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SCIENTIFIC TRANSACTIONS

OF THE

ROYAL DUBLIN SOCIETY.

VOLUME III. (SERIES II.)

V.—ON THE ORIGIN OF FRESHWATER FAUNAS: A STUDY IN EVOLUTION.

BY W. J. SOLLAS, M.A., Dublin; D.Sc., Cambridge; Fellow of St. John's College, Cambridge; Professor of Geology and Mineralogy in the University of Dublin.

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V.—ON THE ORIGIN OF FRESHWATER FAUNAS: A STUDY IN EVOLUTION. By W. J. SOLLAS, M. A., Dublin; D. Sc., Cambridge; Fellow of St. John's College, Cambridge; Professor of Geology and Mineralogy in the University of Dublin.

[Read, May 19, 1884].

"O! what an endlesse worke have I in hand,
To count the seas abundant progeny,
Whose fruitfull seede farre passeth those on land,
And also those which wonne in th' azure sky:
For much more eath to tell the starres on hy,
Albe they endlesse seeme in estimation,
Then to recount the Seas posterity:
So fertile be the flouds in generation,
So huge their numbers, and so numberlesse their nation."

Faërie Queene, Canto xii. Bk. iv.

THE amazing fertility of the sea never fails to excite the wonder of the naturalist, and has often impressed the imagination of the poet. The comparative poverty of our freshwater fauna, though no less astonishing, is seldom remarked upon, and has not been made the subject of systematic investigation. A suggestive Paper* by Von Martens, which appeared in 1857, and a chapter in Semper's thoughtful work, "The Natural Conditions of Existence as they affect Animal Life," are the chief references bearing directly on the subject which I am able to cite.†

One reason for the barrenness of our literature on this subject is to be found in the too readily made assumption that the difference in composition of fresh and salt water is sufficient to account for all the facts. The susceptibility of marine animals to the influence of fresh water is supposed to be so great, that only under

* "On the Occurrence of Marine Animal Forms in Fresh Water," by Dr. E. von Martens, *Ann. and Mag. Nat. Hist.*, 1858, ser. III., vol. i. p. 50 (translated by W. S. Dallas, F. L. S.).

† See incidental remarks on the origin of some freshwater species in Dr. P. M. Duncan's Presidential Address to the Geological Society of London, *Quart. Journ. Geol. Soc.*, 1878, and a chapter on distribution of the freshwater Crayfish, Prof. Huxley (*The Crayfish, International Science Series*).

very exceptional circumstances could they learn to accustom themselves to a freshwater mode of life; and no doubt we have here one cause, and that a potent one, for the exclusion of many marine organisms from our freshwater streams and lakes. But it is by no means the only cause, and probably not the chief; for Beudant, to whose observations Semper has recently called attention, has already shown that several species of marine molluscs can be brought to live in fresh water, if only the sea water in which they are at first placed be freshened with sufficient slowness. Thus in three months he was able to people a freshwater tank with limpets and mussels, which then might have been seen living in strange association with such true freshwater molluscs as *Limnea* and *Paludina* (*v. Semper, l. c., p. 153*).

While Beudant was thus successful in overcoming the repugnance of some marine forms to a change of medium, he failed with others: of fifteen marine species twelve bore the change of medium, and three perished. But it is very possible that, under more favourable conditions, these would have yielded to treatment like the rest. An unfailing supply of appropriate food and a secular slowness in change of medium would seem to be the two conditions essential to success. These given, it is quite possible that all marine animals are susceptible of a freshwater existence. A few considerations will serve to make the probability of this apparent. That the sea is the fertile mother of all life was a poetic fancy which has now become a fair deduction from admitted facts. Indeed, all naturalists are now agreed that all freshwater animals have descended, directly or indirectly, from marine ancestors; so that the adaptation in question must have occurred at some period in the past history of all freshwater races. But some of these are of such a character that it is difficult to admit adaptability for them and to deny it to others. If the freshwater *Hydra* and *Cordylophora* have survived a change of medium, it is difficult to see what reason can be adduced against this being possible in the case of other Hydroid polyps.

Again, so large a proportion of water enters into the composition of all "jelly-fish" that they might be regarded as singularly unlikely to survive a change of medium; and indeed some experiments of Mr. Romanes prove an extreme intolerance on the part of marine *Medusæ* in this respect. No one consequently would have expected to discover *Medusæ* living in fresh water in a state of nature, and yet the occurrence of *Limnocodium* in the tanks of the Botanical Society of London, associated with *Victoria regia*, proves that there is nothing in their nature absolutely incompatible with such a mode of existence. The change from one medium to another has here taken place, and so profoundly have the tissues of *Limnocodium* been modified in consequence, that it is now more susceptible to the fatal action of salt water than its marine relations are to fresh.

G. Romanes remarks, on closing his account of experiments on *Limnocodium*, as follows:—"If an animal so exceedingly intolerant of fresh water as is a marine jelly-fish may yet have all its tissues changed so as to adapt them to thrive in

fresh water, and even die after an exposure of one minute to their ancestral element, assuredly we can see no reason why any animal in earth or sea may not in time become fitted to change its element" (*Nature*, June 24, 1880).

Another cause which has been relied upon in explanation of the poverty of our freshwater faunas, and which no doubt is partially operative, lies in the greater severity of a freshwater climate as compared with a marine one. Von Martens, in his now well-known Paper already referred to, concludes his argument in the following words:—"The great richness of the sea is explained not only by its greater extent, but also by its more uniform temperature. The fresh waters stand in the same relation to it as a continental to an insular climate: their alternation of temperature is the principal hindrance to their becoming populous; and this attains its maximum by freezing in the colder zones; with the increase of temperature the populousness of the fresh waters increases, but is still limited in the sub-tropical zone by partial dessication. In the tropical zone the conditions of temperature of the fresh waters approach most nearly to those of the sea, and with them their populousness."

In support of his thesis Von Martens enumerates several families which, elsewhere exclusively marine, exhibit a mixed or entirely freshwater habit in tropical regions. He mentions *Arca scaphula*, Benson, as living in the Jumna, near Humerpoor, 1000 miles distant from the sea, and *Pholas rivicola*, Sow., which is found in floating timber on the river Pantai, twelve miles about its mouth. He also calls attention to the freshwater prawn of Jamaica, *Palaemon** *jamaicensis*, and to the Thelphusiadæ, a heterogeneous family of freshwater crabs, which occur in sub-tropical regions.

Active as this cause, brought to light by Von Martens, may be, it furnishes by no means a complete solution: the exceptional cases quoted by Von Martens are not numerous enough, and still leave the overwhelming preponderance of marine forms unexplained. If the Unionidæ and other freshwater molluscs have learnt to adapt themselves to a freshwater climate, one sees no good reason why other forms which endure the rigours of our winter along the coast, such as *Patella* and *Littorina*, should not have done so too.

Considering the merciless struggle for existence which the superabundance of marine life involves, sufficient, according to some writers, to drive the less successful competitors into the desolate depths of the abyssal sea, where the only remaining comfort lies in an unchanging uniformity of temperature of about 32° F.—considering the effects of this struggle, one would have expected to find numerous marine animals enterprisingly working their way along the shores of the abundant streams which open all along the coast, and every river characterized by a modified marine fauna derived from the neighbourhood of its mouth.

* The genuine *Palaemon* is now recognized as a freshwater genus.

So far from this being the case, we find that the freshwater forms of Mollusca are remarkably well defined from the marine, and that they maintain their distinctive generic characters throughout a distribution generally world-wide in space, and extending far back into the Mesozoic period in time.

Some other efficient cause or causes must then be sought for in this inquiry, and one—and that a most important one—lies obviously on the surface. Perhaps one of the commonest ways by which marine animals obtain a distribution over extensive areas is by means of free-swimming larvæ. The peopling of the sea by slow-moving or attached forms has certainly been accomplished chiefly, if not almost wholly, in this manner. But obviously no new forms can have been introduced into existing river-systems through the agency of free-swimming larvæ, for these fragile and feeble forms can by no means make headway against the seaward current of a river: indeed, as a matter of observed fact, larvæ are never known to swim against any current, but always along with it. And thus the method which has been most potent in disseminating organisms through the sea must have been wholly inoperative in transferring them to a freshwater *habitat*.*

Furthermore, if any slow-moving animal had managed, in the adult state, to penetrate some little distance up a stream, it could seldom succeed in permanently establishing itself so long as it passed through a free larval stage; for its larvæ would usually be carried away to the sea, where they would perish or resume the ancestral habits. Swift-moving animals, such as fish, would of course be more advantageously situated, since they could rapidly travel a long way up most streams, and might easily find at length some sheltered recess or quiet lagoon, wherein their young could come to maturity. The necessity for some such quiet spot is sufficiently indicated by the long and arduous journies which the freshwater Salmonidæ take to reach it. Excepting fish (and we only propose to discuss the Invertebrates in this Paper) and minute organisms, such as Protozoa, minute Crustacea, Rotifera, and Tardigrades, which are capable of transport in a dessicated

* This has been hinted at by Semper, as I found subsequently; his words are:—"I have already indicated that very often the strength of the current in a river, or the surf at its mouth, its temperature, or the kind of food it affords, must cause quite as great a hindrance to the passage of a marine animal into the fresh water as the necessity for subsequently living in water devoid of salt. Thus, for instance, the remarkably tender bodies of the larva of the Echinodermata, Ascidia, Sea-anemones, Hydroid polypes, and others, are scarcely fitted to overcome such impediments; so that even under the assumption that they might be capable of living in water without salt, their transfer into fresh water seems to be almost impossible; and this is still more probably the case when the fully grown creatures—such as Ascidians, Corals, Polyyps, and others—do not move freely on the sea bottom, but are permanently attached to it" (*Animal Life*, 1881, p. 149). I was quite under the impression that this idea was my exclusive property, and I have previously made use of it in explaining the exclusion of marine forms of Spongiæ from our rivers (Cassell's *Natural History*, article "Spongiæ," p. 328, Part LXX., 1882). But with such a mine of facts and wealth of ideas as occur in Semper's work, how shall one be sure that any idea on this subject is one's own?

state by winds, no inhabitant of freshwater streams ought to propagate, as a rule, or exclusively by means of free-swimming larvæ, for this would be inconsistent with its permanence as a freshwater form. I believe this deduction is capable of being verified by facts. Before proceeding further it will be well to provide ourselves with a list of known freshwater forms, and I have accordingly drawn up the following Table of the Invertebrate sub-kingdom, and marked the various groups *m.* or *f.*, according as they are freshwater or marine; an *o* after *f.* indicates that the group is exclusively freshwater; an *o* before *m.* that it is exclusively marine; *f.m.* indicates that it is both freshwater and marine. It will be observed that most of the great groups are marked *m.f.*; some, however, such as the Brachiopoda, Ascidia, Echinodermata, and other small outlying groups, Enteropneusta, Gephyrea, Chætogonatha, are wholly marine*. Those which are exclusively marine are not further analysed; but those which contain both freshwater and marine forms are resolved step by step into smaller and smaller groups, till a separation into exclusively marine or exclusively freshwater forms is reached; or in case this does not happen, till the families are divided into genera: beyond genera the subdivision has not been carried; but notes are added when a genus, otherwise exclusively marine, presents us with some exceptional freshwater species.

