fitopat.*, Milano. **6**: 19-65. 1934-1935 (1936).
- CAPPE DE BAILLON, P.: Monstres doubles et intersexués chez les phasmides. *Compt. rend. hebd. d. séances d. l'acad. d. sci.* **180**: 1371-1373. 1925a.
- : Sur l'embryogénèse des monstres doubles chez les Phasmides (*Carausius morosus* Br.). *Compt. rend. hebd. d. séances d. l'acad. d. sci.* **181**: 479-481. 1925b.
- : Embryogénie tératologique chez les phasmides (*Menexenus semiarmatus* et *Clitumnus artemis*). *Bull. biol. d. France d. Belg.* **62** (3): 378-387. 1928.
- and FAVRELLE and VICHET: Parthenogénèse et variation chez les phasmes. *Bull. biol. d. France d. Belg.* **72**: 1-46. 1939.
- CAROTHERS, E. E.: The maturation divisions and segregations of heteromorphic homologous chromosomes in Acrididae. *Biol. Bull.* **61**: 324-349. 1931.
- CARRIÈRE, J.: Kurze Mittheilungen aus fortgesetzten Untersuchungen über die Sehorgane. Die Entwicklung und die verschiedenen Arten der ocellen. *Zool. Anz.* **9**: 496-500. 1886.
- : Die Entwicklung der Mauerbiene (*Chalicodoma muraria* Fabr.) im Ei. *Arch. f. Mikrosk. Anat.* **35**: 141-165. 1890a.

- : Zur Embryonalentwicklung der Mauerbiene (*Chalicodoma muraria* Fab.). *Zool. Anz.* **13**: 69–71. 1890b.
- : Die Drüsen am ersten Hinterleibsringe der Insektenembryonen. *Biol. Centr.* **11**: 110–127. 1891a.
- : Zur Graber's Bemerkungen Seite 224 fg. *Biol. Centr.* **11**: 416. 1891b.
- and O. BÜRGER: Die Entwicklungsgeschichte der Mauerbiene (*Chalicodoma muraria* Fabr.) im Ei. *Nova Acta. Abhandl. d. Kaiserl. Leop.-Carol. deut. Akad. d. Naturf.* **69**: 255–420. 1897.
- CARY, L. R.: Plant-house Aleurodes (*Aleurodes vaporariorum*). *Maine Agr. Exp. Sta. Bull.* **96**: 125–144. 1903.
- CHILD, G. P., and R. B. HOWLAND: Observations on early developmental processes in the living egg of *Drosophila*. *Science.* **77**: 396. 1933.
- CHOŁODKOWSKY, N.: Ueber die Bildung des Entoderms bei *Blatta germanica*. *Zool. Anz.* **11**: 163–166. 1888.
- : Studien zur Entwicklungsgeschichte der Insecten. *Zeitschr. f. wiss. Zool.* **48**: 89–100, 301, 302. 1889.
- : Zur Embryologie der *Blatta germanica*. *Zool. Anz.* **13**: 137–138. 1890a.
- : Zur Embryologie der Hausschabe (*Blatta germanica*). *Biol. Centr.* **10**: 425. 1890b.
- : Ueber die Entwicklung des centralen Nerven-systems bei *Blatta germanica*. *Zool. Anz.* **14**: 115, 116. 1891a.
- : Ueber einige Formen des Blastopore bei meroblastischen Eiern. *Zool. Anz.* **14**: 159, 160. 1891b.
- : Zur Embryologie der Insecten. *Zool. Anz.* **14**: 465, 466. 1891c.
- : Die Embryonalentwicklung von *Phyllodromia* (*Blatta*) *germanica*. *Mém. d. l'acad. imp. d. sci. d. St. Petersburg.* 7th ser. **38** (5): 1–121. 1891d. Review: *Jour. Roy. Micr. Soc.* **1892**: 200–201. 1892. In Russian. *Trudui, St. P. Est.* **22**: 39–223. 1892.
- *———: Zur Embryologie der Diplopoden. In Russian, with German résumé. *Soc. Imp. Nat. St. Petersburg.* No. 2: 10–12, 17–18. 1895.
- CHRISTENSEN, P. J. H.: Zur Histologie und Embryologie der überwinterten Eier von *Orygia antiqua*. *Zool. Jahrb. (Anat.)*. **62**: 567–582. 1937.
- *CHRISTOPHERS, S. R.: The development of the egg-follicle in *Anopheles*. *Paludism Simla.* **2**: 73–87. 1911.
- CLAUS, C.: Beobachtungen über die Bildung des Insecteneies. *Zeitschr. f. wiss. Zool.* **14**: 41–54. 1864.
- CLAYPOLE, A. M.: Some points on cleavage among arthropods. *Trans. Amer. Micr. Soc.* **19**, 74–80. 1897 (1898).
- : The embryology and oögenesis of *Anurida maritima*. *Jour. Morphology.* **14**: 219–300. 1898.
- : The embryology of the Apterygota. *Zool. Bull.* **2**: 69–76. 1899.
- *CLEMENT, H.: Contribution à l'étude de la centrifugation expérimentale en biologie. *Rev. gén. sci. pur. et appl.* **18**: 505–510. 1917.
- COCKERELL, T. D. A.: The development of Mantis. *Amer. Naturalist.* **32**: 513–514. 1898.
- CODY, F. P., and I. E. GRAY: The changes in the central nervous system during the life history of the beetle, *Passalus cornutus* Fabr. *Jour. Morphology.* **62**: 503–522. 1938.
- COLE, K. S., and T. L. JAHN: The nature and permeability of grasshopper egg membranes. IV. The alternating current impedance over a wide frequency range. *Jour. Cell. Comp. Physiol.* **10**: 265–275. 1937.

- COMSTOCK, J. H., and C. KOCHI: The skeleton of the head of insects. *Amer. Naturalist*. **36**: 13-45. 1902.
- COMSTOCK, J. H.: "An Introduction to Entomology." Pp. 1-1044. Comstock, Ithaca, N. Y. 1924.
- CRAMPTON, G. C.: The interrelationships and lines of descent of living insects. *Psyche*. **45**: 165-181. 1938.
- CRAVEN, W. N.: Some observations on the embryology of Chironomus. *Proc. Iowa Acad. Sci.* **16**: 221-222. 1909.
- CRAWFORD, A. W.: Glypta rufescutellaris, an ichneumonid larval parasite of the oriental fruit moth. *N. Y. Agr. Exp. Sta., Tech. Bull.* **217**: 1-29, 1933.
- *CZERSKI, S.: Die Entwicklung der Mitteldarmanlage bei Meloe violaceus. *Poln. Arch. Biol. Med. Wiss., Lemberg*. **2**: 259-284. 1904. In Polish. Review: *Zool. Centr.* **1905**: 62, 677-690. 1905.
- DANIEL, D. M.: Macrocentrus ancyllivorus Rohwer, a polyembryonic braconid parasite of the oriental fruit moth. *N. Y. Agr. Exp. Sta., Tech. Bull.* **187**: 1-101. 1932.
- DAVID, K.: Beiträge zur Anatom. und Lebensgeschichte von Osmylus chrysops. *Zeitschr. f. Morph. und u. Oekol. d. Tiere*. **31**: 151-206. 1936.
- DAWYDOFF, C.: "Traité d'embryologie comparée des invertébrés." Pp. 930. Masson et Cie., Paris. 1928.
- DEGENER, PAUL: Entwicklung der Mundwerkzeuge und des Darmkanals von Hydrophilus. *Zeitschr. f. wiss. Zool.* **68**: 113-168. 1900.
- *DELLA CORTE, M.: Lo spessore del guscio delle uova di Bombyx mori nelle principali razze oggi allevate. *Boll. reale staz. sper. gelsicolt. e bach.* **4**: 223-234. 1925.
- *DELLA PIETÀ, S.: Contributo all' embriologia della Pieris brassicae L. *Boll. entomol. oss. filopat., Milano*. **6**: 93-109. 1934-1935 (1936).
- DICKEL, F.: Meine Ansicht über die Freiburger Untersuchungsergebnisse von Bienenen. *Anat. Anz.* **19**: 104-111. 1901a.
- : Ueber die Entwicklungsweise der Honigbiene. *Zool. Anz.* **25**: 39-56. 1901b.
- : Ueber Petrunkevitch Untersuchungsergebnisse von Bienenen. *Zool. Anz.* **25**: 20-27. 1902.
- : Entwicklungsgeschichtliche Studien am Bienenen. *Zeitschr. f. wiss. Zool.* **77**: 481-527. 1904.
- DOBZHANSKY, T.: Interaction between female and male parts in gynandromorphs of Drosophila simulans. *Arch. Entwickl. Mech.* **123**: 719-746. 1931.
- DOHRN, A.: Zur Embryologie der Arthropoden. *Centr. Med. Wiss.* **54**: 849-851. 1866.
- : Ueber die Bedeutung der fundamentalen Entwicklungsvorgänge in den Insecten-eiern für die Systematik der Insecten. *Stett. Entomol. Zeitschr.* **31**: 244-250. 1870.
- : Notizen zur Kenntnis der Insectenentwicklung. *Zeitschr. f. wiss. Zool.* **26**: 112-138. 1876.
- DONCASTER, L.: On the maturation of the unfertilized egg, and the fate of the polar bodies in the Tenthredinidae (sawflies). *Quart. Jour. Micr. Sci.* **49**: 561-589. 1906.
- : On the relations between chromosomes, sex-limited transmission and sex determination in Abraxas grossulariata. *Jour. Genetics.* **4**: 1-21. 1914.
- DRUMMOND, M.: The germinal layers concerned in the formation of the alimentary canal and Malpighian tubules of Ephestia kühniella (Lep). *Quart. Jour. Micr. Sci.* **78**: 533-542. 1936.

- DUBOIS, A. M.: Elimination of chromosomes during cleavage in the eggs of *Sciara* (Diptera). *Proc. Nat. Acad. Sci.* **18**: 352-356. 1932a.
- : A contribution to the embryology of *Sciara*. *Jour. Morphology.* **54**: 161-192. 1932b.
- : Recherches expérimentales sur la détermination de l'embryon dans l'oeuf de *Sialis lutaria*, *Neuroptera*. *Rev. suisse d. zool.*, Geneva. **43**: 519-523. 1936.
- : La détermination de l'ébauche embryonnaire chez *Sialis lutaria* (Megaloptera). *Rev. suisse d. zool.* **45**: 1-92. 1938.
- EASTHAM, L. E. S.: A contribution to the embryology of *Pieris rapae*. *Quart. Jour. Micr. Sci.* **71**: 353-394. 1927.
- : The embryology of *Pieris rapae*. Organogeny. *Phil. Trans. Roy. Soc. London.* Ser. B. **219**: 1-50. 1930a.
- : The formation of germ layers in insects. *Biol. Rev.* **5**: 1-29. 1930b.
- ELSE, F. L.: The developmental anatomy of male genitalia in *Melanoplus differentialis*. *Jour. Morphology.* **55**: 577-610. 1934.
- EMEIS, W.: Ueber Eientwicklung bei den Cocciden. *Zool. Jahrb. (Anat.)*. **39**: 27-78. 1915.
- EPHRUSSI, B.: Sur le chondriome ovarien des *Drosophila melanogaster* et *simulans*. *Compt. rend. hebd. d. soc. d. biol.* **77** (1): 778-780. 1925.
- ESCHERICH, K.: Keimblätterbildung bei den Musciden. *Verhandl. d. deut. Zool. Ges.* **10**: 130-134. 1900a.
- : Ueber die Bildung der Keimblätter bei den Musciden. *Abhandl. d. Kaiserl. Leop.-Carol. deut. Akad. d. Naturf.* **77**: 299-357. 1900b.
- (C. SCHRÖDER): Ueber die Bildung der Keimblätter bei den Insekten. *Zeitschr. allgem. f. Entomol.* **6**: 79. 1901a.
- : Das Insekten-Entoderm. *Biol. Centr.* **21**: 416-431. 1901b.
- : Ueber den sogen. "Mittelstrang" der Insekten. *Biol. Centr.* **22**: 179-181. 1902a.
- : Zur Entwicklung des Nervensystems der Musciden, mit besonderer Berücksichtigung des sog. Mittelstranges. *Zeitschr. f. wiss. Zool.* **71**: 525-549. 1902b.
- EVANS, R.: On the Malayan species of Onychophora. II. The development of *Eoperipatus weldoni*. *Quart. Jour. Micr. Sci.* **45**: 41-88. 1902.
- EWEST, A.: Struktur und erste Differenzierung im Ei des Mehlkäfers *Tenebrio molitor*. *Arch. Entwickl. Mech. Organ.* **135**: 689-752. 1937.
- FALKENHAN, H. H.: Biologische Beobachtungen an *Sminthurides aquaticus* (Collembola). *Zeitschr. f. wiss. Zool.* **141**: 525-580. 1932.
- FAUSSEK, V.: Vergleichend-embryologische Studien. *Zeitschr. f. wiss. Zool.* **98**: 529-625. 1911.
- FERNANDO, W.: The development and homologies of the mouth parts of the head louse. *Quart. Jour. Micr. Sci.* **76**: 231-241. 1933.
- : The early embryology of a viviparous psocid. *Quart. Jour. Micr. Sci.* **77**: 99-119. 1934.
- *FERRIÈRE, C.: Note sur un chalcidien à développement polyembryonique. *Rev. suisse Zool.*, Geneva. **33**: 585-596. 1926.
- FIJALKOWSKA, KALICKA: Le développement embryonnaire de *Margarodes polonicus*. *Compt. rend. hebd. d. séances et mém. d. soc. d. biol.* **99**: 1047-1048. 1928.
- FILIPPI, P. DE: Note sur la génération d'un hyménoptère de la famille des Ptéromaliens. *Ann. d. sci. naturelles.* **15**: 294-297. 1851. (3d ser. Zool.). English translation in *Ann. Mag. Natural Hist.* (2) **9**: 461-464. 1852.
- *FOA, A.: Le nostre conoscenze sulla determinazione del sessa et la loro applicazione al baco da seta. *Boll. reale staz. sper. gelsicolt. e bach. Ascoli Piceno.* **3**: 14-54. 1924.

- *——: Accrescimento e sviluppo nelle razze bivoltine del *Bombyx mori*; probabile correlazione tra l'andamento di questi fenomeni e il rapporto nucleo protoplasmatico delle cellule germinali. *Boll. Zool.*, Torino. **8**: 1-15. 1937.
- FOLSOM, J. W.: The development of the mouth parts of *Anurida maritima*. *Bull. Mus. Comp. Zool. Harvard Coll.* **36**: 87-158. 1900. Review: *Zool. Centr.* **8**: 241-245. 1901.
- FRAENKEL, H.: Die Symbionten der Blattiden im Fettgewebe und Ei in besondere von *Periplaneta orientalis*. *Zeitschr. f. wiss. Zool.* **119**: 53-66. 1921.
- FRIEDERICH, K.: Beiträge zur Entwicklungsgeschichte und Histologie von Arthropoden. 1. Untersuchungen über die Entstehung der Keimblätter und Bildung des Mitteldarms bei Käfern. *Nova Acta. Abhandl. d. Kaiserl. Leop.-Carol. deut. Akad. d. Naturf.* **85**: 259-383. 1906.
- FRIEDMANN, N.: Ein Beitrag zur Kenntnis der embryonalen Entwicklung der Abdominalfüsse bei den Schmetterlingsraupen. *Soc. Sci. Fennica Commentationes Biol.* **4** (10): 1-29. 1934.
- FULINSKI, B.: Ein Beitrag zur Embryonalentwicklung der *Agelastica alni*. *Bull. intern. d. l'acad. sci. d. Cracovie.* **1910**: 12-16. 1910 (1911).
- : "Zur Embryologie von *Agelastica alni*." *Festschr. Nusbaum, Lemberg.* Pp. 197-211. 1911.
- GABRITSCHESKY, E.: Sénescence embryonnaire réjeunissement et déterminisme des formes larvaires de *Miastor metraloas*. *Bull. biol. d. France d. Belg.* **62**: 478-524. 1928.
- : Der umkehrbare Entwicklungszyklus bei *Miastor metraloas*. *Arch. Entwickl. Mech. Organ.* **121**: 450-465. 1930.
- *GALLIARD, H.: Rôle de la mue embryonnaire des réduvidés hématophages dans le processus d'éclosion. *Ann. d. parasit. hum. et comp.* **12**: 345-349. 1934.
- GAMBRELL, F. L. (LYDIA A. JAHN): The embryology of the black fly, *Simulium pictipes* Hagen. *Ann. Entomol. Soc. Amer.* **26**: 641-671. 1933.
- GANIN, M.: Beiträge zur Erkenntnis der Entwicklungsgeschichte bei den Insekten. *Zeitschr. f. wiss. Zool.* **19**: 381-451. 1869a.
- : Ueber die Embryonalhülle der Hymenopteren- und Lepidopteren-Embryonen. *Mém. d. l'acad. imp. d. sci. d. St. Petersburg.* Ser. 7. **14**: 1-18. 1869b.
- *——: Ueber den Mitteldarm der Insekten. *Ber. Warschauer Univ.* 1874.
- GASOW, H.: Ein geeignetes Objekt zur Untersuchung der Embryonalentwicklung von Schmetterlingen. *Mikrokosmos.* **18**: 25-27. 1925.
- GATENBY, J. B.: The embryonic development of *Trichogramma evanescens*, mon-embryonic egg parasite of *Donacia simplex*. *Quart. Jour. Micr. Sci.* **62**: 149-187. 1917.
- : Polyembryony in parasitic Hymenoptera. *Quart. Jour. Micr. Sci.* **63**: 175-196. 1917 (1918).
- *GEIGY, R.: Une anomalie non-héréditaire provoquée par les rayons ultra-violet chez la *Drosophile*. *Compt. rend. soc. phys. et hist. naturelle Genève.* **43**: 143-145. 1926.
- : Production d'anomalies par exposition de drosophiles aux rayons ultra-violet. *Verhandl. schweiz naturf. Ges.* **108**: 191-192. 1927.
- : Action de l'ultraviolet sur le pôle germinal dans l'oeuf de *Drosophila melanogaster* (castration et mutabilité). *Rev. suisse zool.*, Genève. **38**: 187-288. 1931a.
- : Erzeugung rein imaginaler Defekte durch ultra-violette Eibestrahlung bei *Drosophila melanogaster*. *Arch. Entomol. Mech.* **125**: 406-447. 1931b.
- GIARD, A.: Sur le développement de *Litostix truncatellus*. *Bull. d. soc. entomol. d. France.* **67**: 127-129. 1897.