PROTOZOA.

Monera,	<i>f. m.</i>	Radiolaria,	<i>o. m.</i> (Heliozoa, <i>f.</i>)
Protoplasta,	<i>f. m.</i>	Gregarinida,	<i>f. m.</i>
Foraminifera,	<i>o. m.</i> (Gromia, <i>f.</i>)	Infusoria,	<i>f. m.</i>

METAZOA.

Spongiæ,	<i>f. m.</i>	Chætogonatha,	<i>o. m.</i>
Cœlenterata,	<i>f. m.</i>	Nemathelminthia,	<i>f. m.</i>
Platyhelminthia,	<i>f. m.</i>	Mollusca,	<i>f. m.</i>
Rotifera,	<i>f. m.</i>	Crustacea,	<i>f. m.</i>
Brachiopoda,	<i>o. m.</i>	Tracheata,	<i>f. m.</i>
Polyzoa,	<i>f. m.</i>	Echinodermata,	<i>o. m.</i>
Chætopoda,	<i>f. m.</i>	Enteropneusta,	<i>o. m.</i>
Discophora,	<i>f. m.</i>	Ascidia,	<i>o. m.</i>
Gephyrea,	<i>o. m.</i>	Acraniota,	<i>o. m.</i>

* It may be at once observed here that in all these groups propagation is accomplished by means of free-swimming larvæ. This fact sufficiently explains their entire absence from freshwater areas, and their wide distribution in the sea.

METAZOA—*continued.*

Spongiæ.

Myxospongiæ,	<i>o. m.</i>
Ceraospongiæ,	<i>o. m.</i>
Monaxonidæ,	<i>f. m.</i>
Tetractinellidæ,	<i>o. m.</i>
Hexactinellidæ,	<i>o. m.</i>
Calcispongiæ,	<i>o. m.</i>

Monaxonidæ.

Renieridæ,	<i>f. m.</i>
Chalinopsidæ,	<i>o. m.</i>
Desmacidinae,	<i>o. m.</i>
Suberitidæ,	<i>o. m.</i>

Renieridæ.

A large number of sub-families not yet defined,	<i>o. m.</i>
Spongillinae,	<i>f. o.</i>

*Spongillinae.*Section *a*—with statoblasts.

Ephydatia,
Euspongilla,
Tubella,
Parmula,

*Section *b*—without statoblasts.

Lubomirskia,
Potamolepis,
Uruguayia,

Coelenterata.

Hydrozoa,	<i>f. m.</i>
Actinozoa,	<i>o. m.</i>

Hydrozoa.

Hydromedusa,	<i>f. m.</i>
Siphomedusæ,	<i>o. m.</i>

Hydromedusæ.

Gymnoblantica-anthomedusæ,	<i>f. m.</i>
(Hydra and Cordylophora are the only freshwater forms in this group.)	

Calyptriblastica-leptomedusa,	<i>o. m.</i>
Trachomedusæ,	<i>f. m.</i>
(Lymnocodium is the only described freshwater genus in this group.)	

Narcomedusæ,	<i>o. m.</i>
Hydrocorallinae,	<i>o. m.</i>
Siphonophora,	<i>o. m.</i>

Polyzoa.

Ectoprocta,†	<i>o. m.</i>
Entoprocta,	<i>f. m.</i>
Gymnolæmata,	<i>f. m.</i>
Phylactolæmata,	<i>f. o.</i>

* This section was instituted by Dr. Wm. Marshall (*Ann. and Mag. Nat. Hist.* 1883, ser. v. vol. xii.) ; but with the exception of Lubomirskia, the alleged absence of statoblasts is asserted on negative evidence of an incomplete character. Lubomirskia lives in Lake Baikal. Potamolepis inhabits the Congo, occurring as far up as 150 miles by water from the sea, and over 100 metres above its level, with several cataracts intervening. Marshall also mentions *Spongilla stygia*, a transparent sponge, living in the Grotto of Gurk in Carniola, as being devoid of statoblasts.

Those freshwater sponges which do not form statoblasts are the exception: the vast majority of the Spongillinae, world-wide in distribution, are characterized by the occurrence of these structures.

† The Ectoprocta are usually regarded as exclusively marine; but exceptions are recorded. Semper quotes the following:—*Membranipora bengalensis*, Stol.; *Victorella parida*, Kent (*Animal Life*, p. 496).

The Gymnolæmata are almost exclusively marine. Paludicella is the only exception known in this country. Prof. Haddon regards it as a comparatively late immigrant.—Haddon, "On Budding in Polyzoa:" *Quart. Journ. Micro. Sci.*, vol. xxiii., N. S., p. 551.

MOLLUSCA.

<i>Glossophora.</i>		Pyramidellidæ,	<i>o. m.</i>
Gastropoda,	<i>f. m.</i>	Turritellidæ,	<i>o. m.</i>
Scaphopoda,	<i>o. m.</i>	Xenophoridæ,	<i>o. m.</i>
Cephalopoda,	<i>o. m.</i>	Naticidæ,	<i>o. m.</i>
Lamellibranchiata,	<i>f. m.</i>	Entoconchidæ,	<i>o. m.</i>
<i>Gastropoda.</i>		Marsenidæ,	<i>o. m.</i>
Isopleura,	<i>o. m.</i>	Acmaeidæ,	<i>o. m.</i>
Anisopleura,	<i>f. m.</i>	Capulida,	<i>o. m.</i>
<i>Anisopleura.</i>		Littorinidæ,	<i>f. m.</i>
<i>Streptoneura.</i>		Paludinidæ,	<i>f. o.</i>
Zygobranchia,	<i>o. m.</i>	Valvatidæ,	<i>f. o.</i>
Azygobranchia,	<i>f. m.</i>	Ampullaridæ,	<i>f. o.</i>
<i>Euthyneura.</i>		<i>Neritidæ.</i>	
Opisthobranchia,	<i>o. m.</i>	Nerita,	<i>o. m.</i>
Pulmonata,	<i>o. f. t.*</i>	Neritina,	<i>f. o.</i>
<i>Azygobranchia.</i>		Pileolus,	<i>o. m.</i>
Reptantia,	<i>f. m.</i>	Navicella,	<i>f. o.</i>
Natantia,	<i>o. m.</i>	<i>Littorinidæ.</i>	
<i>Reptantia.</i>		Littorina,	<i>f. m.</i>
Holochlamyda,	<i>f. m.</i>	Modulus,	<i>o. m.</i>
Pneumochlamyda,	<i>t.</i>	Lacuna,	<i>o. m.</i>
Siphonochlamyda,	<i>o. m.</i>	Rissoa,	<i>o. m.</i>
<i>Holochlamyda.</i>		Hydrobia,	<i>f. o.</i>
Rhipidoglossa.		Assimineæ,	<i>brackish water.</i>
Trochidæ,	<i>o. m.</i>	<i>Pulmonata.</i>	
Neritidæ,	<i>f. m.</i>	Basommatophora.	
Pleurotomaridæ,	<i>o. m.</i>	Limnæidæ,	<i>f. o.</i>
Ptenoglossa.		Auriculidæ,	<i>f. o.</i>
Scalaridæ,	<i>o. m.</i>	<i>Stylommatophora.</i>	
Janthinidæ,	<i>o. m.</i>	Helicidæ,	<i>t.</i>
Tænioglossa.		Limacidæ,	<i>t.</i>
Cerithiadæ,	<i>o. m.</i>	Oncidiadæ,	<i>o. m.</i>
Melaniidæ,	<i>f. o.</i>	<i>Lamellibranchiata.</i>	
		Isomya.	
		Integropalliata,	
		Arcacea,	<i>o. m.</i>
		Trigonacea,	<i>o. m.</i>
		Unionacea,	<i>f. o.</i>

* *t* signifies land-dwellers

MOLLUSCA—*continued.*

Lucinacea,	<i>o. m.</i>
Cyprinacea,	<i>f. m.</i>
Sinupallia.	
Veneracea,	<i>f. m.</i>
Myacea,	<i>o. m.</i>
Pholadacea,	<i>o. m.</i>
<i>Heteromya.</i>	
Mytilacea,	<i>f. m.</i>
Mulleracea,	<i>f. o.</i>
<i>Monomya.</i>	
Aviculacea,	<i>o. m.</i>
Ostreacea,	<i>o. m.</i>
Veneracea,	
Cypricardia,	<i>o. m.</i>
Tapes,	<i>o. m.</i>
Cyclina,	<i>o. m.</i>
Cytherea,	<i>o. m.</i>
Chione,	<i>o. m.</i>
Venus,	<i>o. m.</i>
Lucinopsis,	<i>o. m.</i>
Sanguinolaria,	<i>o. m.</i>
Psammobia,	<i>o. m.</i>
Tellina,*	<i>f. m.</i>
Donax,	<i>o. m.</i>
Scrobicularia,	<i>m. brackish.</i>

Cumingia,	<i>o. m.</i>
Rangia,	<i>o. m.</i>
Mactra,†	<i>f. m.</i>
Trigonella,	<i>o. m.</i>
Vaganella,	<i>o. m.</i>
Lutraria,	<i>o. m.</i>
Cyprinacea.	
Tridacna,	<i>o. m.</i>
Chama,	<i>o. m.</i>
Dimya,	<i>o. m.</i>
Diceras,	<i>o. m.</i>
Isocardia,	<i>o. m.</i>
Hippopodium,	<i>o. m.</i>
Cardium,	<i>f. m.</i>
Corbicula,	<i>f. æst.</i>
Cyrena,	<i>f. æst.</i>
Cyclas,	<i>f. o.</i>
Pisidium,	<i>f. o.</i>
Cyprina,	<i>o. m.</i>
Mytilacea.	
Mytilus,	<i>o. m.</i>
Modiola,	<i>o. m.</i>
Crenella,	<i>o. m.</i>
Lithodomus,	<i>o. m.</i>
Dreissena,	<i>f. o.</i>
Modiolarca,	<i>o. m.</i>

CRUSTACEA.

<i>Branchiopoda.</i>	
Phyllopoda,	<i>o. m.</i>
Cladocera,	<i>f. o.</i>

Malacostraca.

Nebaliadæ,	<i>o. m.</i>
Schizopoda,	<i>o. m.</i>
Decapoda,	<i>f. m.</i>
Stomapoda,	<i>o. m.</i>
Cumacea,	<i>o. m.</i>
Edriophthalmata,	<i>f. m.</i>

Copepoda.

Eucopepoda.	<i>f. m.</i>
Branchiura.	<i>f.</i>

<i>Cirripedia,</i>	<i>o. m.</i>
<i>Ostracoda,</i>	<i>f. m.</i>

Chætopoda.

Achæta,	<i>f. o.</i>
Polychæta,‡	<i>o. m.</i>
Oligochæta,	<i>f. o. (a few exceptions).</i>

Platyhelminthia.

Turbellaria,	<i>f. m.</i>
Nemertina,	<i>o. m. (one exception).</i>
Trematoda,	<i>m. f.</i>
Cestoida,	

* A sub-genus, *Galatea*, is found in rivers of Africa; otherwise marine.† A sub-genus, *Gnathodon*, lives in fresh water, Gulf of Mexico.‡ A single exception (*Lumbriconereis*) has been recorded by Dr. Kennel as living in fresh water in the river Ortoire, Trinidad.

It will be seen that, as the analysis proceeds, each group furnishes a large number of exclusively marine and a very small number of exclusively freshwater divisions; while the mixed freshwater and marine genera, omitting admittedly exceptional cases, are very few indeed. Thus, to take the Spongiæ as an example, it is divided into six orders, of which only one, the Monaxonidæ, is marked *m. f.*; all the rest are marine. Disregarding these, we find that the Monaxonidæ break up into five families, of which only one, the Renieridæ, is marked *f. m.* This, finally, is resolvable into several sub-families, all of which are marine, except one, the Spongillina, which is exclusively freshwater. When this Paper was first penned the Spongillina were regarded as a compact family, clearly distinguished from other Renieridæ by the possession of "statoblasts"; but recent discoveries have brought to light some ten species, belonging to four or five genera, which are said to be without this characteristic feature; and it is quite possible that some of these new forms may belong to genera otherwise known as marine.

We now approach the inquiry as to how far the exemption we have predicted of freshwater animals, from a free larval existence, is capable of verification. Commencing with the sponges, we find, in this country, the closely allied genera *Euspongilla* and *Ephydatia* or *Meyenia* (*Euspongilla fluviatilis* and *Ephydatia lacustris*). Elsewhere the rest of the world has furnished hitherto some additional seven or eight genera. Such of these (except *Lubomirskia*) as have been exhaustively studied have been found to propagate by means of so-called "winter-eggs" or statoblasts. These are modified internal buds or gemmules, which are provided with a protective horny envelope, and generally one or more layers of surrounding siliceous spicules. Within this protecting case the bud rests during the winter, and on the advent of spring emerges as a young sponge.

In tropical climates the statoblast is produced, not on the approach of winter, but just before the dry season; and it, no doubt, primarily serves, in this case, as a means of protection against the fatal effects of dessication. Since, however, in the dry state, the envelope of these statoblasts contains a considerable volume of air, which materially diminishes their specific gravity, it is possible, as William Marshall has suggested, that their formation may serve a secondary purpose ensuring for the sponge a wide dispersion by the agency of the winds.

The pressing need for a rigid attachment of the reproductive gemmules, which exists in swift streams, or rivers liable to floods, is well illustrated by a case mentioned by Marshall; for he finds that in *Parmula brownii*, from the Rio Negro, the spicular layer of the statoblasts is continuous with that of the hard, dense skeleton of the parent sponge, thus protecting them against all chance of being washed away till they can crawl out as young sponges and shift for themselves. On the whole, so far as definitely ascertained facts go, they point unmistakably to the general, if not universal, occurrence of a peculiar mode of propagation in the case

of those sponges* which are found inhabiting fresh water. In marine sponges, on the other hand, multiplication by free-swimming larvæ is the rule; and when, as in some cases, gemmules are produced as well as larvæ or in place of them, they are generally external; and if internal, never, so far as is known, remain within the parental tissues for any considerable time, but are set free as soon as produced as free-swimming organisms. Moreover, they are never provided with the characteristic protective envelopes which characterise the statoblast of the freshwater sponge.

Thus it appears that the evidence of the Spongillina may be claimed as substantiating, in a very high degree, the truth of our views.

We turn next to the Hydrozoa; and, as the development of the free-swimming *Limnocoedium* is unknown, we must restrict ourselves to the Hydroids, of which, as far as at present known, there are only two freshwater genera, *Hydra* and *Cordylophora*, both belonging to the same family, the Tubularidæ. In *Hydra* the egg is surrounded by a horny case, within which it undergoes its development. There is thus no free-swimming stage, and the young *Hydra* hatches out in the adult form. While *Hydra*, which is by far the commonest freshwater Hydroid, thus favours our view, the other genus, *Cordylophora*, presents us with what appears at first sight a most damaging exception, for the young of this Hydroid are liberated in great numbers as free-swimming planulæ, which persist in a state of great locomotive activity for some time before settling down to a sedentary existence. This exception is otherwise remarkable, as affording, according to Semper, the only known instance in which the progress of the colonization of freshwater streams by a semi-marine genus can be historically traced. The discovery of *Cordylophora* was made by Allman, who found it in the Grand Canal Docks of Dublin in 1854. Since then it has migrated into many rivers, and has already reached the Seine at Paris. One would like to be sure, however, as to how much of this history represents the progress of the discovery of the genus and how much its actual migrations. It is especially interesting as throwing light on the means by which *Cordylophora* has been enabled to carry on its migration, to find it frequently associated with *Dreissena polymorpha*, a mollusc which has, in recent times, colonised many rivers in England. Both *Dreissena* and *Cordylophora* are attached animals, frequently found growing together on floating timber; and it is probably owing to the occasional transport of this up stream by human agency that the introduction of both these forms into our rivers is due. It is also possible that the larvæ of *Cordylophora*, which is known to grow attached to buoys at the mouth of the Elbe, may attach themselves to boats at their moorings, and subsequently be transported by them up stream. Taking into account the

* For much valuable information and suggestive remarks on this subject I would refer to Papers by Carter and Marshall, in the *Annals and Magazine of Natural History*, ser. v., vols. xii. and xiii.

comparative rarity of Cordylophora and its habit of growing attached to floating timber, we need not regard its propagation by free-swimming larva as fatal to our deduction.

The marine Polyzoa propagate exclusively by free-swimming larvæ; but in the freshwater division of the group, statoblasts, similar in essential characters to those of the sponges, are usually developed. A well-known exception is that of Paludicella, in which statoblasts have not been observed. The development of the ovum in this genus, however, has been watched by Professor Allman, who shows that it takes place within the perivisceral cavity of the parent, so that when it escapes, by rupture as he conjectures, of the parental body wall, it is in a condition to settle down at once as a fixed or attached form. This exception, therefore, may be said to prove the rule.

LAMELLIBRANCHIATA.

ISOMYA.		Cyprinacea.	
<i>Integropalliatæ.</i>		Cardium,	<i>f. m.</i>
Unionacea,	<i>f. o.</i>	Cyrena,	<i>f. o.</i>
Cyprinacea,	<i>f. m.</i>	Cyclas,	<i>f. o.</i>
<i>Sinupalliatæ.</i>		Pisidium,	<i>f. o.</i>
Veneracea,	<i>f. m.</i>	<i>Veneracea.</i>	
HETEROMYA.		Tellina (Galatea, <i>f. o.</i>)	
Mytilacea,	<i>f. m.</i>	Scrobicularia.	
Mulleracea,	<i>f. o.</i>	Mactra (Gnathodon, <i>f. o.</i>)	
MONOMYA.		Donax (Fischeria, <i>f. o.</i>)	
Aviculacea,	<i>o. m.</i>	<i>Mytilacea.</i>	
Ostreacea,	<i>o. m.</i>	Dreissena,	<i>f. o.</i>

To give an account of the fresh-water Mollusca of the entire world would require a large monograph to itself; and this, when completed, would leave us in ignorance of many of those points relating to development which are essential to our inquiry. We cannot, therefore, discuss this group except in a very limited manner. Commencing with the Lammellibranchiata, and of these first the Unionacea, we meet in both genera of this family (Unio and Anodon) a most remarkable and well-known course of development, which furnishes a striking illustration of the necessity which exists in the case of slow-moving, freshwater forms of some means of dispersion not involving the production of a free-swimming embryo. The ova in these genera develop up to a certain stage within the gill-pouches of the parent, and remain there as "glochidia" till some passing fish or, it may be, a wading bird comes into their vicinity. The young glochidia then issue into the surrounding water, and, swimming like Pectens by the

flapping of their valves, attach themselves, like external parasites, to the animal whose presence has stimulated their efforts. Becoming encysted by an epidermic outgrowth of the host, they are carried about till they become metamorphosed into young Anodons or Unios; and then, escaping from the cyst, drop to the bottom of the stream, and assume a sedentary mode of life. In this way they become dispersed through the river they inhabit; and when transported by birds may be transferred from one river system to another.