- GIARDINA, A.: Primi stadi embrionali della Mantis religiosa. *Mon. zool. ital.* **8**: 275-280. 1897.
- GILMORE, K. A., and P. W. WHITING: Females from unfertilized eggs in *Habrobracon* and their cytological significance. *Anat. Record.* **51** (supplement): 113. 1931.
- GLASER, R. W.: Biological studies on intracellular bacteria. *Biol. Bull.* **39**: 133-145. 1920.
- GLASGOW, HUGH: The gastric caeca and the caecal bacteria of the Heteroptera. *Biol. Bull.* **26**: 101-170. 1914.
- GOLDSCHMIDT, R.: On a case of facultative parthenogenesis in the Gypsy Moth. *Biol. Bull.* **32**: 35-43. 1917.
- : Die zygotischen sexuellen Zwischenstufen und die Theorie der Geschlechtsbestimmung. *Ergebnisse d. Biol.* **2**: 554-683. 1927.
- : Analysis of intersexuality in the Gypsy Moth. *Quart. Rev. Biol.* **6**: 125-142. 1931.
- : Intersexuality and development. *Amer. Naturalist.* **72**: 228-242. 1938.
- , and K. KATSUKI: Cytologie des erblichen Gynandromorphismus von *Bombyx mori* L. *Biol. Zbl.* **48**: 685-699. 1928.
- GOODRICH, A. L.: The origin and fate of the entoderm elements in the embryology of *Porcellio laevis* and *Armadillidium nasutum*. *Jour. Morphology.* **64**: 401-429. 1939.
- GOOSSENS, T.: L'oeuf du *Papilio machaon*. *Bull. soc. entomol. d. France.* Ser. 6. **5**: CLXXXI-CLXXXIV. 1885.
- GRABER, V.: Vorläufige Ergebnisse einer grösseren Arbeit über vergleichende Embryologie der Insekten. *Arch. f. Mikrosk. Anat.* **15**: 630-640. 1878.
- : "Die Insekten." Vergleichende Entwicklungsgeschichte. Entwicklung im Ei. **2**: 371-448. R. Oldenbourg, Munich. 1879.
- : Ueber die Polypodie bei Insekten Embryonen. *Morph. Jahrb.* **13**: 586-613. 1888a.
- : Vergleichende Studien über die Keimhüllen und die Rückenbildung der Insecten. *Denkschr. d. Kaiserl. Akad. d. Wiss. Wien Math. nat. Cl.* **55**: 109-162. 1888b.
- : Ueber die primäre Segmentirung des Keimstreifs der Insekten. *Morph. Jahrb.* **14**: 345-368. 1888c. Summary: *Jour. Roy. Micr. Soc.* **1888**: 941-942. 1888.
- : Ueber den Bau und die phylogenetische Bedeutung der embryonalen Bauchanhänge der Insekten. *Biol. Centr.* **9**: 355-363. 1889a. Summary: *Jour. Roy. Micr. Soc.* **1889**: 743. 1889.
- : Vergleichende Studien über die Embryologie der Insecten und insbesondere der Musciden. *Denkschr. d. Kaiserl. Akad. d. Wiss. Wien Math. nat. Cl.* **56**: 257-314. 1889b.
- : Bemerkungen zu Dr. K. Heider's Abhandlung über die Embryonalentwicklung von *Hydrophilus piceus*. *Zool. Anz.* **13**: 287-289. 1890a.
- : Vergleichende Studien am Keimstreifen der Insecten. *Denkschr. d. Kaiserl. Akad. d. Wiss. Wien Math. nat. Cl.* **57**: 621-734. 1890b.
- : Beiträge zur vergleichenden Embryologie der Insekten. *Denkschr. d. Kaiserl. Akad. d. Wiss. Wien Math. nat. Cl.* **58**: 803-866. 1891a.
- : Zur Embryologie der Insekten. *Zool. Anz.* **14**: 286-291. 1891b. Summary: *Jour. Roy. Micr. Soc.* **1891**: 729. 1891.
- : Zur Erwiederung Dr. K. Heider's auf meine Bemerkungen zu dessen Embryologie von *Hydrophilus*. *Zool. Anz.* **14**: 8-9. 1891c.
- GRANDORI, R.: Contributo all' embriologia e alla biologia dell' *Apanteles glomeratus*. *Redia.* **7**: 363-428. 1911.

- : Studi sullo sviluppo embrionale del *Bombyx mori*. *Atti d. accad. sci. Veneto-Trentino Istriana*. **6** (3): 225-231. 1914a.
- : Lo sviluppo embrionale del baco da seta. *Mem. l. atti d. accad. sci. Veneto Trentino-Istriana*. **7** (3): 188-270. 1914b (1915).
- : Giactura dell'embrione del baco da seta nell' uovo di avanzata incubazione. *Atti d. reale ist. Veneto d. sci. lettere ed arti*. **74**: (2) 1235-1245. 1915.
- : Anomalie nell' embriogenesi del *Bombyx mori*. *Atti d. reale ist. Veneto d. sci. lettere ed arti*. **75** (2): 1619-1632. 1916.
- : Differenze morfologiche nell' ovicite e nell' uovo di *Bombyx mori*. *Redia*. **14**: 5-42. 1921.
- *———: Segmentazione anomala delle uova partenogeniche di *Bombyx mori*. *Boll. ist. zool. univ. Roma*. **2**: 128-138. 1924.
- : Studi sulla blastocinesi degl' insetti. *Atti d. reale accad. naz. d. Lincei*. **2**: 449-455. 1925.
- : Studi embriologici sulle razze polivoltine del Bombici del gelso. *Atti d. reale accad. naz. d. Lincei*. **8** (6): 717-722. 1928.
- *———: La blastocinesi nel filugello l'industria bacologica. Milan. **4**: 2-5. 1930a.
- : Studi embriologici sulla razze polivoltine del Bombici del gelso. *Boll. d. lab. d. zool. agr. e bach. d. reale ist. sup. agr. d. Milano*. **1**: 9-15. 1930b.
- : Partenogenesi e residui allo schiudimento nelle nova del Filugello. *Loc. cit.* **1**: 75-87. 1930c.
- : Lo sviluppo embrionale del baco da seta. Mem. 2. La diapausa. *Loc. cit.* **1**: 195-237. 1930d.
- : Lo sviluppo embrionale del baco da seta. Mem. 3. Sviluppo primaverile fino alla blastocinesi. *Loc. cit.* **3**: 43-128. 1932a.
- : Osservazioni sullo sviluppo embrionale di *Nyssia florentina* Stefan. *Loc. cit.* **4**: 133-139. 1932b.
- GRASSI, B.: Studi sugli artropodi. Intorno allo sviluppo delle api nell' uovo. *Atti d. accad. Gioenia di sci. nat. Catania*. **18** (3): 145-223. 1884. Review: *Biol. Centr.* **5**: 689-692. 1886.
- : I progenitori degli insetti e dei miriapodi, l'*Japyx* e la Campodea. *Loc. cit.* **19** (3): 1-83. 1885 (1886).
- : Sur le développement de l'abeille dans l'oeuf. *Arch. ital. biol.* **7**: 242-273. Abstract: *Amer. Naturalist*. **20**: 462-464. Summary: *Jour. Roy. Micr. Soc.* **6** (2): 783-787. 1886.
- GRESSION, R. A. R.: Yolk-formation in *Periplaneta orientalis*. *Quart. Jour. Micr. Sci.* **74**: 257-274. 1931.
- GRIMM, O. VON: Zur embryologie von *Phthirus pubis*. *Bull. d. l'acad. imp. d. sci. d. St. Petersburg*. **14**: 513-517. 1870a.
- : Die ungeschlechtliche Fortpflanzung einer *Chironomus*-art. *Mém. de l'acad. imp. d. sci. d. St. Petersburg*. **15**: 1-23. 1870b.
- GROSS, J. B., and R. B. HOWLAND: The early embryology of *Prodenia eridania*. *Ann. Entomol. Soc. Amer.* **33**: 56-75. 1940.
- HAGAN, H. R.: Observations on the development of the mantid *Paratenodera sinensis*. *Jour. Morphology*. **30**: 223-243. 1917.
- : The embryogeny of the Polychaetid, *Hesperoetenes fumarius* Westwood, with reference to viviparity in insects. *Jour. Morphology*. **51**: 3-118. 1931.
- : *Diploptera dytiscoides*, a viviparous roach with elongate pleuropodia. *Ann. Entomol. Soc. Amer.* **32**: 264-266. 1939.
- HAGEN, H.: Die Entwicklung und der innere Bau von *Osmylus*. *Linnaea Entomologica*. **7**: 368-418. 1852.

- HALLEZ, P.: Orientation de l'embryon et formation du cocon chez la *Periplaneta orientalis*. *Compt. rend. hebd. d. séances d. l'acad. d. sci.* **101**: 444-446. 1885.
- : Loi de l'orientation de l'embryon chez les insectes. *Compt. rend. hebd. d. séances d. l'acad. d. sci.* **103**: 606-608. 1886. Summary: *Jour. Roy. Micr. Soc.* **1887**: 72-73. 1887.
- HAMMERSCHMIDT, JOHANN: Beiträge zur Entwicklung der Phasmatiden. *Zeitschr. f. wiss. Zool.* **95**: 221-242. 1910.
- HANDLIRSCH, A.: Die Phylogenie der Insektenordnungen. *Ann. d. Naturh. Mus. in Wien.* **49**: 173-185. 1939.
- HANIN, M.: Neue Beobachtungen über die Fortpflanzung der viviparen Dipteren. *Zeitschr. f. wiss. Zool.* **15**: 375-390. 1865.
- HANSON, F. B., and F. HEYS: The effects of alpha-irradiation from polonium on the developing eggs of *Drosophila melanogaster*. *Amer. Naturalist.* **67**: 567-571. 1933.
- HARDENBURG, J. D. F.: Beiträge zur Kenntnis der Pupiparen. *Zool. Jahrb., (Anat.).* **50**: 497-570. 1929.
- HARRIS, R. G.: Sex of adult Cecidomyiidae (Oligarces) arising from larvae produced by paedogenesis. *Psyche.* **31**: 148-154. 1924.
- HARRISON, J. W. H.: Interspecific hybrids in the Lepidopterous genus *Selenia* with an account of a case of expedited parthenogenesis. *Jour. Genetics.* **27**: 225-232. 1933.
- HARRISON, L.: On some Pauropoda from New South Wales. *Proc. Linnean Soc. N. S. Wales.* **39**: 615-634. 1914 (1915).
- HASPER, M.: Zur Entwicklung der Geschlechtsorgane von *Chironomus*. *Zool. Anz.* **35**: 737-743. 1910.
- : Zur Entwicklung der Geschlechtsorgane von *Chironomus*. *Zool. Jahrb., (Anat.).* **31**: 543-612. 1911.
- HATSCHKE, B.: Beiträge zur Entwicklungsgeschichte der Lepidopteren. *Zeitschr. f. Naturw., Jena.* **11**: 115-148. 1877.
- HEATHCOTE, F. G.: The early development of *Julus terrestris*. *Quart. Jour. Micr. Sci.* **26**: 449-470. 1886. Review: *Amer. Naturalist.* **20**: 662-666. 1886.
- HECHT, O.: Embryonalentwicklung und Symbiose bei *Camponotus ligniperda*. *Zeitschr. f. wiss. Zool.* **122**: 173-204. 1924.
- HEGNER, R. W.: Effects of removing the germ-cell determinants from the eggs of some chrysomelid beetles. *Prelim. Rept., Biol. Bull.* **16**: 19-26. 1908.
- : The origin and early history of the germ-cells in some chrysomelid beetles. *Jour. Morphology.* **20**: 231-296. 1909a.
- : The effects of centrifugal force upon the eggs of some chrysomelid beetles. *Jour. Exptl. Zool.* **6**: 507-552. 1909b.
- : Experiments with chrysomelid beetles. *Biol. Bull.* **19**: 18-30. 1910.
- : **20**: 237-251. 1911a.
- : Germ-cell determinants and their significance. *Amer. Naturalist.* **45**: 385-397. 1911b.
- : The history of the germ cells in the paedogenetic larva of *Miastor*. *Science.* **36**: 124-126. 1912.
- : "The Germ-cell Cycle in Animals." Pp. 1-346. Macmillan, New York. 1914a.
- : Studies on germ cells. The origin of the Keimbahn-determinants in a parasitic hymenopteron, *Copidosoma*. *Anat. Anz.* **46**: 51-69. 1914b.
- : Studies on germ cells. *Jour. Morphology.* **25**: 375-509. 1914c. **26**: 495-561. 1915.

- : The genesis of the organization of the insect egg. *Amer. Naturalist*. **51**: 641-661, 705-718. 1917.
- HEIDER, K.: Ueber die Anlage der Keimblätter von *Hydrophilus piceus*. *Abhandl. K. Acad. Wiss.*, Berlin. **1885**: 1-47. 1885.
- : Die embryonalentwicklung von *Hydrophilus piceus* L. 98 pp. Gustav Fischer, Jena. 1889.
- : Erwiederung auf die Bemerkungen v. Graber's zu meiner Abhandlung über die Embryonalentwicklung von *Hydrophilus piceus* L. *Zool. Anz.* **13**: 428-430. 1890.
- : Ist die Keimblätterlehre erschuttert? *Zool. Centr.* **4**: 725-737. 1897.
- : Entwicklungsgeschichte und Morphologie der Wirbellosen. In "Die Kultur der Gegenwart." Pp. 176-332. Teubner, Leipzig. 1913.
- HENKING, H.: Ueber die Bildung von Richtungs Körpern in den Eiern der Insecten und deren Schicksal. *Nachr. v. d. Kgl. Ges. d. Wiss. Göttingen*. **1888**: 444-449. 1888a.
- : Die ersten Entwicklungsvorgänge im Fliegenei und freie Kernbildung. *Zeitschr. f. wiss. Zool.* **46**: 289-336. 1888b. Summary: *Jour. Roy. Micr. Soc.* **1888**: 573. 1888.
- : Ueber Befruchtungsvorgänge im Insectenei. *Biol. Centr.* **10**: 439-440. 1890.
- : Methoden bei entwicklungsgeschichtlichen Untersuchungen an Insecteneiern. *Zeitschr. f. wiss. Mikrosk.* **8**: 156-167. 1891a.
- : Untersuchungen über die ersten Entwicklungsvorgänge in den Eiern der Insekten. *Zeitschr. f. wiss. Zool.* **49**: 503-564. 1890. **51**: 685-736. 1891b. **54**: 1-274. 1892.
- *HENNEGUY, L. F.: Note sur la structure de l'enveloppe de l'oeuf des phyllies. *Bull. Soc. Philom.* **2** (8): 18-25. 1890. Summary: *Jour. Roy. Micr. Soc.* **1890**: 596. 1890.
- : Contribution à l'embryogénie des chalcidiens. (Note préliminaire). *Bull. Soc. Philom.* **3** (8): 164-167. 1891.
- : Contribution à l'embryogénie des Chalcidiens. *Compt. rend. hebdomad. d. séances d. l'acad. d. sci.* **114**: 133-136. 1892. Summary: *Jour. Roy. Micr. Soc.* **1892**: 357. 1892. *Ann. Mag. Natural Hist.* **10** (6): 271, 272.
- : "Les Insectes." Embryology. Pp. 306-432. Masson et Cie, Paris. 1904.
- HENSCHEN, W.: Entwicklung der Geschlechtsdrüsen von *Habrobracon juglandis* Ash. *Zeitschr. f. Morph. u. Oekol. der Tiere*. **13**: 144-178. 1928 (1929).
- HENSHAW, P. S.: The effect of x-rays on differentiation in *Drosophila* eggs. *Anat. Record*. **60**: supplement: 59. 1934.
- HENSON, H.: The development of the alimentary canal in *Pieris brassicae* and the endodermal origin of the Malpighian tubules in insects. *Quart. Jour. Micr. Sci.* **75**: 283-309. 1932.
- HEROLD, DR.: "Entwicklungsgeschichte der Schmetterlinge." Pp. 1-118. Cassel u. Marburg. 1815.
- : Recherches sur le développement de l'oeuf chez les insectes. *Ann. d. sci. naturelles*. **12** (2): 176-205. 1839.
- HERTWIG, O., and R. HERTWIG: Die Coelomtheorie. *Zeitschr. f. Naturwiss.*, Jena. **15**: 1-150. 1881.
- HERTWIG, P.: Haploide und diploide Parthenogenese. *Biol. Zentr.* **40**: 145-174. 1920.
- HERTWIG, R.: Ueber die Anlage der Keimblätter bei den Insecten. *Sitzb. f.* 1880 (14). *Zeitschr. f. Naturwiss.*, Jena. **14**: 124-128. 1881.