Of the next family of Lammellibranchiata, the Cyprinacea, only three genera are river-dwellers, Cyrena, Cyclas, and Pisidium. In Pisidium the development of the embryo proceeds within the gill-plates of the mother; so that in this case also the young larvæ are secured from a seaward journey. The development of Cyclas is also intraparental; and no free larval stage exists.

With respect to the mode of development of the few forms which, among the Veneracea, are found inhabiting rivers, I can obtain no information.

Passing to the Mytilacea, we find the freshwater Dreissena, common in some English rivers and canals, into which it has been imported within recent times. Although I can find no details respecting its development,* this need not trouble us, as its habit of attaching itself to floating objects will quite readily account for its introduction. I can find no reference to the development of the Mulleracea.

So far as our imperfect examination of the Lammellibranchs permits, we may claim this group as affording evidence in support of our hypothesis.

GASTROPODA.

STREPTONEURA.		EUTHYNEURA.	
<i>Rhipidoglossa.</i>		<i>Pulmonata.</i>	
Neritidæ,	<i>f. m.</i>		
<i>Tænioglossa.</i>		<i>Basommatophora.</i>	
Melaniidæ,	<i>f. o.</i>	Limnæidæ,	<i>f. o.</i>
Entoconchidæ.	<i>o. m.</i>	Auriculidæ.	<i>brackish water.</i>
Littorinidæ,	<i>f. m.</i>		
Paludinidæ,	<i>f. o.</i>	<i>Stylommatophora.</i>	
Valvatidæ,	<i>f. o.</i>	Oneidiada.	<i>salt marshes, t.</i>
Ampullaridæ.	<i>f. o.</i>		

Nerita is a marine genus; but it contains species which dwell in freshwater streams. One species, in the Philippines, climbs trees.

Neritina is a freshwater genus; but *N. fluviatilis*, which is found in British rivers, also occurs in the brackish waters of the Baltic; while *N. viridis* and *N. meleagris* are Indian species which live in the sea.

* Prof. Lankester thinks it probable that the larva of Dreissena is free-swimming, and that both it and Cordylophora are lacustrine rather than fluviatile forms.

Littorina is a marine genus; but it contains two sub-genera, *Lithoglyphus* (S. E. Europe, and Central Africa, *L. tanganyika*) and *Limnotrochus* (*L. tanganyika*), which inhabit fresh water.

Compared with the rich variety of forms which they present in other parts of the world, the freshwater Gasteropoda are but poorly represented in our British streams. The chief genera are *Limnea*, *Ancylus*, *Physa*, *Planorbis*, and *Valvata*, belonging to the euthyneurous Gasteropoda, and *Paludina* and *Bithynia*, belonging to the Streptoneura.

Although not quite germane to our subject, we may stop to point out the remarkable thinness of the shell in these molluscs, and its frequent correlation with a thick epidermis (periostacum). The thinness of shell is suggestive at first sight either of a deficiency of carbonate of lime in fresh water, or of greater difficulty in extricating it from a solution in which sodium chloride is scarcely present. Analyses, however, show that fresh water is usually by no means deficient as compared with sea water in calcium carbonate; and the fact that the Unionidæ frequently secrete quite massive shells indicates that the absence of sodium chloride has no appreciable effect. The erosion of the umbones of *Unio* shells and earlier-formed whorls in *Paludina* seems to suggest an excess of free carbonic acid, and perhaps other acids which might tend to hinder the secretion of solid shell: and possibly the thick epidermis not only represents layers which in a marine shell would be calcified, but also functionally serves to protect the already formed shell from solution.* On the whole it seems most probable that the thin shell has arisen by natural selection, and is correlated with the lower specific gravity of fresh water as compared to salt. This diminished density would render it needful for the free movements of the animal that it should be disburdened of all unnecessary weight. On the other hand, the thicker shells of marine mollusca, so often found broken, are probably correlated with the occurrence of powerful shifting currents and storm waves in the medium which they inhabit.†

Passing on to our main inquiry, we find that the euthyneurous Gasteropoda usually deposit their eggs in jelly, which is attached to some foreign object, and the young emerge in a fully formed state. In the streptoneurous division we have *Bithynia* and *Paludina*: the former attaches its eggs, but the latter—and this is a significant fact—is viviparous, the young molluscs leaving the mantle chamber of the parent as young adults.

The Crustacea furnish us with abundance of freshwater forms, Copepods, Branchiopods, and Ostrapods, Isopods and Amphipods; and *Palæmoninæ*, and *Astacinæ* among the Decapods. But the first three groups contain none but minute forms, which are capable of distribution by birds and probably winds. They

* Semper has already suggested that the epidermis serves this purpose.

† Some interesting remarks bearing on this subject will be found in a Paper by Mr. A. R. Hunt, in the *Proceedings of the Royal Society*, London, 1882, p. 8 (reprint).

pass through a nauplius stage; but Nauplii are strong swimmers, and quite capable of maintaining their position amidst the slowly-moving water in which they teem.

The Amphipods carry their ova about with them, tucked under the abdomen; and the segments and limbs are all formed before hatching.

The marine forms of the Palæmonina usually leave the egg in the zoëa stage, but the freshwater in a stage more advanced than the Mysis, as Fritz Müller shows in his description of the development of a Palæmon living in brooks in Blumenau.

Astacus carries its eggs about, attached to the swimmerets of its abdomen, like the lobster. The young, however, unlike those of the lobster, are provided with sharply-hooked claws, by which they can maintain a hold of the parent after they have entered upon a free existence. Whether this contrivance is to prevent their being swept away by the river, or to afford them, when necessary, maternal protection, like that of a hen for her chickens, seems doubtful.

We have now passed in review many of the chief peculiarities in the mode of development of the members of our freshwater fauna, and find, with a few exceptional cases susceptible of ready explanation, everywhere consistent evidence in favour of our original proposition, that the invertebrate animals inhabiting fresh water might be expected not to propagate exclusively by means of free-swimming larvæ. The passage through a free larval stage in the course of development may be regarded as a real explanation of the exclusion of such marine forms as undergo it from a freshwater *habitat*.

Three causes are therefore admitted as leading to this exclusion: they are—(1) the difference in chemical composition of the medium; (2) the severe character of the freshwater climate; (3) the necessity for the suppression of a free larval existence. The number of animals which can satisfy all these three conditions might be expected to be few; and probably there are other quite as important deterrent causes to be revealed. The absence of suitable food in freshwater streams has been suggested by Semper as one of these, and does probably lead to the exclusion of many marine forms. Thus none of the Gastropods of our streams are carnivorous, in the sense of preying upon other animals of more than microscopic size,* and yet many carnivorous Gastropods are actively locomotive, abound on our coasts between tide marks, endure a rigorous climate, and so dispose their eggs as to preserve them, during development, from destruction or transportation by currents. *Purpura* is a case in point, and *Nassa* another, yet these molluscs are not known to occur in a single freshwater stream. The *Murexes*, some of which are viviparous, and have no severe climate to contend against in the localities where they occur, are likewise exclusively marine. In another order of Mollusca, the Cephalopods, we find characters which one would expect to render

* In rasping the leaves of freshwater plants the gastropods will necessarily devour hosts of Infusoria. Infusoria also help to furnish food for lammellibranchs.

them eminently adapted to a freshwater mode of existence, such as their firm and compact tissues, remarkable activity, and emergence from the egg in a complete state. Yet no such animal as a freshwater cuttlefish is known. In this case a deficiency of appropriate food is probably the efficient barrier, for these molluscs are exceedingly voracious, feeding largely on Crustacea—they have been known to overpower the lobster in fair fight—and the freshwater Crustacea of our streams are probably not numerous enough to furnish them with a dependable meat supply. Like the Murexes, they may also be regarded as amongst the dominant classes of the Mollusca, and, being pre-eminently successful in the struggle for existence, are not forcibly pushed into rivers for a means of subsistence, so that supposing immigration possible, no sufficiently strong reason for it exists. The habits of animals must also be taken into account, for these, in many cases, seem to be as characteristic of the species as are structural peculiarities, and a change from a marine to a freshwater life would therefore only take place under the action of some unusually powerful impelling cause.

Some other impediments to this transformation will be attended to in discussing the next part of our inquiry, *i. e.* as to the mode in which freshwater forms have originated, and the circumstances under which some of their chief peculiarities have been produced.

There are at least three conceivable ways by which freshwater animals may be derived from marine. The latter may—(1) directly migrate into rivers from the sea; (2) the area which they inhabit may be converted into a freshwater basin or lake; (3) they may acquire a terrestrial or marsh-loving *habitat*, and subsequently exchange this for a fluviatile or lacustrine one. Some of our freshwater Gastropods, viz: the freshwater Pulmonata, have most probably acquired their present *habitat* in this circuitous fashion, as also the freshwater Oligochaeta, as Professor Haddon has suggested to me. We shall now confine ourselves to a discussion of the first two alternatives.

With regard to direct emigration from the sea, we may safely dismiss it as an explanation in the case of fixed forms which are not parasitic nor attached to locomotive animals. Such forms as Sponges, Polyzoa, and Hydra, are not likely to have travelled direct from sea to rivers. Only one genus of locomotive Polyzoan is known; and though the Tubularidæ among the Hydrozoa pass through a freely-moving actinula stage; yet, as this is transitory, it is scarcely competent to explain the presence of Hydra in our ponds.* Such locomotive Mollusca and Crustacea as fulfil the three conditions already laid down might, on the other hand, be fairly expected to furnish us with instances of direct colonization. Some such possibly exist, but

* On the other hand, the actinula stage—or one not far removed from it—may, in very early geologic times, have persisted throughout life in the ancestral Tubularidæ, and thus have rendered direct immigration possible. Certain features in the development of Hydra have been regarded, however, as indicating that it is a degraded form of Tubularian, and not a persistent early type.

they are remarkably rare. The actively-moving Crustacea sometimes appear to push their way up stream, as is shown by the occurrence of two species of freshwater *Peneus*, one inhabiting the Sutlej, at the foot of the Himalayas, the other (*P. Braziliensis*) occurring far up the rivers of North America (Semper, p. 437). Some freshwater crabs also appear to be late immigrants into freshwater areas. Of freely-moving molluscs scarcely any good instances of direct immigration can be adduced.