- : (J. S. KINGSLEY): "A Manual of Zoology." 606 pp. Holt, New York. 1912.
- : Ueber den Einfluss der Ueberreife der Eier auf das Geschlechtsverhältnis von Fröschen und Schmetterlingen. *Sitzb. d. math.-physikal. Klasse d. Bayerischen Akad. d. Wiss.* **1921**: 269–294. 1921.
- : Einfluss der Ueberreife der Geschlechtszellen auf das Geschlecht von *Lymantria dispar*. *Sitzb. d. math.-physikal. Klasse d. Bayerischen Akad. d. Wiss.* **1923**: 215–252. 1923.
- HESS, W. N.: Origin and development of the light-organs of *Photurus pennsylvanica* deGeer. *Jour. Morphology*. **36**: 245–277. 1922.
- HEWITT, C. G.: The cytological aspect of parthenogenesis in insects. *Mem. Proc. Manchester Lit. Phil. Soc.* **50** (6): 1–40. 1906.
- HEYMONS, R.: "Die Entstehung der Geschlechtsdrüsen von *Phyllodromia* (Blatta) germanica L." Dissertation. Pp. 1–72. Berlin. 1891a.
- : Die Entwicklung der weiblichen Geschlechtsorgane von *Phyllodromia* (Blatta) germanica L. *Zeitschr. f. wiss. Zool.* **53**: 434–536. 1891b.
- : Entstehung und Ausbildung der Colomsäcke. *Verhandl. d. deut. Zool. Ges.* **1892**: 139–141. 1892.
- : Ueber die Entwicklung des Ohrwurms (*Forficula auricularia*). *Sitzb. d. Ges. Naturf. Freunde*, Berlin. **1893**: 127–131. 1893a.
- : Ueber die Entstehung der Geschlechtszellen bei den Insekten. *Sitzb. d. Ges. Naturf. Freunde*, Berlin. **1893**: 263–269. 1893b.
- : Ueber die Bildung der Keimblätter bei den Insekten. *Sitzb. Akad. Wiss. Berlin*. **1894a**: 23–27. Summary: *Jour. Roy. Micr. Soc.* **1894**: 557–558. 1894a.
- : Übersicht über die neueren Ergebnisse auf dem Gebiete der Insektenembryologie. *Zool. Centr.* **1**: 41–50, 81–92. 1894b.
- : "Die Embryonalentwicklung von Dermapteren und Orthopteren unter besonderer Berücksichtigung der Keimblätterbildung." Pp. 1–136. Gustav Fischer, Jena. 1895a. Review. *Zool. Centr.* **2**: 651–653. 1895a.
- : Die Segmentirung des Insektenkörpers. *Anhang z. d. Abhandl. d. Kgl. Akad. d. Wiss.*, Berlin. **1895**: 1–33. 1895b.
- : Grundzüge der Entwicklung und des Körperbaues von Odonaten und Ephemeriden. *Anhang z. d. Abhandl. d. Kgl. Akad. d. Wiss.*, Berlin. **1896**: 1–66. 1896a.
- : Ein Beitrag zur Entwicklungsgeschichte der Insecta apterygota. *Sitzb. d. kgl. preuss. Akad. d. Wiss.*, Berlin. **1896**: 1385–1389. 1896b.
- : Ueber die Lebensweise und Entwicklung von *Ephemera vulgata* L. *Sitzb. d. Ges. Naturf. Freunde*, Berlin. **1896**: 82–96. 1896c.
- : Ueber die Bildung und den Bau des Darmkanals bei niederen Insekten. *Sitzb. d. Ges. Naturf. Freunde*, Berlin. **1897**: 111–119. 1897. Review: *Zool. Centr.* **4**: 697–698. 1897a.
- : Entwicklungsgeschichtliche Untersuchungen an *Lepisma saccharina* L. *Zeitschr. f. wiss. Zool.* **62**: 583–631. 1897b. Review: *Jour. Roy. Micr. Soc.* **1897**: 372–373. 1897.
- : Ueber die Organisation und Entwicklung von *Bacillus rossii* Fabr. *Sitzb. d. kgl. preuss. Akad. d. Wiss.*, Berlin. **1897**: 363–373. 1897c.
- : Mitteilungen über die Segmentierung und der Körperbau der Myriopoden. *Sitzb. d. kgl. preuss. Akad. d. Wiss.* Pp. XL, XLI. 1897d.
- : Zu Entwicklungsgeschichte der Chilopoden. *Sitzb. d. kgl. preuss. Akad. d. Wiss.*, Berlin. **1898**: 244–251. 1898a.

- : Bemerkungen zu dem Aufsatz Verhoeff's "Noch einige Worte über Segmentanhänge bei Insecten und Myriopoden." *Zool. Anz.* **21**: 173–180. 1898b.
- : Ueber bläschenförmige Organe bei den Gespenstheuschrecken. *Sitzb. d. kgl. preuss. Akad. d. Wiss.*, Berlin. **1899**: 563–575. 1899a.
- : Beiträge zur Morphologie und Entwicklungsgeschichte der Rhynchoten. *Nova Acta. Abhandl. d. Kaiserl. Leop.-Carol. deut. Akad. d. Naturf.* **74**: 351–456. 1899b.
- : Eier, embryonen und junge Larven von *Anisolabis litorea*. *Verhandl. d. deut. Zool. Ges.* **9**: 289–290. 1899c.
- : Die Entwicklungsgeschichte der Scolopendra. *Zoologica*. **13** (33): 1–244. 1901.
- , and H. HEYMONS: Die Entwicklungsgeschichte von *Machilis*. *Verhandl. d. deut. Zool. Ges.* **15**: 123–135. 1905a.
- HEYMONS, R.: Drei neue Arbeiten über Insectenkeimblätter. *Zool. Zentr.* **12**: 677–690. 1905b.
- : Eine Plazenta bei einem Insekt (*Hemimerus*) *Verhandl. d. deut. Zool. Ges.* **19**: 97–107. 1909.
- : Ueber den Genitalapparat und die Entwicklung von *Hemimerus talpodes* Walker. *Zool. Jahrb. Supplement* **15**. **2**: 141–184. 1912.
- HIBBARD, H.: Growth stages in the egg of *Bombyx mori*. *Anat. Record*. **54**: 84. 1932.
- HILL, C. C.: A preliminary account of two Serphoid (Proctotrupoid) parasites of the Hessian fly. *Proc. Entomol. Soc. Washington*. **24**: 109–117. 1922.
- : *Platygaster vernalis*, an important parasite of the Hessian fly. *Jour. Agr. Research*. **25**: 31–42. 1923.
- : *Platygaster hiemalis*, a parasite of the Hessian fly. *Jour. Agr. Research*. **32**: 261–275. 1926.
- , and W. T. EMERY: The biology of *Platygaster herickii* a parasite of the Hessian fly. *Jour. Agr. Research*. **55**: 199–213. 1937.
- HINMAN, E. H.: The presence of bacteria within the eggs of mosquitoes. *Science*. **76**: 106–107. 1932.
- HIRSCHLER, J.: Embryologische Untersuchungen an *Catocala nupta* L. *Bull. intern. d. l'acad. d. sci. d. Cracovie*. **1905**: 802–810. 1905 (1906).
- : Ueber leberartige Mitteldarmdrüsen und ihre embryonale Entwicklung bei *Donacia*. *Zool. Anz.* **31**: 766–770. 1907a.
- : Entwicklungsgeschichtliche Studien an Lepidopteren. *Bull. d. soc. polon. p. l'avance. d. sci. Léopol.* 1907b.
- : Observations sur le développement des embryons des papillons. *Arch. Nauk, Lwow*. **1**: 1–84. 1907c.
- : Beiträge zur embryonalen Entwicklung der Coleopteren. *Bull. intern. d. l'acad. d. sci. d. Cracovie*. **1908**: 508–522. 1908.
- : Ueber die Entwicklung der Keimblätter und des Darmes bei *Gastroidea viridula*. *Bull. intern. d. l'acad. d. sci. d. Cracovie*. **1909**: 284–310. 1909a.
- : Die Embryonalentwicklung von *Donacia crassipes* L. *Zeitschr. f. wiss. Zool.* **92**: 627–744. 1909b.
- : Deux types différents d'embryons dans une même espèce. Etude analytique de la forme et du développement des Aphides. *Lwow księga Pamiątkowa ku uczczeniu Prof. J. Nusbauma*. **1911**: 175–195. 1911.
- : Embryologische Untersuchungen an Aphiden. *Zeitschr. f. wiss. Zool.* **100**: 393–446. 1912.
- : Embryogenese der Insekten. In Schröder's "Handbuch der Entomologie." Chap. 10, pp. 570–824 (1924). Gustav Fischer, Jena. 1928.

- : Sur le développement de la symétrie bilatérale des ovocytes chez *Cicindela hybrida*. *Arch. zool. exp. et gen.*, Paris. **74**: 541-547. 1932.
- HODSON, A. C.: The origin and differentiation of the sex organs of *Tribolium confusum*. *Ann. Entomol. Soc. Amer.* **27**: 278-288. 1934.
- HOFFMANN, R. W.: Zur Kenntnis der Entwicklungsgeschichte der Collembolen. *Zool. Anz.* **37**: 353-377. 1911.
- : Zur Embryonalentwicklung der Strepsipteren. *Nachr. v. d. Kgl. Ges. d. Wiss. z. Göttingen. Math.-Phys. Klasse.* **1913**: 392-408. 1913.
- : Die embryonalen Vorgänge bei den Strepsipteren und ihre Deutung. *Verhandl. d. deut. Zool. Ges.* **24**: 192-206. 1914.
- HOLLANDE, A. C.: La digestion des bacilles tuberculeux par les leucocytes du sang des chenilles. *Arch. zool. exp. et gen.* **70**: 231-280. 1930.
- HOTTES, F. C.: Concerning the structure, function, and origin of the cornicles of the family Aphididae. *Proc. Biol. Soc. Washington.* **41**: 71-84. 1928.
- HOVASSE, R.: Un mode de symbiose nouveau chez les Cochenilles. *Compt. rend. acad. sci. fr.*, Paris. **190**: 322-324. 1930.
- HOWARD, L. O.: Polyembryony and the fixing of sex. *Science.* **24**: 810-818. 1906.
- : Two new instances of polyembryony among Encyrtidae. *Science.* **49**: 43-44. 1919.
- : An obvious new case of polyembryony. *Science.* **62**: 308. 1925.
- : Résumé and conclusions to Paul Marchal's extended paper on the Trichogrammas. *Ann. Entomol. Soc. Amer.* **36**: 551-557. 1937.
- HOWLAND, R. B.: Viability of *Drosophila* spermatozoa in sea water. *Science. New ser.* **76**: 624-625. 1932.
- , and C. W. ROBERTSON: An easily constructed electromicrocauter for use in cellular biology. *Science. New ser.* **80**: 165-166. 1934.
- HUETTNER, A. F.: The origin of the germ cells in *Drosophila melanogaster*. *Jour. Morphology.* **37**: 385-423. 1923.
- : Maturation and fertilization in *Drosophila melanogaster*. *Jour. Morphology.* **39**: 249-265. 1924.
- : Irregularities in the early development of the *Drosophila melanogaster* egg. *Zeitschr. f. Zellf. mikrosk. Anat.* **4**: 599-610. 1927.
- : Octoploidy and diploidy in *Miastor americana*. *Anat. Record.* **60** (supplement): 80. 1934.
- : Nuclear movements in the developing *Drosophila* egg. *Anat. Record.* **64** (supplement): 59. 1935.
- HUETTNER, A. R., and M. RABINOWITZ: Demonstration of the central body in the living cell. *Science. New ser.* **78**: 367-368. 1933.
- HUGHES-SCHRADER, S.: Reproduction in *Aeroschismus wheeleri*. *Jour. Morphology.* **39**: 157-205. 1924.
- : Contributions to the life history of the Iceryine coccids, with special reference to parthenogenesis and hermaphroditism. *Ann. Entomol. Soc. Amer.* **23**: 359-380. 1930.
- HUIE, L. H.: The formation of the germ-band in the egg of the Holly Tortrix Moth. *Proc. Roy. Soc. Edinburgh.* **38**: 154-165. 1918.
- *HUMMEL, C. D.: Entwicklungsgeschichte der *Blatta germanica*. *Oken. Isis.* Pp. 898-908. 1835.
- HUSAIN, M. T.: Yolk formation in some Arthropods. *Nature.* **119**: 817. 1927.
- HUSSEY, P. B.: Studies on the pleuropodia of *Belostoma flumineum* and *Ranatra fusca*, with a discussion of these organs in other insects. *Entomol. Amer.* **7**: 1-80. 1926.

- HUXLEY, J. S., and G. R. DEBEER: "The Elements of Experimental Embryology." Pp. 1-514. Cambridge University Press. 1934.
- *IKEDA, Y.: On the embryology of *Bombyx mori* L. *Nippon Sanshi Kwai Hô Tokio*. **164**: 12-16. **165**: 14-18. 1906.
- IMMS, A. D.: "A General Textbook of Entomology." Pp. 1-727. Methuen, London. 1934.
- : The ancestry of insects. *Trans. Soc. British Entomol.* **3**: 1-32, 1936.
- : "Recent Advances in Entomology." Pp. 1-431. Churchill, London. 1937.
- INKMANN, F.: Beiträge zur Entwicklungsgeschichte des Kornkäfers (*Calandra granaria*). Die Anfangsstadien der Embryogenese. *Zool. Jahrb., (Anat.)*. **56**: 521-558. 1933.
- JACKSON, D. J.: The biology of *Dinocampus* (*Perilitus*) *rutilus*, a braconid parasite of *Sitona lineata*. *Proc. Zool. Soc. London*. **1928**: 597-630. 1928.
- JACKSON, H. W.: "The Morphology and Histogenesis of the Blood of the Mealworm (*Tenebrio molitor*) with Observations on Its Embryology." Thesis abstracts, Cornell University. 1939.
- JANET, C.: Sur les nerfs céphaliques, les corpora allata et le tentorium de la fourmi (*Myrmica rubra*). *Mém. d. soc. zool. d. France*. **12**: 295-335. 1899.
- *JAWOROWSKY, A.: Ueber die Entwicklung des Rückengefäßes und speciell der Musculatur bei *Chironomus* und einigen anderen Insecten. *Sitzb. Akad. Wien*. **80** (1): 238-258. 1880.
- JEFFREY, W. R.: Further notes on the development of the embryo in eggs of *Botys hyalinis*. *Entomol. Monthly Mag.* **23**: 173-178. 1887.
- JENTSCH, S.: Ovoviviparie bei einer einheimischen Copeognathenart (*Hyperetes guestphalicus*). *Zool. Anz.* **116**: 287-289. 1936.
- JOHANSEN, O. A.: Paedogenesis in *Tanytarsus*. *Science*. **32**: 768. 1910.
- : Parthenogenesis and paedogenesis in *Tanytarsus*. Insect notes for 1910. *Maine. Agr. Exp. Sta. Bull.* **187**: 3-4. 1911.
- : Development of the germ-band and embryonic envelopes in *Diacrisia virginica*. *Anat. Record*. **41**: 71. 1928.
- : Some phases in the embryonic development of *Diacrisia virginica*. *Jour. Morphology*. **48**: 493-541. 1929.
- : Aquatic Diptera, Part 4. Chironomidae, subfamily Chironominae. *Cornell Univ. Agr. Exp. Sta. Mem.* **210**: 1-56. 1937.
- JOHNSON, C. G.: The absorption of water and the associated volume changes occurring in the eggs of *Notostira erratica* (Hemiptera, Capsidae) during embryonic development under experimental conditions. *Jour. Expl. Biol., London*. **14**: 413-421. 1937.
- *JOLY, N.: Etudes sur l'embryogénie des éphémères, notamment chez la *Palingenia virgo*. *Mém. acad. Toulouse*. **1875**: 1-12. 1875. Review: *Ann. Mag. Natural Hist.* **17**: (4): 481-484. 1876.
- JORDAN, K.: Anatomie und Biologie der Physapoda. *Zeitschr. f. wiss. Zool.* **47**: 541-62C. 1888.
- : Notes on the anatomy of *Hemimerus talpoides*. *Novitates Zoologicae*. **16**: 327-330. 1909.
- JOUBERT, M.: Recherches pour servir à l'histoire de la génération chez les insectes. *Compt. rend. hebd. d. séances d. l'acad. d. sci.* **93**: 975-977. 1881 (1882).
- *JUCCI, C.: La capacità di sviluppo dell'uovo vergine o fecondato, nei bachi da seta (*Bombyx mori*). *Boll. ist. Zool. Roma*. **3**: 86-99. 1926.
- : Ricerche di genetica sui bachi da seta. *Boll. soc. nat. Napoli*. **45**: 3-20. 1933 (1934).

- KAHLE, W.: Die Pädogenese der Cecidomyiiden. *Zoologica*, Stuttgart. H55: 1-80. 1908.
- *KARAWAJEW, W.: Du développement embryonnaire de *Pyrrhocoris apterus*. *Zapiski Kiev. Abshch.* 13: 1-34. In Russian. 1893.
- KELLICOTT, W. E.: "A Textbook of General Embryology." 376 pp. Holt, New York. 1913.
- KENNEDY, C. H.: The habits and early stages of the dragonfly, *Gomphaeschna furcillata*. *Proc. Indiana Acad. Sci.* 45: 315-322. 1935 (1936).
- *KENNEL, J.: Entwicklungsgeschichte von *Peripatus edwardsi* und *Peripatus torquatus*. *Arb. aus. d. zool. Inst. Würzburg.* 7: 95. 1884. 8: (2): 1-94. 1886. Review: *Leistungen im Gebiete d. Entomol.* 1884: 73-75. 1885. 1886: 107-111. 1887.
- KERSHAW, J. C.: Development of an embiid. *Jour. Roy. Micr. Soc.* 1914: 24-27. 1914.
- KESSEL, E. L.: The embryology of fleas. *Smithsonian Misc. Coll.* 98 (3): 1-78. 1939.
- KING, R. L., and E. H. SLIFER: Genetic analysis of parthenogenesis in Nabour's Grouse Locusts. *Amer. Naturalist.* 67: 80-81. 1933.
- : Insect development. VIII. Maturation and early development of unfertilized grasshopper eggs. *Jour. Morphology.* 56: 603-620. 1934.
- KING, S. D.: Note on the oögenesis of *Peripatopsis capensis*. *Quart. Jour. Micr. Sci.* 70: 553-558. 1926.
- KIRCHNER, H.: Biologische Studien über *Carabus cancellatus*. *Zeitschr. f. Morph. u. Oekol. d. Tiere.* 7: 489-534. 1927.
- KLEVENHUSEN, F.: Beiträge zur Kenntnis der Aphidensymbiose. *Zeitschr. f. Morph. u. Oekol. d. Tiere.* 9: 97-165. 1927.
- KLOTS, A. B.: Ovoviviparity in *Colias*? *Entomol. News.* 46: 58. 1935.
- KNOWER, H. M.: The development of a termite (*Eutermes rippertii*?). *Johns Hopkins Univ. Circ.* 15: 86-87. 1896. Reproduced: *Amer. Naturalist.* 18: 277-282. 1896. *Abstr. Zool. Centr.* 3: 740. 1896.
- : The embryology of a termite (*Eutermes rippertii*?). *Jour. Morph.* 16: 505-568. 1900. Review: *Zool. Centr.* 7: 505-508. 1900.
- KOCH, A.: Die Symbiose von *Oryzaephilus surinamensis* (Cucujidae). *Zeitschr. f. Morph. u. Oekol. d. Tiere.* 23: 389-424. 1931.
- KÖLLIKER, A.: Observationes de primâ insectorum genesi adjectâ articulorum evolutionis cum vertebratorum comparatione. *Ann. d. sci. naturelles.* 20: 253-284. 1843.
- KOROTNEFF, A.: Entwicklung des Herzens bei *Gryllotalpa*. *Zool. Anz.* 6: 687-690. 1883.
- : Die Embryologie der *Gryllotalpa*. *Zeitschr. f. wiss. Zool.* 41: 570-604. 1885. Review: *Biol. Centr.* 5: 689-692. 1886. *Amer. Naturalist.* 20: 460-462. 1886.
- : Zur Entwicklung des Mitteldarmes bei den Arthropoden. *Biol. Centr.* 14: 433-434. 1894.
- KORSCHULT, E.: Ueber die Bildung des Chorions und die Micropylen bei den Insecteneiern. *Zool. Anz.* 7: 394-398, 420-425. 1884.
- : Zur Frage nach dem Ursprung der verschiedenen Zellenelemente der Insectenovarien. *Zool. Anz.* 8: 581-599. 1885.
- : Ueber die Entstehung und Bedeutung der verschiedenen Zellenelemente der Insectenovariums. *Zeitschr. f. wiss. Zool.* 43: 537-720. 1886.
- : Zur Bildung der Eihüllen der Mikropylen und Chorionanhänge. *Nova Acta d. Kaiserl. Leop.-Carol. deut. Akad. d. Naturf.* 51: 181-252. 1887a.

- : Ueber einige interessante Vorgänge bei der Bildung der Insecteneier. *Zeitschr. f. wiss. Zool.* **45**: 327–397. 1887b.
- : Zur Embryonalentwicklung des *Dytiscus marginalis*. *Zool. Jahrb. Supplement* 15. **2**: 499–532. 1912.
- , and K. HEIDER: "Textbook of the Embryology of Invertebrates." Vol. III, pp. 1–441. Macmillan. 1899.
- : "Vergleichende Entwicklungsgeschichte der Tiere." Vol. II, pp. 535–1314. Gustav Fischer, Jena. 1936.
- KOULAGUINE: see Kulagin.
- KOWALEWSKI, A.: Embryologische Studien an Würmern und Arthropoden. *Mém. d. l'acad. imp. d. sci. d. St. Petersburg.* 7th ser. **16**: (12): 31–71. 1871.
- : Zur embryonalen Entwicklung der Musciden. *Biol. Centr.* **6**: 49–56. 1886. Summary: *Jour. Roy. Micr. Soc.* Pp. 429–430. 1886.
- KRAUSE, G.: Analyse erster Differenzierungsprozesse im Keim der Gewächshaus-schrecke durch Künstlich erzeugte Zwillingsdoppel und Mehrfachbildungen. *Arch. Entwickl. Mech.* **132**: 115–205. 1934.
- : Einzelbeobachtungen und typische Gesamtbilder der Entwicklung von Blastoderm und Keimanlage im Ei der Gewächshaus-schrecke, *Tachycines asynamorus*. *Zeitsch. f. Morph. und Oekol. d. Tiere.* **34**: 1–78. 1938a.
- : Die Ausbildung der Körpergrundgestalt im Ei der Gewächshaus-schrecke *Tachycines asynamorus*. *Zeitschr. f. Morph. und Oekol. d. Tiere.* **34**: 499–564. 1938b.
- : Die Eitypen der Insekten. *Biol. Centr.* **59**: 495–536. 1939.
- KÜKENTHAL, W.: "Handbuch der Zoologie." Insecta. Pp. 1–30. De Gruyter, Berlin. 1926–1938.
- KULAGIN, N.: Zur Entwicklungsgeschichte der *Platygaster intricator* (femorator). *Zool. Anz.* **13**: 418–424. 1890. Review: *Jour. Roy. Micr. Soc.* **1890**: 713–714. 1890.
- : Zur Entwicklungsgeschichte der parasitischen Hautflügler. *Zool. Anz.* **15**: 85–87. 1892a. Summary: *Jour. Roy. Micr. Soc.* **1892**: 470–471. 1892.
- : (Koulaguine) Notice pour servir à l'histoire du développement des hyménoptères parasites. Congrès intern. de zool. 2d sess. **1892**: 253–277. 1892b.
- : Zur Entwicklungsgeschichte der parasitischen Hymenopteren. *Tagebl. d. zool. abth. d. Ges. d. Fr. d. Naturw.* Moskau. Protokolle. **2**: 35. In Russian. 1894.
- : Beiträge zur Kenntnis der Entwicklungsgeschichte von *Platygaster*. *Zeitschr. f. wiss. Zool.* **63**: 195–235. 1897. *Zool. Centr.* V: 91–94. 1898. Summary: *Jour. Roy. Micr. Soc.* **1898**: 73. 1898.
- *KUPFFER, C.: "De embryogenesi apud Chironomos observationes, Kiliae." Dissertation. 1866a.
- : Ueber das Faltenblatt an den Embryonen der Gattung *Chironomus*. *Arch. f. Mikrosk. Anat.* **2**: 385–398. 1866b.
- LAMEERE, A.: "Précis de zoologie." Masson et Cie, Paris. **4**: 1–468. 1935. **5**: 1–536. 1938.
- LANG, A.: Beiträge zu einer Trophocöltheorie. *Zeitschr. f. Naturw., Jena.* **38**: 1–376. 1903.
- LASSMANN, G. W. P.: The early embryological development of *Melophagus ovinus*, with special reference to the development of the germ cells. *Ann. Entomol. Soc. Amer.* **29**: 397–413. 1936.
- LAUTENSCHLAGER, F.: Die Embryonalentwicklung der weiblichen Keimdrüse bei der Psychide *Solenobia triquetrella*. *Zool. Jahrb. (Anat.)*. **56**: 121–162. 1932.
- LAWSON, C. A.: The significance of germaria in differentiation of ovarioles in female aphids. *Biol. Bull.* **77**: 135–145. 1939.

- LEADORO, G.: Sulla embriologie della cocciniglie. *Redia*. **14**: 137-141. 1920 (1921).
- LÉCAILLON, A.: Sur les feuillets germinatifs des coléoptères. *Compt. rend. hebdom. d. séances d. l'acad. d. sci.* **125**: 876-879. 1897a.
- : Note préliminaire relative aux feuillets germinatifs des coléoptères. *Compt. rend. hebdom. d. séances et mém. d. la soc. d. biol.* **4**: 1014-1016. 1897b.
- : Contribution à l'étude des premiers phénomènes du développement embryonnaire chez les insectes particulièrement chez les coléoptères. *Arch. d'anat. micr.* **1**: 205-224. 1897c.
- : Sur les enveloppes ovulaires de quelques chrysomélides. *Arch. d'anat. micr.* **2**: 89-117. 1898a.
- : Recherches sur le développement embryonnaire de quelques chrysomélides. *Arch. d'anat. micr.* **2**: 118-176, 189-250. 1898b.
- : Remarques au sujet d'un mémoire récent relatif à l'origine des feuillets germinatifs et la formation de l'intestin moyen des Coléoptères. *Compt. rend. hebdom. d. séances et mém. d. la soc. d. biol.* **59**: 583-585, 634-636. 1907.
- LEHMANN, F. E.: see Leuzinger, Wiesmann, and Lehmann.
- LEIBY, R. W.: The polyembryonic development of *Copidosoma gelechiae*, with notes on its biology. *Jour. Morphology*. **37**: 195-285. 1922.
- : The origin of mixed broods in polyembryonic Hymenoptera. *Ann. Entomol. Soc. Amer.* **19**: 290-299. 1926.
- : Polyembryony in Insects. IV. Intern. Congr. Entomol., Ithaca. **2**: 873-887. 1928 (1929).
- , and C. C. HILL: The twinning and monembryonic development of *Platygastr hiemalis*, a parasite of the Hessian fly. *Jour. Agr. Research*. **25**: 337-350. 1923.
- : The polyembryonic development of *Platygastr vernalis*. *Jour. Agr. Research*. **28**: 829-840. 1924 (1925).
- LEMOINE, V.: Recherches sur le développement des podurelles. *Assoc. fran. pour l'avance. d. sci.* **11**: 483-520. 1882 (1883).
- : Sur le *Phylloxera punctata*. 1. Développement des oeufs. *Jour. d. microgr.* **11**: 85-87. 1887.
- : Notes on Hemiptera embryology. *Bull. soc. entomol. d. France*. **61**: clxiv-clxv. 1892.
- : Etude comparée du développement de l'oeuf dans la forme agame aptère, dans la forme agame ailée et dans la forme sexuée du *Phylloxera*. *Zool. Anz.* **16**: 140-142, 145-149. 1893a.
- : Etude comparée du développement de l'oeuf chez le Puceron vivipare et ovipare. *Bull. soc. entomol. d. France*. **62**: LXXXIX-XCVII. 1893b.
- LENGERKEN, H. VON: Ueber die Entstehung bilateral-symmetrischer Insekten-gynander aus verschmolzenen Eiern. *Biol. Zbl.* **48**: 475-509. 1928.
- LEUCKART, R.: Ueber die Mikropyle und den feinern Bau der Schalenhaut bei den Insekteneiern. *Arch. f. Anat. u. Physiol. u. wiss. Medicin.* **1855**: 90-264. 1855.
- : Die Fortpflanzung und Entwicklung der Pupiparen. Nach Beobachtungen an *Melophagus ovinus*. *Abhandl. d. Naturf. Ges., Halle*. **4**: 145-226. 1858a.
- : "Zur Kenntniss des Generationswechsels und der Parthenogenese bei den Insekten." 112 pp. Meidinger Sohn & Comp., Frankfurt. 1858b.
- : Die ungeschlechtliche Fortpflanzung der Cecidomyienlarven. *Arch. f. Naturg.* **31** (1): 286-303. 1865.
- LEUZINGER, H., R. WIESMANN, and F. E. LEHMANN: "Zur Kenntnis der Anatomie und Entwicklungsgeschichte der Stabheuschrecke *Carausius morosus*." Pp. I-IX, 1-414. Gustav Fischer, Jena. (1925) 1926.

- *LEYDIG, F.: Die Dotterfurchung nach ihrem Vorkommen in der Thierwelt und nach ihrer Bedeutung. *Oken. Isis*. **3**: 161-193. 1848.
- : Einige Bemerkungen über die Entwicklung der blattläuse. *Zeitschr. f. wiss. Zool.* **2**: 62-66. 1850.
- : Beiträge zur Kenntnis des thierischen Eies im unbefruchteten Zustande. *Zool. Jahrb. (Anat.)*. **3**: 287-432. 1889.
- LIGNAU, N.: Ueber die Entwicklung des Polydesmus abchasius. *Zool. Anz.* **37**: 144-153. 1911a.
- : Die Embryonalentwicklung des Polydesmus abchasius. Ein Beitrag zur Morphologie der Diplopoden. 249 pp. Thesis. Odessa. 1911b. *Odessa Mem. Soc. Nat.* **38**: 57-305. In Russian. 1912.
- LOWNE, B. J.: "The Anatomy, Physiology, Morphology, and Development of the Blow-fly." Vol. 1, pp. 230-261. R. H. Porter, London. 1890-1892.
- *LUDWIG, H.: Die Eibildung in Thierreiche. *Arb. a. den Zool. Inst. Würzburg*. Vol. 1. 1874.
- MACBRIDE, E. W.: "Textbook of Embryology." Invertebrate. 692 pp. Macmillan. 1914.
- MCNABB, J. W.: A study of the chromosomes in meiosis, fertilization, and cleavage in the grasshopper egg (Orthoptera). *Jour. Morphology*. **45**: 47-96. 1928.
- MALOEUF, N. S. R.: The physiology of Arthropoda development with special reference to insects. *Bull. d. la soc. roy. Entomol. d'Egypte*. **1937**: 88-152. 1937.
- MANSOUR, K.: The development of the larval and adult mid-gut of Calandra oryzae. The Rice Weevil. *Quart. Jour. Micr. Sci.* **71**: 313-352. 1927.
- : Preliminary studies on the bacterial cell mass (accessory cell mass) of Calandra oryzae (the rice weevil). *Quart. Jour. Micr. Sci.* **73**: 421-436. 1930.
- : The development of the adult mid-gut of coleopterous insects and its bearing on systematics and embryology. *Egyptian Univ. Bull. Fac. Sci.* **2**: 1-34. 1934a.
- : On the so-called symbiotic relationship between Coleopterous insects and intracellular microorganisms. *Quart. Jour. Micr. Sci.* **77**: 255-271. 1934b.
- : The entoderm problem in Insecta. *Compt. rend. XII^e Congrès international de Zoologie. Lisbonne*. **1935**: 567-570. 1936.
- MARCHAL, P.: Contribution à l'étude du développement embryonnaire des Hyménoptères parasites. *Compt. rend. hebd. d. séances et mém. d. la soc. d. biol.* **4** (2): 1084-1086. 1897.
- : Le cycle évolutif de l'Encyrtus fuscicollis. *Bull. d. la soc. entomol. d. France*. **67**: 109-111. 1898a.
- : La dissociation de l'oeuf en un grand nombre d'individus distincts et le cycle évolutif chez l'Encyrtus fuscicollis. *Compt. rend. hebd. d. séances d. l'acad. d. sci.* **126**: 662-664. 1898b.
- : Un exemple de dissociation de l'oeuf. Le cycle de l'Encyrtus fuscicollis. *Compt. rend. hebd. d. séances et mém. d. la soc. d. biol.* **5** (10): 238-240. 1898c.
- : Comparaison entre le développement des hyménoptères parasites à développement polyembryonnaire et ceux à développement monoembryonnaire. *Compt. rend. hebd. d. séances et mém. d. la soc. d. biol.* **1**: 711-713. 1899.
- : Le cycle évolutif du Polygonotus minutus. *Bull. d. la soc. entomol. d. France*. **72**: 90-93. 1903.
- : Sur la formation de l'intestin moyen chez les Platygasters. *Compt. rend. hebd. d. séances et mém. d. la soc. d. biol.* **56**: 1091. 1904a.