Had our streams become populated by direct colonization from the sea, one might fairly expect to find more frequent cases of the process still in progress. Marine forms becoming estuarine, and estuarine passing into fluviatile forms, should be processes of common occurrence; as a matter of fact, they are so rare that one is led to suspect that the *Peneus* of freshwater streams has been derived rather from descending lacustrine species than ascending marine ones. It would appear that some very serious obstacle besides those already suggested must exist about the debouchment of rivers to hinder the inland progress of marine animals: it is possible that in some cases this is of the nature of a thinly-peopled zone or desert margin, which none but swiftly-moving animals, such as fish or Crustacea, find it possible to traverse. Such a desert might well be produced by the comingling of the fresh and of the muddy water of a river with the sea. Such rivers as I am acquainted with are remarkably bare of vegetation along their seaward banks, and the fatal action of salt water on many of the minute organisms they bear to sea would probably produce unwholesome conditions extending over a considerable distance. Again, the percentage of salt may decrease too rapidly from sea to river to permit individual animals to cross from one to another in the course of a lifetime, though one would not rest much on this, as Semper mentions oysters which flourished at the mouth of a river where they were alternately bathed, according to the state of the tides, with fresh and salt water; and if oysters are capable of withstanding such rapid alternations of medium, no doubt other locomotive molluscs may be also. Direct immigration appears less probable than the second alternative already suggested; and I would rely for an explanation of the existence of freshwater animals on those wide changes in the distribution of land and sea, which we know to have taken place in the course of geological time. The conversion of continental seas swarming with various kinds of life into terrestrial areas, diversified by extensive systems of lakes, has occurred not once or twice only in the history of the earth. As lakes began to be produced by a rising of the sea-floor, they would probably remain in connexion at first with the open sea, and rivers discharging into them would only slightly sweeten their waters; but as elevation slowly continued, connexion with the sea would be severed at one point and another, till eventually it would cease altogether, except in so far as rivers might flow into the sea from the lake. The waters of a lake so formed would continually freshen at a rate depending on the size of the lake and the area and rainfall of its catchment basin.

Of the marine forms existing in this transformed area, few would probably migrate so long as the tidal waters of the ocean ebbed and flowed in it. As elevation progressed, many active locomotive forms, to whom the new conditions were distasteful, would escape seawards, and others less enterprising, in whom fixity of habit was a pronounced feature, would lag behind till escape became impossible. The attached forms would be unable to escape, and would therefore be entrapped. With complete isolation of the lake would commence a sorting out of the remaining fauna: some members would succumb, others would survive, and, adapting themselves to their altered circumstances, give rise to a freshwater fauna.

The Baltic has often been quoted as a marine area in which some such change as that described is in progress, and no doubt with truth, but one cannot but admit that the change is here taking place under somewhat unfavourable circumstances. The climate of the Baltic is severe, and a selection by means of climatal conditions proceeds apace with that due to freshening of the waters. The elevation is also proceeding with that slowness which characterises the terrestrial movements of the present day. Finally, the Baltic has only just emerged, geologically speaking, from a glacial episode which left its fauna poorer than it found it. In past times much more favourable transformations of marine into lacustrine areas must have occurred. To look no further back than the beginning of Tertiary times, we know that then there existed a far more uniform, which is the same as saying "less severe" climate than characterises the temperate regions of the existing period. We have reason to believe that the relative level of land and sea was subject to more rapid changes. Glacial epochs did not interfere, and the newly-raised rocks need not have always been schists and gneisses, but were sometimes probably composed of softer and more porous materials, which, retaining a certain quantity of salt water in their interstices, may have given a brackish character to the first-formed running streams. If the origin of our freshwater fauna dates back to a time when climatal conditions were more uniform or less severe, then the characters which freshwater animals now possess in adaptation to the existing climate would have been subsequently produced, and might have been acquired with secular slowness.

If now we turn to the evidences of geology, we find that the first recognized appearance of lakes is to be found in the Old Red Sandstone period. The previously existing Silurian marine areas became gradually differentiated into the Old Red Lakes and the Devonian Seas, and a freshwater fauna might very well have been contemporaneously developed. It is unfortunate that the explored Old Red Sandstone strata, like so many deposits of probably freshwater origin, should have proved so remarkably unfossiliferous; still we know of one fossil far from rare in the Kiltoreen beds of Kilkenny, which has been pronounced by no less an authority than Edward Forbes to be a genuine ancestor of existing pond mussels. This shell, known as *Anodonta Jukesii*, is altogether different in character from the

described lamellibranchs of the marine Devonian strata, and, from its large size, rivalling that of existing Anodons, appears to have flourished under remarkably favourable circumstances. If at this early period a glochidian stage was then characteristic of the Anodonta, it would have secured a wide distribution to the species by means of the contemporaneously existing fish. Although *Anodonta Jukesii* is the only fossil found in the Old Red Sandstone which has been referred to the freshwater Mollusca, others may undoubtedly have existed. Indeed the presence of numerous remains of fish which are supposed to have possessed the habits of the Salmonidæ directly suggests this, since, judging from their teeth, they must have required animals to feed upon during their sojourn in fresh water.

The world-wide distribution of the Unionidæ and their extraordinary richness in subgenera and species are quite in harmony with this early appearance of Anodonta; and I feel disposed to assign quite as early a date to the appearance of the Limnæidæ: their world-wide distribution, and the difficulty of assigning them any close alliance with marine forms, suggests a high antiquity for the family. The Valvatidæ, so curiously distinguished by the persistence of an archaic character in their gill plumes, might also have inhabited the Old Red Sandstone rivers and lakes. No one supposed that the terrestrial gastropods had originated already in the Palæozoic period, yet the discovery of Pupa and Conulites (*Helix*) in the coal-measures leaves no doubt on this point.

The Helicidæ are amongst the nearest allies, and are possibly ancestors, of the Limnæidæ, and the latter may be fairly looked for in strata of corresponding age. It must here be added that the Helicidæ, though at least as old as the Carboniferous period, may be much older, and may have existed in the Devonian forests, so similar in the general character of their flora to those of the succeeding Carboniferous period.

The next great lacustrine epoch occurred in Permo-Triassic times, when extensive lakes covered a large part of the northern continental areas. Some of these were evidently inland salt seas, but probably not all: indeed Ramsay regards the Bunter beds of the Trias as in all probability the deposits of a freshwater lake, which subsequently became salt. In such freshwater lakes a part of the enclosed post-carboniferous fauna may have slowly become modified, and thus have contributed additional genera to our freshwater fauna. The Trias has not, however, as yet furnished us with any fossiliferous freshwater deposits, and consequently we must look to later Mesozoic strata for signs of the freshwater genera which had thus early come into existence. But scant evidence is however afforded until we reach the Purbeck and Neocomian strata: thus in the Lias we find *Cyrena*, *Neritina*, and, according to Moore, *Planorbis* (one species) and *Valvata* (two species). In the inferior Oolite we meet with *Corbula*, *Neritina*, *Planorbis*, *Paludina* (?), *Melania*, *Hydrobia*, and *Cyrena*. Of these genera, *Planorbis*, *Paludina*, and *Valvata* may be, and probably are, very ancient forms which originated in Devonian lakes; but with the other genera—*Cyrena*, *Neritina*, *Melania*, and *Hydrobia*—the case is different;

for we can easily find close alliances for them amongst marine molluscan families from which we may regard them as directly or collaterally descended. Further, as fossil remains of marine molluscs are comparatively abundant, we shall be able from the first appearance of these to gather some idea as to the probable date of the first appearance of their freshwater relations; always, however, bearing in mind that the determinations of many Palæozoic Mollusca are to a certain extent doubtful. Setting these aside, we find that the Cyprinidæ (*in sensu restricto*) date from the Trias, and thus Cyrena, which is allied to this family, in all probability may be regarded as post-Triassic in age. The Neritinæ are included in the family Neritidæ, which is also first found in the Trias, while Hydrobia belongs to the Rissoidæ, first met with in the Jura, though it may of course have made its appearance earlier, and probably did. Thus the genera Cyrena, Neritina, and Hydrobia cannot safely be pushed farther back than the Trias, but may very possibly have then originated in the lakes of that period.