- : Le déterminisme de la polyembryonie spécifique et le déterminisme du sexe chez les hyménoptères à développement polyembryonnaire. *Compt. rend. hebd. d. séances et mém. d. la soc. d. biol.* **56**: 468–470. 1904b.
- : Recherches sur la biologie et le développement des hyménoptères parasites. La polyembryonie spécifique ou germinogonie. *Arch. d. zool. exptl. et gen.* **2**: 257–335. 1904c.
- : Recherches sur la biologie et le développement des Hyménoptères parasites. Le Platygasters. *Arch. d. zool. exptl. et gen.* 4th ser. **4**: 485–640. 1906.
- MARIANI, G.: Contributo alla conoscenza dello sviluppo embrionale della *Saturnia pyri* Schiff. *Boll. zool. agr. bach.*, Torino. **7**: 205–215. 1936 (1937).
- MARSHALL, W. S.: Contributions towards the embryology and anatomy of *Polistes pallipes*. II. The early history of the cellular elements of the ovary. *Zeitschr. f. wiss. Zool.* **86**: 173–213. 1907.
- : The development and structure of the eyes, ocelli of the female black scale, *Saissatia oleae*. *Jour. Morphology.* **57**: 571–595. 1935.
- and P. H. DERNEHL: Contributions toward the embryology and anatomy of *Polistes pallipes*. I. The formation of the blastoderm and the first arrangement of its cells. *Zeitschr. f. wiss. Zool.* **80**: 122–154. 1905.
- MARTIN, F.: Zur Entwicklungsgeschichte des polyembryonalen Chalcidiers *Ageniaspis* (*Encyrtus*) *fuscolis*. *Zeitschr. f. wiss. Zool.* **110**: 419–479. 1914.
- *MASERA, E.: Flora microbica nelle uova di *Bombyx mori* L. *Rivista biol.*, Rome. **18**: 98–115. 1935.
- MAYER, P.: Ueber Ontogenie und Phylogenie der Insekten. *Zeitschr. f. Naturw.*, Jena. **10**: 125–221. 1876.
- MECZNIKOFF: see Metschnikoff.
- MEGUŠAR, F.: Einfluss abnormaler Gravitationswirkung auf die Embryonalentwicklung bei *Hydrophilus aterrimus*. *Arch. Ent. Mech.* **22**: 141–148. 1906.
- MEINERT, F.: Weitere Erläuterungen über die von Prof. Wagner beschriebene Insectenlarve, welche sich durch Sprossenbildung vermehrt. *Zeitschr. f. wiss. Zool.* **14**: 394–398. 1864.
- MEISENHEIMER, J.: "Entwicklungsgeschichte der Tiere." Vol. I, pp. 1–137; Vol. II, pp. 1–132. Sammlung Götschen. 1917.
- MEISSNER, G.: Beobachtungen über das Eindringen der Samenelemente in den Dotter. II. *Zeitschr. f. wiss. Zool.* **6**: 272–295. 1855.
- MELLANBY, H.: The early embryonic development of *Rhodnius prolixus*. *Quart. Jour. Micr. Sci.* **78**: 71–90. 1936a.
- : The later development of *Rhodnius prolixus*. *Quart. Jour. Micr. Sci.* **79**: 1–42. 1936b.
- MELNIKOW, N.: Beiträge zur Embryonalentwicklung der Insekten. *Arch. f. Naturg.* **35**: 136–189. 1869.
- MELVIN, R.: Oxygen consumption of insect eggs. *Bio. Bull.* **55**: 135–142. 1928.
- MERCIER, M. L.: Les corps bactérioides de la *Blatta* (*Periplaneta orientalis*): *Bacillus cucenoti* n. sp. *Compt. rend. hebd. d. séances et mém. d. la soc. d. biol.* **58**: (II): 682–684. 1906.
- METCALFE, M. E.: The germ-cell cycle in *Phytophaga destructor*. *Quart. Jour. Micr. Sci.* **77**: 585–604. 1935.
- METSCHNIKOFF, E. (Mecznikoff): Ueber die Entwicklung der Cecidomyienlarven aus dem Pseudovum. *Arch. f. Naturg.* **31**: (1): 304–310. 1865.
- : (Mecznikow) Untersuchungen über die Embryologie der Hemipteren. *Zeitschr. f. wiss. Zool.* **16**: 128–132. 1866a.

- : (Mecznikow) Embryologische Studien an Insekten. *Zeitschr. f. wiss. Zool.* **16**: 389–500. 1866b.
- : Embryologie der doppeltfüssigen Myriapoden (Chilognatha). *Zeitschr. f. wiss. Zool.* **24**: 253–283. 1874.
- : Embryologisches über Geophilus. *Zeitschr. f. wiss. Zool.* **25**: 313–322. 1875.
- METZ, C. W.: Chromosome behavior, inheritance and sex determination in *Sciara*. *Amer. Naturalist.* **72**: 485–520. 1938.
- MIALL, L. C., and A. DENNY: "The Structure and Life-history of the Cockroach." 224 pp. Lovell Reeve & Co., London. 1886.
- MIALL, L. C., and A. R. HAMMOND.: "The Structure and Life-history of the Harlequin fly (*Chironomus*)." Pp. 1–196. Clarendon Press, Oxford. 1900.
- MILLER, A.: "The Egg and Early Development of the Stonefly, *Pteronarcys proteus*." Abstracts of theses, Cornell University. **1938**: 259–261. 1939a.
- : The egg and early development of the stonefly *Pteronarcys proteus*. *Jour. Morphology.* **64**: 555–609. 1939b.
- : Embryonic membranes, yolk cells, and morphogenesis of the stone-fly *Pteronarcys proteus*. *Ann. Entomol. Soc. Amer.* **33**: 437–477. 1940.
- *MORGAN, T. H.: Mosaics and gynandromorphs in *Drosophila*. *Proc. Soc. Exptl. Biol. Med.* **11**: 191–192. 1914.
- : "Experimental Embryology." Macmillan, New York. 1927.
- : "Embryology and Genetics." 258 pp. Columbia University Press, New York. 1934.
- , and C. B. BRIDGES: The origin of gynandromorphs. *Carnegie Inst. Pub.* **278**: 1–122. 1919.
- , A. H. STURTEVANT, and C. B. BRIDGES: The constitution of the germ material in relation to heredity. *Carnegie Inst. Yearbook.* **22**: 283–287. 1923 (1924).
- MOSELEY, H. N.: On the structure and development of *Peripatus capensis*. *Phil. Trans. Roy. Soc. London.* **164**: 757–782. 1874.
- MUIR, F., and J. C. KERSHAW: On the later embryological stages of the head of *Pristhesancus papuensis* (Reduviidae). *Psyche.* **18**: 75–79. 1911.
- : The development of the mouth parts in the Homoptera, with observations on the embryo of *Siphanta*. *Psyche.* **19**: 77–89. 1912.
- MUKERJI, R. N.: The "nuclear reaction" in *Apanteles* sp. with special reference to the secondary nuclei and the germ-cell determinant in the egg. *Proc. Roy. Soc. London.* **106** (B): 131–139. 1930.
- MÜLLER, J.: Ueber die Entwicklung der Eier im Eierstock bei den Gespenstheuschrecken. *Nova Acta Phys.-Med. Acad. Leop. Carol.* **12** (2): 553–672. 1825.
- MÜLLER, K.: Histologische Untersuchungen über den Entwicklungsbeginn bei einem Kleinschmetterling (*Plodia interpunctella*). *Zeitschr. f. wiss. Zool.* **151**: 192–242. 1938.
- *MUNCHBERG, P.: Ueber die Entwicklung und die Larve der Libelle *Sympetrum pedemontanum allioni*, zugleich ein Beitrag über die Anzahl der Häutungen der Odonatenlarve. *Arch. f. Naturg.* **7** (N. F.): 559–568. 1939.
- MURPHY, H. E.: Notes on the biology of some of our North American species of Mayflies. *Bull. Lloyd Library, Entomol. Ser.* **2**: 3–39. 1922.
- MURRAY, A.: On the early stages of development of orthopterous insects. *Jour. Proc. Linnean Soc.* **7**: 97–105. 1864.
- MURRAY, M. R.: Secretion in the amitotic cells of the cricket egg follicle. *Biol. Bull.* **50**: 210–234. 1926.
- NACHTSHEIM, H.: Cytologische Studien über die Geschlechtsbestimmung bei der Honigbiene (*Apis mellifica*). *Arch. f. Zellforsch.* **11**: 169–241. 1913.

- NATH, V.: Egg-follicles of *Culex*. *Quart. Jour. Micr. Sci.* **69**: 151-175. 1925.
- , and T. HUSAIN: Origin of yolk in the eggs of *Scolopendra*. *Nature*. **118**: 660-661. 1926.
- NEEDHAM, J.: "Chemical Embryology." 3 vols. Pp. 1-2021. Cambridge University Press. 1931.
- NEEDHAM, J. G., J. R. TRAVER, and Y. HSU: "The Biology of May Flies." 759 pp. Comstock Publishing Company Inc., Ithaca, N. Y. 1935.
- NEL, R. I.: Studies on the development of the genitalia and genital ducts in insects. I. Female of Orthoptera and Dermaptera. *Quart. Jour. Micr. Sci.* **73**: 25-85. 1930.
- NELSEN, O. E.: Life cycle, sex differentiation, and testis development in *Melanoplus differentialis* (Acridae, Orthoptera). *Jour. Morph. Phys.* **51**: 467-525. 1931.
- : The segregation of the germ cells in the grasshopper *Melanoplus differentialis*. *Jour. Morphology*. **55**: 545-574. 1934.
- NELSON, J. A.: The origin of the rudiments of the mesenteron in the honey bee. *Science*. **33**: 273-274. 1911.
- : A peculiar structure in the embryo of the honey bee. *Science*. **35**: 475. 1912.
- : A pair of tracheal invaginations on the second maxillary segment of the embryo of the honey bee. *Science*. **39**: 437. 1914.
- : "The Embryology of the Honey Bee." Pp. 1-282. Princeton University Press. 1915.
- NEWPORT, G.: The organs of reproduction and the development of the Myriapoda. *Phil. Trans. Roy. Soc. London*. **1841**: 99-130. 1841.
- : On the natural history, anatomy, and development of the oil beetle *Meloe*, more especially *Meloe cicutricosus*. *Trans. Linnean Soc.* **20**: 297-357. 1851.
- NICETA, E.: La partenogenesi naturale nel *Bombyx mori* L. *Boll. d. lab. d. zool. agr. e bach. d. reale ist. sup. agr. d. Milano*. **1**: 139-160. 1930.
- NICHOLSON, A. J.: The development of the ovary and ovarian egg of a mosquito, *Anopheles maculipennis*. *Quart. Jour. Micr. Sci.* **65**: 395-448. 1921.
- NIKLAS, O.: Die Eientwicklung der Feuerwanze. *Mikrokosmos*. **28**: 185-189. 1935.
- NOACK, W.: Beiträge zur Entwicklungsgeschichte der Musciden. *Zeitschr. f. wiss. Zool.* **70**: 1-57. 1901.
- NOSKIEWICZ, J., and G. POLUSZYŃSKI: Embryologische Untersuchungen an Strepsipteren. (1) Embryogenesis der Gattung *Stylops*. *Bull. intern. acad. Sci. Cracovie*. **3**: 1093-1226. 1927.
- : Embryologische Untersuchungen an Strepsipteren. II. Teil. Polyembryonie. *Zool. Polon.* **1**: 53-94. 1935.
- : Un nouveau cas de polyembryonie chez les insectes (Strepsiptères). *Compt. rend. d. séances d. la soc. biol.* **90**: 896-898. 1938.
- NUSBAUM, J.: Vorläufige Mittheilung über die Chorda der Arthropoden. *Zool. Anz.* **6**: 291-295. 1883.
- : Bau, Entwicklung und morphologische bedeutung der Leydig'schen Chorda der Lepidoptera. *Zool. Anz.* **7**: 17-21. 1884a.
- *———: Ueber die Entwicklungsgeschichte der Ausführungsgänge der Sexualdrüsen bei Insekten. *Kosmos*. Lemberg. In Polish with German résumé. **9**. 1884b.
- : The embryonic development of the cockroach. In Miall and Denny, "The Structure and Life-history of the Cockroach." Pp. 181-204. 1886.
- : Die Entwicklung der Keimblätter bei *Meloe proscarabaeus*. *Biol. Centr.* **8**: 449-452. 1888.

- : Zur Frage der Segmentierung der Keimstreifens und der Bauchanhänge der Insektenembryonen. *Biol. Centr.* **9**: 516–522. 1889.
- : Zur Frage der Rückenbildung bei den Insektenembryonen. *Biol. Centr.* **10**: 110–114. 1890a.
- *———: Studya nad Morfologija zweierzat. Przyczynek do embryologii maika (Meloë proscarabaeus). *Kosmos*. Lemberg. **15**: 17–47. In Polish. 1890b.
- , and B. FULIŃSKI: Ueber die Bildung der Mitteldarmanlage bei *Phyllodromia* (*Blatta*) *germanica*. *Zool. Anz.* **30**: 362–381. 1906.
- : Zur Entwicklungsgeschichte des Darmdrüsenblattes bei *Gryllotalpa vulgaris*. *Zeitschr. f. wiss. Zool.* **93**: 306–348. 1909.
- *OKA, H.: Experimental studies on the embryonic development of a cricket. *Ann. zool. Jap.*, Tokyo. **14**: 373–376. 1934.
- *OKADA, Y. K.: Origin and development of the photogenic organs of Lampyrids, with special reference to those of *Luciola cruciata* and *Pyrocoelia rufa*. *Mem. Coll. Sci., Kyoto Imp. Univ.* (B). **10**: 209–228. 1935.
- OSBORNE, J. A.: On the embryology of *Botys hyalinalis*. *Sci. Gossip.* **21**: 32–36. 1885.
- OULGANINE: see Uljanin.
- PACKARD, A. S.: On the development of a dragon-fly (*Diplax*). *Proc. Boston Soc. Natural Hist.* **11**: 365–372. 1868.
- : The embryology of *Chrysopa*, and its bearing on the classification of the Neuroptera. *Amer. Naturalist.* **5**: 564–568. 1871a.
- : Embryological studies on *Diplax*, *Perithemis* and the thysanurous genus *Isotoma*. *Mem. Peabody Acad. Sci.* **1** (2): 1–24. 1871b.
- : Embryological Studies on hexapodous insects. *Mem. Peabody Acad. Sci.* **3**: 1–18. 1872a.
- : Embryology of *Isotoma*, a genus of Poduridae. *Proc. Boston Soc. Natural Hist.* **14**: 13–15. 1872b.
- : The embryological development of the locust. *U.S. Entomol. Comm.* **3**: 263–279. 1883a.
- : The development of the bark-boring beetles *Hylurgops* and *Xyleborus*. *U.S. Entomol. Comm.* **3**: 280–282. 1883b.
- : "A Textbook of Entomology." Pp. 1–729. Macmillan, New York. 1903.
- PAGENSTECKER, H. A.: Die ungeschlechtliche Vermehrung der Fliegenlarven. *Zeitschr. f. wiss. Zool.* **14**: 401–416. 1864.
- PARKER, G. H.: Possible pedogenesis in the blow-fly (*Calliphora erythrocephala*). *Psyche.* **29**: 127–131. 1922.
- PARKER, H. L.: *Macrocentrus gifuensis*, a polyembryonic Braconid parasite in the European corn borer. *U.S. Dept. Agr., Tech. Bull.* **230**: 1–63. 1931.
- PARKS, H. B.: Cleavage patterns in *Drosophila* and mosaic formation. *Ann. Entomol. Soc. Amer.* **29**: 350–392. 1936.
- PATERSON, N. F.: A contribution to the embryological development of *Euryope terminalis*. *S. African Jour. Sci.* Pt. 1, The early embryological development. **28**: 344–371. 1931. Pt. 2, Organogeny. **29**: 414–448. 1932.
- : Observations on the embryology of *Corynodes pusis*. *Quart. Jour. Micr. Sci.* **78**: 91–132. 1936.
- PATTEN, W.: The development of phryganids with a preliminary note of *Blatta germanica*. *Quart. Jour. Micr. Sci.* **24**: 549–602. 1884.
- : Studies on the eyes of arthropods. *Jour. Morphology.* **1**: 193–226. 1887. **2**: 97–190. 1888a.
- : Segmental sense-organs of arthropods. *Jour. Morphology.* **2**: 600–602. 1888b.

- PATTERSON, J. T.: Observations on the development of *Copidosoma gelechiae*. *Biol. Bull.* **29**: 333-372. 1915.
- : Studies on the biology of *Paracopidosomopsis*. I. Data on the sexes. *Biol. Bull.* **32**: 291-305. 1917a. III. Maturation and fertilization. **33**: 57-62. 1917b. IV. The asexual larvae. **35**: 362-376. 1918.
- : The development of *Paracopidosomopsis*. *Jour. Morphology.* **36**: 1-69. 1921.
- : Polyembryony in animals. *Quart. Rev. Biol.* **2**: 399-426. 1927.
- PAULI, M. E.: Die Entwicklung geschnürter und zentrifugierter Eier von *Calliphora erythrocephala* und *Musca domestica*. *Zeitschr. f. wiss. Zool.* **129**: 483-540. 1927.
- PAYNE, F.: A study of the cytoplasm in insect ova. *Jour. Morphology.* **53**: 523-591. 1932.
- PAYNE, N. M.: Regional growth rates in insects. *Anat. Record.* **60** (supplement): 29. 1934.
- PEDASCHENKO, D.: Obrazovanie zarodischevoi polosti u *Notonecta glauca*. *Viestnik estestvoznaniia izdaniia C. Peterburgskago Obschestva.* **1**: 358-362. 1890.
- PETRUNKEWITSCH, A.: Ueber die Entwicklung des Herzens bei *Angelastica alni*. *Zool. Anz.* **21**: 140-143. 1898.
- : Die Richtungskörper und ihr Schicksal im befruchteten und unbefruchteten *Bienenei*. *Zool. Jahrb. (Anat.)*. **14**: 573-608. 1901.
- : Das Schicksal der Richtungskörper im Drohneei. Ein Beitrag zur Kenntnis der natürlichen Parthenogenese. *Zool. Jahrb. (Anat.)*. **17**: 481-516. 1903.
- PFLUGFELDER, O.: Ueber den Mechanismus der Segmentbildung bei Embryonalentwicklung und Anamorphose von *Platyrrhacus amauros*. *Zeitschr. f. wiss. Zool.* **140**: 650-723. 1932.
- *———: Vergleichend-anatomische, experimentelle und embryologische Untersuchungen über das Nervensystem und die Sinnesorgane der Rhynchoten. *Zoologica*, Stuttgart. **34** (93): 1-102. 1937.
- PHILIPTSCHENKO, J.: Zur Kenntnis der Apterygotenembryologie. *Zool. Anz.* **39**: 43-49. 1912a.
- : Beiträge zur Kenntnis der Apterygoten. III. Die Embryonalentwicklung von *Isotoma cinerea*. *Zeitschr. f. wiss. Zool.* **103**: 519-660. 1912b.
- PHILLIPS, E. F.: A review of parthenogenesis. *Proc. Amer. Phil. Soc.* **42**: 275-345. 1903.
- PHILLIPS, W. J.: Further studies of the embryology of *Toxoptera graminum*. *Jour. Agr. Research.* **4**: 403-404. 1915.
- *PICTET, A.: Des diapauses embryonnaires, larvaires, et nymphales chez les insectes lépidoptères. *Bull. soc. lépidopt. Genève.* **1**: 98-153. 1906.
- *PIERANTONI, H.: Studi sullo sviluppo di *Icerya purchasi*. (2) Origine ad evoluzione degli organi sessuali maschili. *Ermafroditismo.* **7**: 27-49. (3) Osservazione di embriologie. *Arch. ital. Napoli.* **7**: 243-274. 1914.
- PIERANTONI, U.: L'organo simbiotico sullo sviluppo di *Calandra oryzae*. *Rend. dell' accad. d. sci. fisiche e mat.* **33** (3): 244-250. 1927.
- PIETI, S. D.: Contributo all' embriologia della *Pieris brassicae*. *Boll. d. lab. d. zool. agr. e bach. d. reale ist. sup. agr. d. Milano.* **6**: 93-109. 1934 (1935).
- PLAGNIOL, E. DE: "Embryologie de l'oeuf du ver à soie." 55 pp. Privas, impr. du Patriote, 1886.
- PLATNER, G.: Die erste Entwicklung befruchteter und parthenogenetischer Eier von *Liparis dispar*. *Biol. Centr.* **8**: 521-524. 1888.
- *POLUSZYŃSKI, G.: O tworzeniu się listka spodniego, zarwiazka pleciowego i o blastokinezie u czerwców (*Coccidae*). *Księga pam. XI. zjazdu Lek. i Przyrod. Polsk. Kraków.* 1911.

- POULSON, D. F.: Embryology of *Drosophila*. *Genetics*. **22**: 204. 1937.
- : "The Embryonic Development of *Drosophila melanogaster*." 51 pp. Hermann et Cie, Paris. 1937.
- PRATT, H. S.: Imaginal discs in insects. *Psyche*. **8**: 15-30. 1897.
- : The embryonic history of imaginal discs in *Melophagus ovinus*, together with an account of the earlier stages in the development of the insect. *Proc. Boston Soc. Natural Hist.* **29** (13): 241-272. 1900. Review: *Zool. Centr.* **8**: 245-248. 1901.
- PROVASOLI, L.: Contributo alla biologia ed all' embriologia della *Galerucella luteola* e del suo endofago *Tetrastichus xanthomelaenae*. *Bol. d. lab. d. zool. agr. e bach. d. reale ist. sup. agr. d. Milano*. **3**: 53-56. 1932.
- *PROWAZEK, S.: Bau und Entwicklung der Collembolen. *Arb. Zool. Inst. Wien*. **12** (3): 335-363, 364-370. 1900a.
- : Structure and development of Collembola. *Jour. Roy. Micr. Soc.* **1900**: 580-581. 1900b.
- RABINOWITZ, M.: Studies on the cytology and early embryology of the egg of *Drosophila melanogaster*. *Genetics*. **22**: 204-205. 1937.
- RABITO, L.: Sull' origine del' intestino medio nella *Mantis religinosa*. *Il Naturalista siciliano*. **2**: 181-183. 1897.
- RATHKE, H.: Zur Entwicklungsgeschichte der Maulwurfsgrille (*Gryllotalpa vulgaris*). *Arch. f. Anat. Physiol. wiss. Med.* **1844**: 27-37. 1844.
- : Studien zur Entwicklungsgeschichte der Insekten. *Entomol. Zeitschr. Stett.* **22**: 169-191, 229-240. 1861. **23**: 389-408. 1862.
- RAU, P., and N. RAU: The biology of *Stagmomantis carolina*. *Trans. Acad. Sci. St. Louis*. **22**: 1-58. 1913.
- *RAVETTA, E.: Il poliploidismo della cellule somatiche dei Ditteri. *Boll. zool.* **2**: 47-56. 1931.
- REDI, F.: "Esperienze intorno alla generazione degl' insetti fatte." Napoli. 1671. ("Experiments on the Generation of Insects." Trans. by H. Bigelow.) 160 pp. Open Court. 1909.
- REITH, F.: Entwicklung des Musca-Eies nach Ausschaltung verschiedener eibereiche. *Zeitschr. f. wiss. Zool.* **126**: 181-238. 1925.
- : Zur experimentellen Analyse der Primitiventwicklung bei Insekten. *Naturwissenschaften*. **19**: 398-399. 1931a.
- : Versuche über die Determination der Keimesanlage bei *Camponotus ligniperda*. *Zeitschr. f. wiss. Zool.* **139**: 664-734. 1931b.
- *———: Über entwicklungsmechanische Untersuchungen an Insekten. *Jahresber. Schles. Ges. wasserl. Cult.*, Breslau. **104**: 56-63. 1931 (1932a).
- : Ueber die Localisation der Entwicklungsfaktoren im Insektenkeim. I. Zentrifugerversuche an Ameiseneiern. *Arch. Entomol.-Mech.* **127**: 283-299. 1932b.
- : Ueber die Determination der Keimesanlage bei Insekten. *Zeitschr. f. wiss. Zool.* **147**: 77-100. 1935.
- REITHFELDT C.: Entwicklung der Insektenlarve im Ei. *Mikrosk.* **18**: 201-205. 1925.
- RICHARDS, A.: "Outline of Comparative Embryology." 444 pp. Wiley, New York. 1931.
- RICHARDS, A. G.: Comments on the origin of the midgut in insects. *Jour. Morphology*. **53**: 433-441. 1932.
- , and A. MILLER: Insect development analyzed by experimental methods: A review. Pt. 1, Embryonic stages. *Jour. N. Y. Entomol. Soc.* **45**: 1-60. 1937.

- RICHTER, G.: Untersuchungen an Homopterensymbionten. 1. Die Symbionten der Diaspinen und Asterolekanien. 2. Die Symbionten einiger exotischer Zikaden. *Zeitschr. f. Morph. u. Oekol. d. Tiere.* **10**: 174–206. 1928.
- RIES, E.: Die Symbiose der Läuse und Federlinge. *Zeitschr. f. Morph. u. Oekol. d. Tiere.* **20**: 233–367. 1931.
- : Die prozesse der Eibildung und des Eiwachstums bei Pediculiden und Mallophagen. *Zeitschr. Zellf. u. Mikrosk. Anat.* **16**: 314–388. 1932.
- RILEY, W. A.: The embryological development of the skeleton of the head of Blatta. *Amer. Naturalist.* **38**: 777–810. 1904.
- : Polymbryony and sex-determination. *Science.* **25**: 106–107. 1907.
- RITTER, R.: Die Entwicklung der Geschlechtsorgane und des Darmes bei Chironomus. *Zeitschr. f. wiss. Zool.* **50**: 408–427. 1890.
- RITTERSHAUS, K.: Eine neue Art von Eisprengeern bei Lamellicornierlarven (Phyllopertha horticola und Anomala aenea). *Zool. Anz.* **62**: 31–33. 1925.
- RIZZI, M.: Sullo sviluppo dell' uovo di Bombyx (Sericaria) mori. *Redia.* **8**: 323–359. 1912.
- ROBIN, C.: Mémoire sur la production des cellules du blastoderme sans segmentation du vitellus chez quelques articulés. *Compt. rend. hebdomad. séances d. l'acad. d. sci.* **54**: 150–153. 1862a.
- : Mémoire sur les phénomènes qui se passent dans l'ovule avant la segmentation du vitellus. *Jour. d. la physiol. d. l'homme et d. animaux.* **5**: 67–109. 1862.
- *ROONWAL, M. L.: Fate of the embryonic membranes in insects. *Current Sci., Bangalore.* **4**: 317–318. 1935.
- : The growth-changes and structures of the egg of the African Migratory Locust, *Locusta migratoria*. *Bull. Entomol. Res.* **27**: 1–14. 1936.
- : Studies on the embryology of the African migratory locust, *Locusta migratoria migratorioides*. I. The early development, with a new theory of multiphased gastrulation among insects. II. Organogeny. *Phil. Trans. Roy. Soc. London. Ser. B.* **226**: 391–421. 1936. **227**: 175–244. 1937.
- : On a new law of the bi-triangular medial concentration of the cephalic appendages in the Chilopoda and the Insecta. *Jour. Morphology.* **64**: 1–8. 1939a.
- : Some recent advances in insect embryology, with a complete bibliography of the subject. *Jour. Roy. Asiatic Soc. Bengal.* **4**: 17–105. 1939b.
- ROSTAND, J.: Demi-larves de mouches obtenues par ligature des oeufs. *Bull. d. la soc. entomol. d. France.* **1927**: 163, 215–216. 1927.
- RYDER, J. A.: The origin of the amnion. *Amer. Naturalist.* **20**: 179–185. 1886a.
- : The development of *Anurida maritima*. *Amer. Naturalist.* **20**: 299–302. 1886b.
- SACHTLEBEN, H.: "Ueber die Entwicklung der Geschlechtsorgane von Chironomus mit besondere Berücksichtigung der keimbahnbegleitenden Substanzen." Dissertation. 60 pp. University of Munich Press, Munich. 1918.
- *SAINT HILAIRE, K. K.: Die Bildung des Eies von *Dytiscus*. *Compt. rend. soc. natural.* St. Petersburg. **1895**: 21–33. In Russian. German summary. 1895.
- SAITO, S.: A study on the development of the tusser worm, *Antheraea pernyi*. *Jour. Coll. Agr., Hokkaido Imp. Univ., Sapporo.* **33**: 249–266. 1934.
- : On the development of the tusser, *Antheraea pernyi*, with special reference to the comparative embryology of insects. *Jour. Coll. Agr., Hokkaido Imp. Univ., Sapporo.* **40**: 35–109, 1937.
- SALING, T.: Zur Kenntnis der Entwicklung der Keimdrüsen von *Tenebrio molitor*. *Zeitschr. f. wiss. Zool.* **86**: 238–303. 1907.

- SCHAEFER, P. E.: The embryology of the central nervous system of *Phormia regina*. *Ann. Ent. Soc. Amer.* **31**: 92-111. 1938.
- SCHEINERT, W.: Symbiose und embryonalentwicklung bei Rüsselkafern. *Zeitschr. f. Morph. u. Oekol. d. Tiere.* **27**: 76-127. 1933.
- SCHLEIP, W.: "Die Determination der Primitiventwicklung." XII + 914 pp. Akademische Verlagsgesellschaft, Leipzig. 1929.
- *SCHMIDT, F.: Die Bildung des Blastoderms und des Keimstreifens der Musciden. *Sitzb. Naturf. Ges. Dorpat.* **8**: 366-371. 1889.
- SCHMUCK, M. L., and C. W. METZ: The maturation divisions and fertilization in eggs of *Sciara coprophila*. *Proc. Nat. Acad. Sci. Washington.* **18**: 349-352. 1932.
- SCHNEIDER, A.: Die Entwicklung der Geschlechtsorgane der Insecten. *Zool. Beitr.* (Schneider). **1**: 257-300. 1885a.
- : Chironomus grimmii und seine Parthenogenesis. *Zool. Beitr.* (Schneider). **1**: 301-302. 1885b.
- SCHNETTER, M.: Physiologische Untersuchungen über das Differenzierungszentrum in der Embryonalentwicklung der Honigbiene. *Arch. Entwickl. Mech. Organ.* **131**: 285-323. 1934a.
- : Morphologische Untersuchungen über das Differenzierungszentrum in der Embryonalentwicklung der Honigbiene. *Zeitschr. f. Morph. u. Oekol. d. Tiere.* **29**: 114-195. 1934b.
- SCHÖLZEL, G.: Die Embryologie der Anopluren und Mallophagen. *Zeitschr. f. Parasitenkunde.* **9**: 730-770. 1937.
- SCHRADER, F.: The origin of the mycetocytes in *Pseudococcus*. *Biol. Bull.* **45**: 279-309. 1923.
- SCHRÖDER, C.: see Hirschler.
- SCHWANGART, F.: Studien zur Entodermfrage bei den Lepidopteren. *Zeitschr. f. wiss. Zool.* **76**: 167-212. 1904. Review: *Zool. Zentr.* **12**: 677-690. 1905.
- : Zur Entwicklungsgeschichte der Lepidopteren. *Biol. Centr.* **25**: 721-729; 777-789. 1905.
- : Ueber die Beziehungen zwischen Darm- und Blutzellenbildung bei *Endromis versicolor*. *Sitzb. Ges. Morph. Phys., München.* **22**: 95-113. 1906-(1907).
- SCHWARTZE, E.: Zur Kenntnis der Darmentwicklung bei Lepidopteren. *Zeitschr. f. wiss. Zool.* **66**: 450-496. 1899.
- SLATER, W. L.: On the early stages of the development of a South American species of *Peripatus*. *Quart. Jour. Micr. Sci.* **28**: 343-363. 1888.
- SCOTT, A. C.: Paedogenesis in the Coleoptera. *Zeitschr. f. Morph. u. Oekol. d. Tiere.* **33**: 633-653. 1938.
- SEBESS VON ZILAH: Chironomiden Studien. *Arb. d. erste. Abt. d. Ung. biol. Forschungsinst.* **5**: 77-84. 1932.
- SEDGWICK, A.: The development of *Peripatus capensis*. *Quart. Jour. Micr. Sci.* **25**: 449-468. 1885.
- : The development of the Cape species of *Peripatus*. *Quart. Jour. Micr. Sci.* **26**: 175-212. 1886. **27**: 467-550. 1887. **28**: 373-396. 1888.
- SEHL, A.: Furchung und Bildung der Keimanlage bei der Mehlmotte *Ephestia Kühniella*, nebst einer allgemeinen übersicht über den Verlauf der Embryonalentwicklung. *Zeitschr. f. Morph. u. Oekol. d. Tiere.* **20**: 535-598. 1931.
- SEIDEL, F.: Die Geschlechtsorgane in der embryonalen Entwicklung von *Pyrhocoris apterus*. *Zeitsch. f. Morph. u. Oekol. d. Tiere.* **1**: 429-506. 1924.
- : Die Determinierung der Keimanlage bei Insekten. *Biol. Centr.* **46**: 321-343. 1926. **48**: 230-251. 1928. **49**: 577-607, 695. 1929a.
- : Untersuchungen über das Bildungsprinzip der Keimanlage im Ei der Libelle *Platynemis pennipes*. *Arch. f. Entwickl. d. Organ.* **119**: 322-440. 1929b.

- : Die reaktionsfolgen im Determinationsgeschehen des Libellenkeimes. *Verhandl. deut. Zool. Ges.*, Leipzig. **34**: 193–200. 1931.
- : Die Potenzen der Furchungskerne im Libellenei und ihre Rolle bei der Aktivierung des Bildungszentrums. *Arch. f. Entwickl. Mech. d. Organ.* **126**: 213–276. 1932.
- : Das differenzierungszentrum im Libellenkeim I. Die dynamischen Voraussetzungen der Determination und Regulation. *Arch. f. Entwickl. Mech. d. Organ.* **131**: 135–187. 1934.
- : Der Anlagenplan im Libellenei, zugleich eine Untersuchung über die allgemeinen Bedingungen für defekte Entwicklung und Regulation bei Dotterreichen Eiern. *Arch. f. Entwickl. Mech. d. Organ.* **132**: 671–751. 1935.
- : Entwicklungsphysiologie des Insekten-Keims. *Verhandl. d. deut. Zool. Ges.* **38**: 291–336. 1936.
- : Entwicklungsphysiologie. In Hartmann: *Fortschritte Zool.*, Jena (N. F.) 1: Insecta, pp. 413–421. 1937.
- SEILER, J.: Furchung des Schmetterlingeis ohne Beteiligung des Kernes. *Biol. Centr.* **44**: 68–71. 1924.
- *SELVATICO, S.: Sullo sviluppo embrionale dei Bomicini. *Boll. di bach.*, Padova. **8**: 1881. Reviews: *Bull. Entomol. Ital.* **14**: 250–251. 1882. *Zool. Record*, Insecta. **19**: 154. 1882.
- SELYS-LONGCHAMPS, M. DE: Recherches sur développement embryonnaire de l'appendice de premier segment abdominal chez *Tenebrio molitor*. *Bull. d. la class d. sci. acad. roy. Belg.* **1904**: 235–236, 413–447. 1904.
- SEN, P.: On the function and development of the sternal spatula in the Cecidomyiidae or gall midges as exemplified by *Rhabdophaga saliciperda*. *Jour. Morphology.* **65**: 1–13. 1939.
- SHARP, L. W.: "An Introduction to Cytology." Pp. 1–567. Mc-Graw-Hill, New York. 1934.
- SHELDON, L.: On the development of *Peripatus Novae-Zelandiae*. *Quart. Jour. Micr. Sci.* **28**: 205–237. 1887.
- SHINJI, G.: Embryology of coccids, with special reference to the formation of the ovary, origin and differentiation of the germ cells, germ layers, rudiments of the midgut, and the intracellular symbiotic organisms. *Jour. Morph.* **33**: 73–167. 1919.
- SHULL, A. F.: Control of gamic and parthenogenetic reproduction in winged aphids by temperature and light. *Zeitschr. f. ind. Abstamm. Vererb.* **55**: 108–126. 1930a.
- : Order of embryonic determination of the differential features of gamic and parthenogenic aphids. *Zeitschr. f. ind. Abstamm. Vererb.* **57**: 92–111. 1930b.
- : Order of embryonic segregation in intermediate aphids not reversed by low temperature. *Amer. Naturalist.* **65**: 469–473. 1931.
- SIEBOLD, VON C. T. E.: "Wahre Parthenogenesis bei Schmetterlingen und Bienen." Wm. Engelmann, Leipzig. Pp. 1–144. 1856.
- : *Miastor metraloas*. *Zeitschr. f. wissen. Zool.* **14**: 398–399. 1864.
- SIKES, E. K., and V. B. WIGGLESWORTH.: The hatching of insects from the egg and the appearance of air in the tracheal system. *Quart. Jour. Micr. Sci.* **74**: 165–192. 1931.
- SILVESTRI, F.: Sulla morfologia dei Diplopodi. Sviluppo del *Pachyiulus communis*. *Atti d. reale accad. d. Lincei.* **7**: 178–180. 1898.
- : Sviluppo dell' *Ageniaspis fuscicollis*. *Atti d. reale accad. d. Lincei.* **15** (I): 650–657. 1906a.