Passing now to the Purbeck-Wealden deposits, we encounter the numerous freshwater genera detailed in the following list:—Unio, Cyrena, Corbula, Cardium, Valvata, Hydrobia, Amnicola, Neritina, Planorbis, Lioplax, Bithynia, Paludina(?), Physa, Limnæus, Gnathodon, Pleuroceras, Goniobasis, Leptoxis, Plychostylus, Carychium, and Auricula. Of the genera which here appear for the first time, Gnathodon, a sub-genus of Maetra, may have become specially modified in Jurassic times, for the genus is not known earlier than the Coral-rag. Unio, however, may be regarded as a descendant of the Devonian Anodonta. The list is more especially interesting as affording evidence of the abundant development of the freshwater Melaniinæ in our own area during the Mesozoic period, from which, as well as from Northern Europe generally, they are now entirely absent, though widely spread in other regions, particularly the warmer zones of the earth. Considering the small part of the earth's crust that has been at all carefully studied, it is of the highest interest to find the same genera of freshwater shells occurring at widely-separated points in beds of approximately contemporaneous age, and so far remote from the present as Cretaceous times (Cenomanian or Senonian). Thus in North America, where the Cretaceous rocks have been grouped as follows:—Laramie, Fox Hill, Colorado, and Dakota groups, they have afforded Unio (one species), Cyrena (one species), Neritina (three species), Physa, and Valvata, from the Fox Hill beds; and Unio, Corbicula, Acella, Leptolimnea, Limnophysa, Limnæa, Neritina, Melanopsis, Campelosis, Pyrgulifera, and others, from the Laramie beds. With regard to the fauna of the Fox Hill beds, Clarence King well remarks that "the discovery of this singularly tertiary-like group deep in the Cretaceous should only open our eyes to the early specialisation of freshwater molluscan types." And Dr. White, referring to the Laramie fossils and their similarity to existing forms, speaks more strongly still, as when he says: "The lines of descent of the numerous types which have reached us unbroken seem to be almost parallel, so little

have they changed with the lapse of time. So slightly divergent are these lines, considered as lines of differentiation, that if we bound them all by two imaginary straight lines we should have an evolutionary parallax that would carry back the origin of these types to a period inconceivably remote."*

It is not only in North America that we find, however, the same freshwater genera as in Europe: India also furnishes us with an instructive list: thus from the lower Intertrappean freshwater beds (Cenomanian or Senonian in age) have been obtained—*Unio*, *Physa* (one sp.), *Paludina* (twelve sp.), *Valvata* (four sp.), *Limnæa* (six sp.), and *Pisidium* (one sp.)

Thus we find several freshwater genera of Mollusca already distributed in Cretaceous times over parts of the Palæarctic, Neartic, and Oriental regions.

Proceeding in our review to the Tertiary period, we encounter an epoch of gigantic mountain building, and consequently of extensive lake formation. Many great mountain ranges now existing took their rise after the Eocene, Miocene, and Pliocene periods; and with them, I doubt not, several of our existing great lakes and inland seas, such as the Caspian, lake Baikal, and the lake system of Central Africa.

Some marine forms were probably enclosed in these basins, and became converted into freshwater genera; but the majority of the freshwater inhabitants of the Tertiary lakes and rivers were derived from previously-existing freshwater species, as is shown by the fact that they belong to genera already in existence in Mesozoic times. There are, however, some fresh acquisitions: thus the Littorinidæ, which might, from their hardy habits and universal distribution, have been expected to have furnished earlier some freshwater species, are now represented by the freshwater genus *Lithoglyphus*, which is found in Lower Pliocene strata (*i. e.* subsequent in time to the upheaval of the Siwalik hills, and previous to the upheaval of the Sub-Apennines). The Mytilidæ again, of which the absence of earlier freshwater modifications is equally remarkable, are now represented by numerous species of *Dreissena*, which first appears in the Upper Eocene.

Passing now to the existing lakes, which we regard as the modified descendants of Tertiary seas, we find that those of the northern hemisphere have been subjected to singularly unfavourable conditions: thus the lakes of North America, Europe, and Asia have endured all the rigours of a glacial climate, and in some cases have been submerged beneath a glacial sea; while the Caspian, in addition, suffers from an excessive concentration of its waters. Singularly unwholesome as it has thus become, it yet retains, however, a fragmentary relic of a Tertiary fauna. So much has been written on the subject of the Caspian and its fauna, that I make no excuse

* Let us add, it by no means follows that we are bound to carry back their origin to a period so determined. The probabilities are that, if we could trace the lines of descent backwards, we should finally find them rapidly converging as they entered a region of geographical change—such, for instance, as that of the conversion of a continental sea into a system of freshwater lakes.

for here inserting the following list, compiled from a monograph on its Invertebrate fauna, by O. A. Grimm, which appeared in 1876 and 1877, with 273 pages of letterpress, nine plates, and a folding map. As, with the exception of the scientific names of species, it is written throughout in Russian, I have to regret that I am not able to extract any further information from a work* which must be a veritable mine of interesting facts:—

RHIZOPODA.

Heliozoa.

Protastrum marina (Grm.)

Schulzia pelagica (Grm.)

Radiolaria

Heliosphæra ? hæckeli (Grm.)

Foraminifera

Rotia veneta (M. Salch.)

Textularia caspia (Grm.)

INFUSORIA.

Acineta tuberosa (Ehb.)

Lacrymaria caspia (Grm.)

Paramecium, sp.

Colpoda pigerima (Cohn.)

Nassula flava (Clp.)

Pleuronema (?)

Climacostomum longissimum (Grm.)

Euplotes charon (Ehb.) (?)

Stylonichia, sp.

Tintinnus mitra (Grm.)

Carchesium, sp.

SPONGIÆ.

Amorphina caspia (Grm.)

Reniera flava (Grm.)

Metschnikowia tuberculata (Grm.)

M. intermedia (Grm.) (larval form).

TURBELLARIA.

Plagiostomum caspium (Grm.)

Polycelis schulmanii (Grm.)

HIRUDINEI.

Archæobdella esmontii (Grm.)

Piscicola respirans (Trosch.)

P. littoralis (Johnst.)

Clepsine cœcum (Grm.)

C. affinis (Diesg.)

PLATYHELMINTHES.

Distomum tumidulum (Rud.)

Amphilina foliacea (G. Wg.)

Ligula monogramma (Crepl.)

L. digramma (Crepl.)

NEMATODES.

Monhysteria bulbosa (Grm.)

Eustrongylus tubifex (Nitsch.)

Ascaris cuneiformis (Rud.)

A. acus (Bloch.)

A. constricta (Rud.)

ACANTHOCEPHALA.

Echinorhyncus strumosus

OLIGOCHATA.

Nais, sp.

Tubifex deserticola (Grm.)

Limnodrilus bogdanowii (Grm.)

Limnodrilus, (?) sp.

Enchytræus, sp.

Amphicteis invalida (Gb.)

A. brevispina (Gb.)

A. kowalewski (Grm.)

POLYCHÆTA.

Ampharete kowalewskii (Grm.)

* *Fauna of the Caspian*, by O. A. Grimm, 1876 and 1877.

POLYZOA.

Laguncula repens	(Farr.)
Bowerbankia densa	(Farr.)
Stichoporina ?	

LAMELLIBRANCHIATA.

Corbicula fluminalis	(Müll.)
Cardium edule	(Linn.)
C. edule, var. rusticum	
C. caspium	(Eich.)
C. crassum	(Eich.)
C. trigonoides	(Pall.)
C. trigonoides, var. crassum	(Grm.)
C. pyramidatum	(Grm.)
C. baeri	(Grm.)
C. longipes	(Grm.)
C. barbot-de-marnii	(Grm.)
C. catillus	(Eich.)
C. pseudocatillus	(Abich.)?
Adacna læviuscula	(Eich.)

A. edentula	(Pall.)
A. plicata	(Eich.)
A. vitrea	(Eich.)
Anadonta ponderosa	(Pfr.)
Dreissena polymorpha	(Ben.)
D. caspia	(Eich.)
D. rostriformis	(Desh.)
D. brardii, Brgn. var. caspia	(Grm.)

GASTROPODA.

Neritina littorata	(Eich.)
N. schulzii	(Grm.)
Hydrobia caspia	(Eich.)
H. dimidiata	(Eich.)
H. spica	(Eich.)
H. stagnalis	(Linn.)
Eulima conus	(Eich.)?
Bithynia eichwaldi	(Krynicky.)
Lithoglyphus ? caspius	(Krynicky.)
Planorbis micromphalus	(Fuchs.)?

Separating the Mollusca, we have the following list of genera, in which I have added the name of the group of beds in which each genus is first known to occur :

Corbicula,	1 sp.,	Lower Eocene.
Cardium,	12 sp.,	Upper Jura.
Adacna,	4 sp.,	Lower Pliocene.
Anodonta,	1 sp.,	Devonian.
Dreissena,	5 sp.,	Upper Eocene.
Neritina,	2 sp.,	Lias.
Hydrobia,	4 sp.,	Middle Jura.
Eulima,	1 sp.,	Trias.
Bithynia,	1 sp.,	Middle Jura.
Lithoglyphus,	1 sp.,	Lower Pliocene.
Planorbis,	1 sp.,	Lias.

It is generally admitted that this Molluscan fauna has its closest affinities with that of the "Congerien" strata of Upper Pliocene age, and I therefore add a list of the latter for comparison.

* Fossils of "Congerien" Strata. Sandberger, p. 676, etc.

<i>Dreissena subglobosa</i>	(Partsch.)	<i>P. loxostomia</i>	(Sandb.)
<i>D. triangularis</i>	(Partsch.)	<i>P. achatinoides</i>	(Desh.)
<i>D. subcarinata</i>	(Desh.)	<i>P. duboisi</i>	(C. Mayer).
<i>D. simplex</i>	(B. de Marny.)	<i>Melantho sadleri</i>	(Partsch.)
<i>D. schrockingeri</i>	(Fuchs.)	<i>Tulotoma zelebori</i>	(Hörnes).
<i>Didacna conjungens</i>	(Partsch.)	<i>T. rudis</i>	(Neumayer).
<i>Unio vukotinovici</i>	(Hörnes.)	<i>T. avellana</i>	(Neumayer).
<i>U. flabellatus</i>	(Gdt.)	<i>Bithynia verneulii</i>	(C. Mayer).
<i>Pisidium priscum</i>	(Eich.)	<i>B. tentaculata</i>	(Linn.)
<i>Neritina</i> , sp.		<i>Valvata balatonica</i>	(Rolle).
<i>Melanopsis martiniana</i>	(Férussac)	<i>V. piscinalis</i>	(Müll.)
<i>M. bouei</i>	(Férussac)	<i>Planorbis varians</i>	(Fuchs.)
<i>Melania escheri</i>	(Brgn.)	<i>Carinifer quadrangularis</i>	
<i>Goniochilus costulatum</i>	(Fuchs.)		(Neumayer).
<i>Turbonella inaspecta</i>	(Fuchs.)	<i>Limnæus velutinus</i>	(Desh.)
<i>Paludina vukotinovici</i>	(Frauenfeld)	<i>Valenciennia annulata</i>	(Rousseau).