- : Contribuzioni alla conoscenza biologica degli Imenotteri parassiti. 1. Biologia del *Litomastix truncatellus*. 2e Nota preliminare. *Ann. scuola agr. d. Portici*. **6**: 1-51. 1906b.
- : Contribuzioni alla conoscenza biologica degli Imenotteri parassiti. Biologia del *Litomastix truncatellus*. *Boll. d. lab. d. zool. gen. e agr. d. Portici*. **1**: 17-64. 1907.
- : Appunti sulla *Prospalta berlesei* e specialmente sui primi stati del suo sviluppo. *Boll. d. lab. d. zool. gen. e agr. d. Portici*. **3**: 22-28. 1908a.
- : Contribuzioni alla conoscenza biologica degli Imenotteri parassiti. *Boll. d. lab. d. zool. gen. e agr. d. Portici*. **3**: 29-84. 1908b (1909).
- : Notizie preliminari sullo sviluppo del *Copidosoma buyssoni*. *Mon. zool. ital.* **21**: 296-298. 1910.
- : Prime fasi di sviluppo del *Copidosoma buyssoni*. Imenottero Chalcidide. *Anat. Anz.* **47**: 45-56. 1914.
- : Struttura dell' ovo e prime fasi de sviluppo di alcuni Imenotteri parassiti. *Boll. d. lab. d. zool. gen. e agr. d. Portici*. **10**: 66-88. 1915.
- : Sulla maturazione dell' ovo, fecondazione e formazione del trophamnios nel *Platygaster dryomyiae*. *Atti reale accad. d. Lincei*. **25** (II): 121-128. 1916.
- : Contribuzioni alla conoscenza biologica degli Imenotteri parassiti. V. Sviluppo del *Platygaster dryomyiae*. *Boll. d. lab. d. zool. gen. e agr. d. Portici*. **11**: 299-326. 1921.
- : Sulle appendici del capo degli "Japygidae" (Thysanura entotropha) e rispettivo confronto con quelle dei Chilopodi, dei Diplopodi e dei Crostacei. *V^e Congrès intern. d'entomol.* II. Travaux. **1932**: 329-343. 1933.
- : Insect polyembryony and its general biological aspects. *Bull. Mus. Comp. Zool.* **81**: 469-498. 1937.
- SLIFER, E. H.: Blastokinesis in the living grasshopper egg. *Anat. Record*. **51** (supplement): 61. 1931a.
- : Insect development. II. Mitotic activity in the grasshopper embryo. *Jour. Morphology*. **51**: 613-618. 1931b.
- : Insect development. III. Blastokinesis in the living grasshopper egg. *Biol. Zentr.* **52**: 223-229. 1932a.
- : Insect development. IV. External morphology of grasshopper embryos of known age and with a known temperature history. *Jour. Morphology*. **53**: 1-22. 1932b.
- : Insect development. VI. The behavior of grasshopper embryos in anisotonic balanced salt solutions. *Jour. Exptl. Zool.* **67**: 137-157. 1934.
- : Morphology and development of the femoral chordotonal organs of *Melanoplus differentialis*. *Jour. Morphology*. **58**: 615-637. 1935.
- : The origin and fate of the membranes surrounding the grasshopper egg; together with some experiments on the source of the hatching enzyme. *Quart. Jour. Micr. Sci.* **79**: 493-506. 1937.
- : The formation and structure of a special water-absorbing area in the membranes covering the grasshopper egg. *Quart. Jour. Micr. Sci.* **80**: 437-457. 1938.
- and R. L. KING: Parthenogenesis and haploidy in grasshoppers. *Proc. Sixth Intern. Genet. Congr.* **2**: 187. 1932.
- : Insect development. VII. Early stages in the development of grasshopper eggs of known age and with a known temperature history. *Jour. Morphology*. **56**: 593-602. 1934.
- SMITH, E. L.: Extra-genic effects in offspring arising from x-rayed gametes in *Drosophila melanogaster*. *Amer. Naturalist*. **69**: 78. 1935.

- SMITH, R. C.: The biology of the Chrysopidae. *Mem. Cornell Univ. Agr. Exp. Sta.* **58**: 1293-1298. 1922.
- SMITH, S. G.: Thelytokous parthenogenesis in *Cephus cinctus*. *Can. Entomol.* **70**: 259-260. 1938.
- *SMREČZYŃSKI, S.: Embryological investigation on the development of the head of *Silpha obscura*. *Rozpr. Wydz. mat.-przyr. Akad. Um., Krakow.* (B) **71** (1): 1-29. 1931.
- : Embryologische Untersuchungen über die Zusammensetzung des Kopfes von *Silpha obscura* L. *Zool. Jahrb. (Anat.)*. **55**: 233-314. 1932a.
- : Embryologische Untersuchungen über die Entwicklung des Kopfes von *Silpha obscura*. *Bull. Intern. acad. Sci. Cracovie.* **B.II.** 649-651. (1931) 1932b.
- : Beitrag zur Kenntnis der Entwicklungsgeschichte des Rüsselkäfers *Phyllobius glaucus*. *Bull. Intern. acad. Sci. Cracovie.* **B.II.** 287-312. 1934.
- : Entwicklungs-mechanische Untersuchungen am Ei der Käfers *Agelastica alni*. *Zool. Jahrb.* **59**: 1-58. 1938.
- SNODGRASS, R. E.: "Anatomy and Physiology of the Honey Bee." Pp. 1-327. Development. Pp. 284-295. McGraw-Hill, New York. 1925.
- : From an egg to an insect. *Smithsonian Rept.* **1925**: 373-414. 1927.
- : Morphology and evolution of the insect head and its appendages. *Smithsonian Misc. Coll.* **81** (3): 1-158. 1928.
- : Evolution of the insect head and the organs of feeding. *Smithsonian Rept.* **1931**: 443-489. 1932.
- : The history of an insect's stomach. *Smithsonian Rept.* **1933**: 363-387. 1935a.
- : "Principles of Insect Morphology." Pp. 1-667. Development: 14-47. McGraw-Hill, New York. 1935b.
- : Morphology of the insect abdomen. II. The genital ducts and the ovipositor. III. The male genitalia. *Smithsonian Misc. Coll.* **89** (8): 1-148. 1933. **95** (14): 1-96. 1936.
- : The male genitalia of Orthopteroid insects. *Smithsonian Misc. Coll.* **96**: 1-107. 1937.
- : Evolution of the Annelida, Onychophora, and Arthropoda. *Smithsonian Misc. Coll.* **97** (6): 1-159. 1938.
- SOGRAFF, N.: see Zograf.
- SONNENBLICK, B. P.: Normal development of *Drosophila melanogaster* following removal of pre-blastodermic ooplasm. *Anat. Record.* **60** (supplement): 60. 1934.
- SPEMANN, H.: "Embryonic Development and Induction." Pp. 1-401. Yale University Press, New Haven. 1938.
- SPEYER, W.: Die Embryonalentwicklung und das Ausschlüpfen der Junglarven von *Psylla mali*. *Zeitschr. f. wiss. Insektenbiol.* **24**: 215-220. 1929.
- STECKER, A.: Die Anlage der Keimblätter bei den Diplopoden (Chilognathen). *Arch. f. Mikrosk. Anat.* **14**: 6-17. 1877.
- STEVENS, N. M.: A study of the germ cells of *Aphis rosae* and *Aphis oenotherae*. *Jour. Exptl. Zool.* **2**: 313-333. 1905.
- STILES, K. A.: The time of embryonic determination of sensoria and antennal color and their relation to the determination of wings, ocelli, and wing muscles in aphids. *Biol. Bull.* **76**: 442-447. 1939.
- STRASBURGER, E. H.: Ueber den Formwechsel des Chromatins in der Eientwicklung der Fliege *Calliphora erythrocephala*. *Zeitschr. f. Zellforsch.* **17**: 83-117. 1933.
- : Ueber die Zellbewegungen bei der Eifurchung der Fliege *Calliphora erythrocephala*. *Zeitschr. f. wiss. Zool.* **145**: 625-641. 1934.

- : "Drosophila melanogaster Meig. Eine Einführung in den Bau und die Entwicklung." 60 pp. Julius Springer, Berlin. 1935.
- : Ueber Störungen der Eientwicklung bei Kreuzungen von *Epilachna chripomelina* mit *E. capensis*. *Zeitschr. indukt. Abst. u. Vererb. Lehre*. **71**: 538–545. 1936.
- STREBEL, O.: Beiträge zur Biologie, Oekologie und Physiologie einheimischer Collembolen. *Zeitschr. f. Morph. u. Oekol. d. Tiere*. **25**: 30–153. 1932.
- STRINDBERG, H.: Einige Stadien der Embryonalentwicklung bei *Myrmica rubra* unter besonderer Berücksichtigung der sogenannten entodermfrage. *Zool. Anz.* **41**: 512–521. 1913a.
- : Embryologische Studien an Insekten. *Zeitschr. f. wiss. Zool.* **106**: 1–227. 1913b.
- : Zur Kenntnis der Hymenopteren-Entwicklung. *Vespa vulgaris* nebst einigen Bemerkungen über die Entwicklung von *Trachusa serratulae*. *Zeitschr. f. wiss. Zool.* **112**: 1–47. 1914a.
- : Beiträge zur Kenntnis der Entwicklung der Orthopteren. *Dixippus morosus*. *Zool. Anz.* **45**: 7–14. 1914b.
- : Zur Entwicklung der Hymenopteren nebst einigen damit zusammenhängenden Fragen. *Zool. Anz.* **45**: 248–260. 1915a.
- : Ueber die Bildung und Verwendung der Keimblätter bei *Bombyx mori*. *Zool. Anz.* **45**: 577–597. 1915b.
- : Embryologisches über *Forficula auricularia* L. *Zool. Anz.* **45**: 624–631. 1915c.
- : Hauptzüge der Entwicklungsgeschichte von *Sialis lutaria*. *Zool. Anz.* **46**: 167–185. 1915d.
- : Noch eine Ameise ohne Serosa (*Tetramorium caespitum*). *Zool. Anz.* **46**: 198–202. 1915e.
- : Zur Entwicklungsgeschichte und Anatomie der Mallophagen. *Zeitschr. f. wiss. Zool.* **115**: 382–459. 1916a.
- : *Azteca* sp. Eine Ameise mit totaler Eifurchung. *Zool. Anz.* **48**: 155–158. 1916b.
- : Ueber die Embryonalentwicklung von *Pulex erinacei*. *Zool. Anz.* **48**: 258–263. 1917a.
- : Neue Studien über Ameisen embryologie. *Zool. Anz.* **49**: 177–197. 1917b.
- : Zur Entwicklungsgeschichte der oviparen Cocciden. *Zool. Anz.* **50**: 113–139. 1919a.
- : Die Eifurchung von *Tapinoma erraticum*. *Zool. Anz.* **50**: 204–207. 1919b.
- STUART, R. R.: The development of the mid-intestine in *Melanoplus differentialis*. *Jour. Morphology*. **58**: 419–438. 1935.
- STUHLMANN, F.: Die Reifung des Arthropodeneies nach Beobachtungen an Insecten, Spinnen, Myriapoden und Peripatus. *Ber. Freib. Naturf.-Gess.* **1**: 1–128. 1886.
- STURTEVANT, A. H.: The claret mutant type of *Drosophila simulans*: a study of chromosome elimination and of cell-lineage. *Zeitschr. f. wiss. Zool.* **135**: 323–356. 1929.
- *ŠULC, K.: Pseudovitellus und ähnliche Gewebe der Homopteren sind Wohnstätten symbiontischer Saccharomyceten. *Sitz. kgl. böhm. Ges. Wiss. Prag.* **3**: 1–39. 1910.
- TAKAHASHI, I.: Variation in condition of the embryo of silkworms (annual) during hibernation. *Sci. Rept. Sericult. Inst.* **42**: 291–312, 313–342. 1911.
- TANGL, F.: Embryonale Entwicklung und Metamorphose von energetischen Standpunkte aus betrachtet. *Arch. f. d. gesamte Physiol.* **130**: 55–89. 1909.

- TANNREUTHER, G. W.: History of the germ cells and early embryology of certain aphids. *Zool. Jahrb. (Anat.)*. **24**: 609-642. 1907.
- TANQUARY, M. C.: Biological and embryological studies on Formicidae. *Bull. Illinois State Lab. Natural Hist.* **9**: 417-479. 1913.
- TCHANG, Y. T.: La structure et les rénovations successives de l'épithélium du mésentéron chez l'embryon du lépidoptère: *Galleria mellonella*. *Compt. rend. hebdomadaire de la soc. de biol.* **100**: 809-812. 1929.
- TEODORO, G.: Sulla embriologia della cocciniglia. *Redia*. **14**: 137-141. 1921.
- THOMAS, A. J.: The embryonic development of the stick-insect, *Carausius morosus*. *Quart. Jour. Micr. Sci.* **78**: 487-512. 1936.
- TICHOMIROFF, A.: Ueber die Entwicklungsgeschichte des Seidenwurms. *Zool. Anz.* **2**: 64-67. 1879.
- *———: On the ontogeny of the *Bombyx mori* within the egg. *Izvyest. Imp. Obshch. Lyubit. estest. Antrop. i. Ethnog.*, Moscow. **32**: 4. In Russian. 1882.
- : Chemische Studien über die Entwicklung der Insekten. *Zeitschr. f. Physiol. Chem.* **9**: 518-532, 566-567. 1885. Review: *Jour. Roy. Micr. Soc.* **5** (2): 441. 1885. *Nature*. **36**: 620. 1885.
- *———: Ueber die Entwicklung der *Calandra granaria*. *Versamml. russisch. Naturf.*, St. Petersburg. **8**. 1890.
- : "Aus der Entwicklungsgeschichte der Insekten." *Festschr. z. 70sten Geburtstag Leuckarts*. Leipzig. **1892**: 337-346.
- : Ueber die Entwicklung von *Calandra*. *Biol. Centr.* **10**: 424. 1900.
- TICHOMIROV: see Tichomiroff.
- TICHOMIROVA, O.: Zur Embryologie von *Chrysopa*. *Biol. Centr.* **10**: 423. 1890a.
- : Article on *Pulex serraticeps*. *Obshchestvo ljubitelei estestvoznaniia, antropologii i etnografii. Izvestiia Moscow Universitet.* **67**, 3. 1890. Review: *Biol. Centr.* **10**: 427. 1890b.
- : Sur l'histoire du développement de *Chrysopa perla*. L'origine du mésoderme des cellules vitellines. *Congrès intern. de zool.* 2me sess., Moscou. **1892**: 112-119. 1892.
- TIEGS, O. W.: Embryology of the Symphyla. *Nature*. **143**: 334-335. 1939.
- , and F. V. MURRAY: The embryonic development of *Calandra oryzae*. *Quart. Jour. Micr. Sci.* **80**: 159-284. 1938.
- TICHOMIROVA, O.: see O. Tichomirova.
- TILLYARD, R. J.: "The Biology of Dragonflies." Embryology. Pp. 229-242. Cambridge University Press, Cambridge. 1917. Review: Calvert, P. P. *Entomol. News*. **28**: 475-479.
- TIRELLI, M.: Ipotesi spaziale e meccanica sulla blastocinesi degli insetti. *Zool. Jahrb. (Zool.)*. **49**: 59-68. 1931.
- : Studi su alcuni fenomeni fisiologici nelle uova ibride del *Bombyx mori*. *Zool. Jahrb. (Zool.)*. **53**: 367-410. 1934.
- *———: Per la migliore conoscenza degli stadi embrionali tipici illustrati dal Grandori nel *Bombyx mori*. *Arch. zool. (ital.)*, Torino. **21**: 479-502. 1935.
- : Caracteres morfológicos y propiedades fisiológicas de la siero de los huevos de los insectos (*Bombyx mori*). *Mém. d. la soc. Cubana d. hist. naturelle*. **13**: 177-188. 1939.
- *TOKUNAGA, Y.: Studies on the development of the head of the silkworm (*Bombyx mori*). [In Japanese.] *Dobuts, Zasshi*, Tokyo. **40**: 229-237. 1929. Abstract in *Jap. Jour. Zool.*, Tokyo. **2**: 105. 1929.
- TONON, A.: Variabilità dei caratteri embriologici nell' uova di filugello durante la diapausa. *Atti d. reale ist. Veneto d. sci. lettere ed arti*. **85** (10): 1137-1146. 1925-1926.

- TÓTH, L.: Ueber die frühembryonale Entwicklung der viviparen Aphiden. *Zeitschr. f. Morph. u. Oekol. der Tiere.* **27**: 692-731. 1933.
- : Beiträge zur Kenntnis der Aphidenspeicheldrüse. *Zeitschr. f. Morph. u. Oekol. d. Tiere.* **30**: 496-505. 1935a.
- *———: Furchungsteilung der viviparen Aphiden. *Állat, Közlem.* Budapest. **32**: 119-122. 1935b.
- : Entwicklungszyklus und Symbiose von Pemphigus spirothecae. *Zeitschr. f. Morph. u. Oekol. Tiere.* **33**: 412-437. 1937.
- TOWNSEND, C. H. T.: "Manual of Myology." Vol. I. Pp. 1-280. C. Townsend & Filhos, Sao Paulo. 1934.
- TOYAMA, K.: Contributions to the study of silk-worms. 1. On the embryology of the silk-worm. *Bull. Coll. Agr. Tokyo Imp. Univ.* **5**: 73-118. 1902.
- TSCHUPROFF, H.: Ueber die Entwicklung der Keimblätter bei den Libellen. *Zool. Anz.* **27**: 29-34. 1903.
- TUR, J.: Observations sur l'oogénèse chez le hanneton (*Melolontha vulgaris*). *Bull. biol. d. France Belg.* **54**: 37-57. 1920.
- UICHANCO, L. B.: Studies on the embryogeny and postnatal development of the Aphididae with special reference to the history of the "symbiotic organ" or "mycetom." *Phil. Jour. Sci.* **24**: 143-247. 1924.
- ULJANIN, W. N.: Observations on the development of thrips (Physopoda). *Izviestiia Imp. Ob. Liubit. Estest. Anth. Ethnogr.* **10**: 39-44. In Russian. 1874. Abstract: Uzel (1895).
- (Oulganine): Beobachtungen über die Entwicklung der Poduren (In Russian). *Izviestiia Imp. Ob. Liubit. Estest. Anth. Ethnogr.* **16**: 3. 1875. Review: *Arch. d. zool. exptl. et Gén.* **4**: 39-40. 1875.
- : Développement des Podurelles. *Arch. d. zool. exptl. et gén.* **5**: 17-19. 1876.
- ULRICH, H.: Experimentelle Untersuchungen über den Generations-wechsel der heterogonen Cecidomyids *Oligarees paradoxus*. *Zeitschr. f. Abst.-lehre.* **71**: 1-60. 1936.
- UMEYA, Y.: Preliminary note on experiments of oöplasm transfusion of silk-worm eggs with special reference to the development of embryo. *Proc. Imp. Acad. Japan, Tokyo.* **13**: 378-380. 1937.
- UZEL, H.: "Monographie der Ordnung Thysanoptera." Pp. 1-472. In Czech; German summary. B. E. Tolman, Königgratz. 1895.
- : Vorläufige Mittheilung über die Entwicklung der Thysanuren. *Zool. Anz.* **20**: 125-132. 1897a.
- : Beiträge zur Entwicklungsgeschichte von *Campodea staphylinus*. *Zool. Anz.* **20**: 232-237. 1897b.
- : "Studien über die Entwicklung der apterygoten Insecten." 76 pp. K. Friedländer & Sohn, Berlin. 1898. Review: *Zool. Centr.* **5**: 852-855. 1898.
- VAN BAMBEKE, C.: Contribution pour servir à l'histoire de la vesicule germinativ. *Bull. d. l'acad. roy. d. sci., lettres, beaux-arts, Belg.* **11** (3): 14-28. 1886.
- VANCE, A. M.: *Apanteles thompsoni*, a braconid parasite of the European corn borer. *U.S. Dept. Agr., Tech. Bull.* **233**: 1-28. 1931.
- VANEY, C., and A. CONTE: Recherches sur le développement de l'oeuf univoltin du ver à soie. *Labor, étud. soie, Lyons.* **14**: 127-152. 1911.
- VATERNAHM, T.: Die Entwicklung des Eies von *Dilina tiliae*. *Zeitschr. f. wiss. Insektenbiol.* **13**: 83-84. 1918.
- VERHEIN, A.: Die Eibildung der Musciden. *Zool. Jahrb. (Anat.)* **42**: 149-212. 1921.
- VERHOEFF, K. W.: Chilopoda. *Bronn's Klassen und Ordnungen des Tierreichs.* **5**, **2**: 1-725. 1925.

- VERSON, E.: Zur Entwicklung des Rückengefäßes bei *Sericaria mori*. *Zool. Anz.* **34**: 313-316. 1909.
- VIALLANES, H.: Sur quelques points de l'histoire du développement embryonnaire de la Mante religieuse. *Rev. biol. d. Nord d. France.* **2**: 479-488. 1890. Also: *Assoc. franç. pour l'avance d. sci.* **19**: 479-488. 1890. Also: *Ann. d. sci. naturelles.* 7th ser. Zool. **11**: 282-328. 1891.
- VOELTZKOW, A.: Vorläufige Mittheilung über die Entwicklung im Ei von *Musca vomitoria*. *Zool. Anz.* **11**: 235-236. 1888.
- : Entwicklung im Ei von *Musca vomitoria*. *Arb. aus dem zool. zoot. Inst. Würzburg.* **9**: 1-48. 1889a. Summary: *Leistungen im Geb. d. Entomol.* **1889**: 100-101. 1890. *Jour. Roy. Micr. Soc.* **1889**: 505-506. 1889.
- *———: *Melolontha vulgaris*; Ein Beitrag zur Entwicklung im Ei bei Insekten. *Arb. aus dem zool. zoot. Inst. Würzburg.* **9**: 49-74. 1889b. Summary: *Jour. Roy. Micr. Sci.* **1889**: 506. 1889.
- *VON BAER, C. E.: "Ueber Entwicklungsgeschichte der Thiere." Beobachtung und Reflection. Privately published, Königsberg. 1828.
- WADDINGTON, C. H.: "How Animals Develop." 127 pp. Allen & Unwin, London. 1935.
- WAGNER, J.: Einige Betrachtungen über die Bildung der Keimblätter, der Dotterzellen und der Embryonalhüllen bei Arthropoden. *Biol. Centr.* **14**: 361-375. 1894.
- WAGNER, N.: Ueber die viviparen Gallmückenlarven. *Zeitschr. f. wiss. Zool.* **15**: 106-117. 1865.
- WAGNER, N. P.: Ueber die Organisation von *Smynturus*. *Biol. Centr.* **10**: 428-429. 1900.
- WALCZUCH, A.: Studien an Coccidensymbionten. *Zeitschr. f. Morph. u. Oekol. d. Tiere.* **25**: 623-729. 1932.
- WALDEYER, W.: "Eierstock und Ei." Pp. 1-174. Wm. Engelmann, Leipzig. 1870.
- WEBER, H.: "Biologie der Hemipteren." Pp. 1-543. Julius Springer, Berlin. 1930.
- : "Lehrbuch der Entomologie." Pp. 1-724. Gustav Fischer, Jena. 1933.
- : Morphologie und Entwicklungsgeschichte der Arthropoden. *Fortschritte d. Zool. N. F.* **2**: 67-86. 1937.
- WEBSTER, F. M., and W. J. PHILLIPS.: The spring grain-aphis or Green bug. *U.S. Dept. Agr., Bur. Entomol. Bull.* **110**: 94-103. 1912.
- WEISMANN, A.: Die Entwicklung der Dipteren im Ei. *Zeitschr. f. wiss. Zool.* **13**: 107-220. 1863.
- : Zur Embryologie der Insecten. *Arch. f. Anat., Physiol. und wiss. Med.* **1864**: 265-277. 1864.
- : Beiträge zur Kenntniss der ersten Entwicklungsvorgänge im Insektenei. *Beitr. z. Anat. u. Embryol. Als Festgabe J. Henle*, Bonn. **1882**: 80-111. 1882.
- WEISS, P.: The so-called organizer and the problem of organization in amphibian development. *Phys. Rev.* **15**: 639-674. 1935.
- : "Principles of Development." Holt, New York. 1939.
- WEYER, F.: Untersuchungen über die Keimdrüsen bei Hymenopterenerbeiterinnen. *Zeitschr. f. wiss. Zool.* **131**: 345-501. 1928.
- WHEELER, W. M.: Ueber drüsenartige Gebilde im ersten Abdominalsegment der hemipterenembryonen. *Zool. Anz.* **12**: 500-504. 1889a.
- : The embryology of *Blatta germanica* and *Doryphora decemlineata*. *Jour. Morphology.* **3**: 291-386. 1889b. Summary: *Jour. Roy. Micr. Soc.* **1890**: 32, 33. 1890.
- : Homologues in embryo Hemiptera of the appendages to the first abdominal segment of other insect embryos. *Amer. Naturalist.* **23**: 644-645. 1889c.

- : Ueber ein eigenthümliches Organ im Locustenembryo. *Zool. Anz.* **13**: 475-480. 1890a. Summary: *Jour. Roy. Micr. Soc.* **1890**: 716. 1890.
- : New glands in Hemipterous embryo. *Amer. Naturalist.* **24**: 187. 1890b.
- : Note on the oviposition and embryonic development of *Xiphidium ensiferum*. *Insect Life.* **2**: 222-225. 1890c.
- : Neuroblasts in the arthropod embryo. *Jour. Morphology.* **4**: 337-344. 1891a.
- : The embryology of the common fly. *Psyche.* **6**: 97-99. 1891b.
- : The germ-band of insects. *Psyche.* **6**: 112-115. 1891c.
- : Concerning the "blood-tissue" of the Insecta. *Psyche.* **6**: 216-220, 233-236, 253-258. 1892a.
- : On the appendages of the first abdominal segment of embryo insects. *Trans. Wisconsin Acad. Sci., Arts, and Letters.* **8**: 87-140. 1892b.
- : A contribution to insect embryology. *Jour. Morphology.* **8**: 1-160. 1893a.
- : The primitive number of Malpighian vessels in insects. *Psyche.* **6**: 457-460, 485-486, 497-498, 509-510, 539-541, 545-547, 561-564. 1893b.
- : The embryonic development of the Wall-bee (*Chalicodoma muraria* Fabr.). *Amer. Naturalist.* **32**: 794-498. 1898.
- WHITING, P. W.: Some anomalies in *Habrobracon* and their bearing on maturation, fertilization and cleavage. *Anat. Record.* **29**: 146. 1924.
- : Sex-determination in Hymenoptera. *Biol. Bull.* **65**: 357-358. 1933a.
- : Selective fertilization and sex-determination in Hymenoptera. *Science*. New ser. **78**: 537-538. 1933b.
- : Egg trinuclearity in *Habrobracon*. *Biol. Bull.* **66**: 145-151. 1934.
- and K. A. GILMORE: Genetic analysis of synapsis and maturation in eggs of *Habrobracon*. *Proc. Sixth Intern. Genet. Congr.* **2**: 210-211. 1932.
- WIEBE, A. H.: Artificial fertilization of aquatic insects. *Ann. Entomol. Soc. Amer.* **18**: 45-48. 1925.
- WIELOWIEJSKI, H. V.: Zur Kenntniss der Eibildung bei der Feuerwanze. *Zool. Anz.* **8**: 369-375. 1885.
- WIEMAN, H. L.: The pole disc of chrysomelid eggs. *Biol. Bull.* **18**: 180-187. 1910.
- WIESMANN, R.: see Leuzinger, Wiesmann, and Lehmann.
- : Untersuchungen über den weiblichen Genitalapparat, das Ei und die Embryonalentwicklung des Apfelwicklers *Carpocapsa* (*Cydia*) *pomonella* L. *Mitt. d. schweiz. ent. Ges.* **16**: 370-377. 1935.
- WIGGLESWORTH, V. B.: The physiology of ecdysis in *Rhodnius prolixus* (Hemiptera). II. Factor controlling moulting and "Metamorphosis." *Quart. Jour. Micr. Sci.* **77**: 191-222. 1934.
- : "The Principles of Insect Physiology." Pp. 1-434. Dutton, New York. 1939.
- WILL, L.: Zur Bildung des Eies und des Blastoderms bei den viviparen Aphiden. *Arb. d. Zool. Inst. Würzburg.* **6**: 217-258. 1883.
- : Ueber die Entstehung des Dotters und die Epithelzellen bei den Amphibien und Insecten. *Zool. Anz.* **7**: 272-276, 288-291. 1884.
- : Entwicklungsgeschichte der viviparen aphiden. *Zool. Jahrb. (Anat.).* **3**: 201-286. 1888a.
- : Zur Entwicklungsgeschichte der viviparen Aphiden. *Biol. Centr.* **8**: 148-155. 1888b.
- WILLEY, A.: "Anatomy and Development of *Peripatus Novae-Britanniae*." *Zool. Results.* Willey, Cambridge. Vol. I, pp. 1-52. 1898.
- : Trophoblast and serosa. A contribution to the morphology of the embryonic membranes of insects. *Quart. Jour. Micr. Sci.* **41**: 589-609. 1899.

- WILLIAMS, C. B., and P. A. BUXTON: On the biology of *Sphodromantis guttata*. *Trans. Entomol. Soc. London*. **1916**: 86-100. 1916.
- WILLIAMS, F. X.: Photogenic organs and embryology of Lampyrids. *Jour. Morphology*. **28**: 145-207. 1916.
- WILSON, E. B.: The embryology of the earthworm. *Jour. Morphology*. **3**: 387-462. 1888.
- WINCHELL, A.: Notes on *Selandria cerasi* as it occurs at Ann Arbor, Mich. *Proc. Boston. Soc. Natural Hist.* **9**: 321-325. 1863 (1865).
- WINKLER, H.: "Verbreitung und Ursache der Parthenogenesis im Pflanzen- und Tierreiche." Gustav Fischer, Jena. Pp. 1-231. 1920.
- WITLACZIL, E.: Entwicklungsgeschichte der Aphiden. *Zeitschr. f. wiss. Zool.* **40**: 559-696. 1884.
- WOLFF, C. F.: *Theoria generationis* (Halae ad Salem. 1759). Translation by P. Samassi. Pt. 1, 96 pp.; pt. 2, 98 pp. Leipzig. 1896.
- WOLFF, L. K., and G. RAS: Effect of mitogenetic rays on the eggs of *Drosophila melanogaster*. *Nature*. **133**: 499. 1934.
- WONG, W. S., and H. H. LI: A study on gonad and embryonic development of the silkworm, *Bombyx mori*. *Lignan Sci. Jour.* **13**: 475-485. 1934.
- WOODWORTH, C. W.: Studies on the embryological development of *Euvanessa antiopa*. In Scudder's "Butterflies of the Eastern United States and Canada." Vol. I. Pp. 95-104. 1889.
- WOSKRESSENSKY, N. M.: Ueber die Wirkung der Röntgenbestrahlung auf das embryonale Wachstum. *Arch. f. Entwickl. d. Organ.* **113**: 447-461. 1928.
- WRAY, D. L.: The embryology of *Calendra callosa*; the southern Corn Billbug. *Ann. Entomol. Soc. Amer.* **30**: 361-409. 1937.
- ZACHARIAS, O.: Neue Untersuchungen über die Entwicklung der viviparen Aphiden. *Zool. Anz.* **7**: 292-296. 1884.
- ZADDACH, G.: "Untersuchungen über die Entwicklung und den Bau der Gliedertiere." I. Die Entwicklung des Phryganiden-eies. Reimer, Berlin. Pp. 1-138. 1854.
- *——: Ueber die Entwicklung der Insecten. *Schrift d. Kgl. phys.-oekon. Ges. Königsberg. Sitzb.* **8**: 1867.
- *ZAKOLSKA, Z.: Sur quelques anomalies dans l'oogenèse chez *Dixippus morosus*. *Compt. rend. soc. sci. Varsovie.* **10**: 1917.
- ZANINI, E.: Lo sviluppo embrionale della uova del filugello di razza bivoltina. *Boll. d. zool. agr. e bach.* **1**: 111-137. 1930.
- ZAVREL, J.: *Tanytarsus connectens*. *Pub. d. la fac. d. sci. d. l'univ. Masaryk.* **65**: 1-47. 1926.
- ZOGRAF, N. V. (SOGRAFF): Zur Embryologie der Chilopoden. *Zool. Anz.* **5**: 582-585. 1882.
- : Materialien zur Kenntnis der embryonalentwicklung von *Geophilus ferrugineus* und *G. proximus*. *Nachr. d. Ges. d. Freunde d. Naturk. Anthrop. und Ethnogr.*, Moscow. In Russian. **1883**: 1-77. 1883. Review: *Zool. Jahrb.* **1883** (II): 90-92. 1884.
- : Sur l'origine et les parentés des arthropodes, principalement des arthropodes trachéates. *Congrès intern. d. zool.* 2d. sess. 1 part. **1892**: 278-302. 1892.

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