It will be seen that the Melaniina of the Congerien beds have disappeared from the Aralo-Caspian area, as indeed they have from all the northern Palæarctic zone, but *Adacna* and *Dreissena* are common in both the Caspian and Congerien faunæ. One species of the last-named genus (*Dreissena simplex*) is of particular interest, for it is stated by Sandberger to be closely allied to *D. Brardii*, a species which occurs in Lower Miocene deposits, and which is preceded by a very similar form, *D. unguiculus* of the Headon Hill strata (Upper Eocene). Since *Dreissena Brardii* (var. *caspius*) also occurs in the Caspian according to Grimm, we have in this species a series of forms which, commencing with *D. unguiculus* in the Upper Eocene, has persisted with scarcely more than varietal modification down to existing times.

If the genus *Dreissena* originated in Europe in Eocene times, it has acquired an extensive distribution since, for it is now found living in Eastern Europe, Asia, Africa, and America.

In the lakes of Central Africa, which have not experienced the severe climate and other trying conditions of the northern lakes, we find a remarkable assemblage of freshwater Mollusca. Those of Tanganyka and Nyassa, which are best known, are given in the following list, compiled from Mr. Edgar Smith's descriptions.*

Some of these forms have a very marine aspect, particularly *Neothauma*, *Tiphobia*, *Paramelania*, *Limnotrochus*, and *Syrnolopsis*, so that at first sight one might be disposed to regard them as of comparatively very recent origin: further consideration, however, will render this view improbable. On the next page the molluscan genera of Lake Tanganyka are assigned to their respective families, and

* *Proceedings, Zool. Soc.* 1880, p. 334; 1881, p. 276 and p. 558.

the date of their earliest known existence appended. It will be seen that *Neothauma* is a Paludinid, and consequently a modified freshwater genus—not marine.

Genera of Mollusca living in Lake Tanganyka.	Date of first known Appearance.	Families to which the Genera are assigned.	Date of first known Appearance of Families.
Tiphobia,	L. Eocene or Up. Cret.	Melaniina, .	Mid. Jura (Inf. Oolite).
Paramelania, . .	" "		
(= Pyrgulifera ?)			
Melania,	Mid. Jura, (Inf. Oo.) .		
Melanella,	L. Pliocene,		
Paludomus,	Mid. Cret.,		
Paludina,	Up. Cret.,	Paludinidæ, .	Mid. Jura (Inf. Oolite).
Unio,	Up. Jura,	Unionidæ, .	Devonian.
Pleiodon,	(?),		
Ætheria,	Recent,	Mutelidæ, .	Up. Cret.
Spatha,	Up. Cret.,		
Mutela,	L. Eocene,		
Corbicula,	L. Eocene,	Cyrenidæ, .	Lias.
Cyrena,	Lias,		
Planorbis,	Lias,	Planorbinæ, .	Lias.
Neothauma, . . .	Recent,		
Segmentina, . . .	Up. Eocene,		
Limnæa,	Up. Jura,	Limnæinæ, .	Up. Jura.
Physa,	"		
Limnotrochus, . .	L. Pliocene,	Littorinidæ, .	Silurian.
Lithoglyphus, . .	Recent,		
Syrnolopsis,* . . .	Recent,	Pyramidellidæ,	Cambrian.
Lanistes,	Recent,	Ampullariidæ,	Up. Cret.

Tiphobia, which Mr. Smith regards as one of the most marine-looking of the whole fauna, is not only a Melanian, and therefore a genuine freshwater genus, but includes Paramelania as a sub-genus; and this is closely allied to, if not identical with, Pyrgulifera, which is known as a freshwater form so low down as the Laramie beds of North America. Limnotrochus, which Smith speaks of as exceedingly like a Trochus, both in general form and sculpture, is assigned by him to the Littorinidæ, a family which is already represented by one freshwater genus in the lower Pliocene beds of Europe; and since Lithoglyphus occurs together with Limnotrochus in the lake, it is quite possible that both have descended

* This genus may belong to the Melaniinæ.

from early Pliocene freshwater ancestors. It is, on the other hand, possible that the modification of some marine Littorinid into *Limnotrochus*, as well perhaps as *Syrnolis* into *Syrnolopsis*, may have taken place during the conversion of some part of the Tertiary sea into the African lakes; but whether these two genera are special modifications confined to the African area or not, future research alone can decide.

The lakes of the northern hemisphere must now be briefly referred to. Some of them, as those of Norway and the British Isles, were probably submerged beneath the sea during the middle of the glacial episode. The same is probably true of the North American lakes. This short, temporary submergence, while it must have destroyed the freshwater inhabitants of the lakes, probably introduced into them the marine and Arctic Crustacea, *Mysis relicta* and *Pontoporeia affinis*, which became isolated from the sea on the subsequent re-emergence of the land. The rest of the present inhabitants of these lakes must have been subsequently supplied by the rivers which discharge into them. It is probably owing to the severe climate which culminated in glacial conditions that the Melanidæ are no longer to be found in Northern Europe. The cold and the glaciers would, no doubt, have operated quite as effectually in North America; but in this case the structure of the country has made it possible for the Strepomatidæ to return from their southern exile, and once more to occupy their pre-glacial *habitat*. The great size also of the American lakes might have saved the Melanidæ from extinction during the first and most severe part of the glacial period; and during the great submergence, when the climate was warmer, they might have sought refuge from the sea-water in the freshly restored river-systems.

We have, finally, to consider the causes which have led to some of the more marked modifications which characterise freshwater genera. In the first place they are seldom shared by their nearest marine relations: no marine mollusc is known to pass through a glochidium stage; no marine Polyzoan nor sponge produces a winter bud or statoblast; no marine Phyllopod an ephippium; and no Tubularian an egg within a horny shell like that of *Hydra*. A large number of marine molluscs, however, lay their eggs in capsules, and some, such as *Cymba*, are viviparous.

The winter eggs of sponges and Polyzoa, since they appear in correspondence with a seasonal change, are probably, as Semper has suggested, produced as a protection against cold or drought. If they are adaptations to a freshwater climate they must have appeared subsequently to the isolation of the organism from the sea; and thus, though now available as a means of distribution, could not have been the means by which the organisms producing them exchanged a marine for a freshwater *habitat*. The ephippium of *Daphnia* and the incapsuled embryo of *Hydra* may also be regarded as modifications induced by the severity of a freshwater climate. The fact that the embryo of *Hydra* hatches out soon after it is laid in a freshwater tank

is not opposed to this view, as the water in such tanks is maintained at the temperature of the laboratory, and not at that proper to the season.

On the origin of the glochidium in the Unionidæ it is, in the absence of data, almost useless to speculate. One might suggest that it is the specialised descendant of a form of larvæ once of very general occurrence, and of which, as the development of the Mollusca becomes better known, some traces may still be found to exist. Its marked persistence in the Unionidæ would be clearly owing to modifications giving it a functional importance as a means of distribution.

The causes which have led to the viviparous character of Paludina and the attachment of the eggs of other freshwater Mollusca and Crustacea need special discussion, and we must now enter upon a somewhat lengthy argument, though I fear it will not appear so extensive and detailed as its importance demands.

I will begin by stating the following proposition:—The higher the position an animal occupies in the scale of organised beings, the higher, as a rule, the stage at which it assumes a free existence. Thus the lowest classes of animals, such as the sponges, coelenterates, and echinoderms, almost invariably commence an independent existence as free-swimming larvæ, very unlike the parent in outward form and general structure. So do most of the Vermes, including the whole of the Brachiopoda and Polyzoa.

The Mollusca, Arthropoda, and Vertebrata, exhibit instructive gradations in this respect.

The young of all classes of the Vertebrata are always born in full possession of the characters distinguishing that sub-kingdom. (I here follow Balfour in regarding Amphioxus as a member of the Chordata, but not of the Vertebrata.) In the Ichthyopsida, the lowest division of the Vertebrata, the young, however, frequently undergo a remarkable metamorphosis before assuming the adult state; at the same time they always enter upon existence as evident Ichthyopsida. In the higher subdivisions Sauropsida and Mammalia, no considerable metamorphosis takes place, and the young are always born with the same generic or at least family characteristics as distinguish their parents. In the Mollusca we find the lower forms, such as the Chitons, commence life as free-swimming larvæ: so do some of the Gastropoda, but others do not. Thus the first hatched young of Murex, one of the culminating genera of the marine Gastropoda, are in all important respects similar to the parents. The case is similar with the Lammellibranchiata, the young being sometimes born as free larvæ; at others as young adults. But in the Cephalopoda, the crown of the molluscan sub-kingdom, the young animals never are hatched otherwise than as young cuttlefish. In the Arthropoda a similar gradation exists. The lower orders of Crustacea are characterised by passing through a free nauplius stage; the higher, such as the Decapoda (except in the case of Penæus), are not hatched until they have reached the zoëa stage, or it may be until they have completed their development, as in the case of the lobster.

The Tracheata furnish some interesting exceptions which, like most exceptions to a general rule, lend a helping hand to its interpretation. A young cockroach, for instance, is born with nearly all the parental characters, yet it is a less specialised form than a butterfly, which starts in life as an humble grub, and long remains so. Still, even in the Insecta, we find the highest forms, such as bees and ants, postponing a free existence till the larval state is passed. Taken broadly, then, the statement that the higher the organism the more advanced the stage at which it enters upon a free and independent existence, may be regarded as a sound generalization. We may next seek for an explanation of this rule, and we begin by the inquiry—What is the use of the more complex organization of a higher form to it, and how has it been produced? Its use, or one use, is to give an advantage in the struggle for existence; and it has been evolved by the constant superposition of successful inherited varietal modifications. This much being admitted—as it is universally admitted by modern naturalists—it is clearly a disadvantage for a highly organized animal to produce young which have to start afresh from the same level as the inferior competitors, which it has already distanced in the race, to repeatedly fight the same battle over again, or to run the gauntlet in its ontogenetic development of other competitors in each and every of the less highly organized states through which it has passed in its phylogenetic history. As a gastrula, it would have to compete with other gastrulæ, and not with gastrulæ only, but with older and more formidable competitors, more advanced in their development than itself. Not only would it be exposed to the dangers of direct competition, but also those of the inorganic world—to the violence of currents in particular. The very fact that the adult possesses a higher organization is a proof of the less efficiency of the lower organization which marks its earlier embryological stages. Thus it would be clearly of immense advantage to the race for the organism—(1) to abbreviate its larval history; (2) and to pass through that history in a state of seclusion—withdrawn, as far as possible, from the accidents and competition of the outer world.

On the higher forms these advantages are always conferred, so that a great part of their development takes place in concealment, and many larval stages are passed through with surprising rapidity, or even substantially curtailed.

But the more complete the seclusion of the developing animal, the less the possibility of its obtaining food by its own exertions, and hence food must be provided for it.*

In the lower forms of life in which a free larval state is the rule, the resources of the parent are greatly taxed in producing a vast number of embryos, compara-

* Probably the appearance of secondary nourishment in connexion with the ovum was the first variation to occur, and secluded development followed as an effect. The advantage which this conferred insured more certain survival and continued variation in the same direction.

tively few of which survive the chances of destruction which await them in the outer world.

In the higher animals the resources of the parent are less taxed in this direction, but more in another—that of providing food for the secluded embryos. The parent either contributes yolk to the essential part of the ovum, or in addition she lays up with it a store of additional food, such as honey, or a store of captured prey, or, as in the case of the Mammalia and some elasmobranch fishes, she nourishes it with her own blood. In some cases, when a number of ova are left to hatch in the same capsule, one of them having proved its superiority by outgrowing the rest, proceeds to devour them, and thus obtains the requisite additional nourishment by feeding on its brothers and sisters. A remarkable instance of this occurs in the freshwater genus *Hydra*—one ovum devouring the rest while still in its ovary; so that this *Hydrozoon* produces only one or two young, instead of the countless numbers which are born to its marine relations.*

Cases of this class are of great interest, partly because they illustrate in a strikingly simple manner the supercession of “safety in numbers” by “safety in secluded development,” and partly since they seem to suggest a return on the part of the ova to “plasmodial” formation, the stimulating effect of which is so well known amongst the Protozoa.

Thus by providing food for the ovum, the full inheritance of the adult organism is secured to the embryo. Herewith a secondary advantage of great importance follows to the race. Cells, like complexes of cells, have a life-history of their own, bounded on either hand by life and death. These machines for converting energy are liable to wear out, to become clogged by residual effete products, or perhaps to become converted into some metameric modification under the degrading action of constant molecular motion. However this may be, they have power to convert only a limited quantity of energy: when they have received and expended a definite but unknown amount they cease to work. Hence the necessity for the reproductive process. If this assumption be not capable of proof, it is at any rate extremely probable. Let us see what it involves. A free-swimming embryo which repeats the ancestry spends its time in swimming rapidly about by means of its vibratile cilia, in obtaining food and digesting it, and while performing these various functions it expends the balance of its resources in undergoing structural change. On exchanging the gastrula state for some other it has still to work for its own living, and when finally it reaches the adult state it has already to a considerable extent worn out its machinery, and expended its powers of converting energy.

In the lower classes of animals, such as the coelenterates and echinoderms, the larval state is not sufficiently prolonged, and the larval changes are not sufficiently

* The same phenomenon is met with in other Hydrozoa, however, *ex. gr.* *Tubularia*.

numerous to make this result of a free larval existence clearly appear, so that the not very highly endowed animal may enjoy the adult state for a very considerable period. To rightly estimate the value of this hypothesis, we ought to know at least approximately the limits of age of various animals in the adult state, and the length of time they respectively pass in the larval state, as well as the changes which they pass through; and these data are almost wholly wanting, and not unnaturally, since no intelligent man, unprompted by some suggestions such as here made, would care to set about the laborious investigation which their ascertainment would involve, merely for the sake of tabular results. Something, however, may be learnt from various of the higher animals. Thus we may point to the Ephemeridæ, which, after a prolonged larval existence, die soon after attaining maturity. So, too, the butterflies and moths, which do not live long after oviposition. A still more important consequence, however, would seem to follow from the premature ageing due to a free larval existence; and that is the comparatively early exhaustion of the power of undergoing transformational change; the adult or comparatively stable state is reached sooner than it otherwise would be, and the chances of further development are correspondingly diminished.

If we pass to the consideration of the opposite case, we find that the embryo within the egg is in a much superior position to the free larva. In most cases, all that it has to do, besides undergoing transformational changes, is to feed upon nourishment already prepared for it, needing scarcely any preliminary digestion, but capable of immediate absorption by the cells of the embryo. When the embryo is hatched, it enters upon the world with its cells scarcely used; their capacity for work has comparatively had small demands made upon it, and thus a longer life awaits them in the mature state, when the faculties of the organism are most highly endowed.

Thus, in contrast with the Ephemeridæ, we may cite the ants and bees, which, while in the larval stage, are carefully nourished at the expense of the community, and some of which, after leading the life of grubs, enjoy an interesting and protracted existence. Further, the cells of a young animal just born would appear to be in a particularly plastic state, so that they are peculiarly ready to respond to the action of the environment. Many changes might be induced in the young animal at this critical period, the effects of which would be afterwards manifested as variations in its offspring.

Again, the longer life in the mature state, acquired by those forms which are saved from the drudgery of a larval existence, offers increased opportunities for evolution to the adult animals, so that a progressive development starting from higher and higher platforms is directly favoured.

But not only is a longer existence assured to the adult—existence in the embryonic state is shortened, and perhaps here the influence of seclusion is most

clearly exhibited; for the energy which would be expended by a free larva in activities other than those involved in producing structural change is here solely devoted to that end, and hence the embryonic stages are passed over by secluded forms with comparative rapidity. Thus, while it takes several days to produce no higher form than an *Echinus* from its larva, the chick repeats its enormously longer ancestral history in so short a time as three weeks! Thus we find an explanation for another generalization, viz., that the higher the organism the greater the tendency to pass rapidly through its embryological development, involving the abbreviation of one or more of its larval states, or it may even be their total suppression. That it should take nine months for the development of a man and only three weeks for that of a chick may seem strong adverse commentary upon this statement; but we have here to take into account not only the much higher state of organization in which the young child is born, but also its much greater relative size and the lower temperature at which the development is conducted. But it is in the Mammalia that the most perfect method is met with for insuring to the embryo immunity from all work but that of development. For here there is no useless expenditure of energy in maintaining temperature or carrying on respiration. Nourishment is obtained without the intervention of the stomach by direct absorption in the veins, and thus the ancestral history vastly longer in the Mammalia, especially in the higher orders of Mammalia, than in the other groups, is repeated in a conveniently short period.*

With this kind of intra-uterine development is probably connected the development of mammæ, since the young embryo when born possesses an unused stomach, and must, consequently, if no other reason existed, be dependent for a while upon the mother for appropriate support. In some of the elasmobranch fishes, where intra-uterine development likewise occurs, nourishment is obtained at first from yolk, and subsequently from the vessels of the yolk-sac, and hence the stomachal parts being put to some use in the course of development, there is no need for a digestive education, and the young dog-fish may obtain food for itself as soon as born.

In the Sauropsida the embryos are nourished by the yolk of the yolk-sac, which, however, is partly employed in supplying blood to the blood-vessels, but it remains quite possible that some of it is directly absorbed by the walls of the alimentary canal. Thus it happens that many birds, as soon as hatched, fall to picking up grain and feed upon it; but certain exceptions even here seem to show the advantage of a gastric education, for some graminivorous birds, such as pigeons, do not take at once to a grain diet, but are fed by the mother bird with a kind of milk, which is secreted by her crop. So, too, the flamingo pours down

* The earlier phases are passed through more rapidly than the later, probably owing to their having been far more frequently repeated.

the throat of her young a sanguineous fluid which is probably similarly derived. Even when the diet is so digestible as fish, the young bird is not put to feed upon it always in the unprepared state, but is allowed to take it from the crop of the parent where it has probably undergone a partial digestion.

The feeding of young pigeons with milk has been hitherto explained by the comparative helplessness of the young bird; but in that case what necessity is there for the special secretion of milk? One would have thought a grain diet could have been provided for it by the parent at a smaller expense to the parental resources.

We have now to end this digression by pointing to one further consequence which follows upon the comparatively late assumption of an independent existence in the case of the higher animals. It is that in seclusion, where the play of incident forces is as little varied as possible, variations from the usual course of development are unlikely to occur, and consequently the variations which so constantly appear in a species are, as a rule, to be traced to the action of incident forces on the adult animal. A form that passes through a free larval development is liable to modification at any point of its development: one that does not is chiefly susceptible of modification after birth. Hence, as no crustacean appears upon the world at an earlier stage than a nauplius, so no crustacean can diverge from the phylum at a point lower down than that of the nauplius; while the lobster, being born fully formed, cannot develop into fresh varietal modifications except as these are moulded on the lobster type. This helps us to understand the tree-like form of zoological classifications.

Returning now to the viviparous character of the development of Paludina, we find that it is not an isolated case amongst the Mollusca, for it occurs also among the Murexes; and further, that it is an illustrative case of a general tendency towards development in seclusion, the advantages of which are in most cases great, but particularly so in relation to a freshwater mode of existence.

The views here advanced as to the origin of freshwater faunas may be briefly summarised as follows:—

1. The conversion of comparatively shallow continental seas into freshwater lakes has taken place on a large scale several times in the history of the earth; and has been accompanied by the transformation of some of the marine into freshwater species.

2. At their inception these species may have been phanerogenous; if so, they have since nearly all become cryptogenous. This change has been accomplished by the selective action of climate and river currents on varietal modifications induced by change of climate (Hydra, Spongilla), or of food (? Paludina, pseudoparasitic glochidium), or otherwise.

3. While apparently the only probable explanation of the origin of sedentary freshwater forms, the hypothesis will serve equally well to account for others which are locomotive; though in their case another explanation is possible, that of direct migration from the sea.

NOTE I.—Since this Paper was in type, Professor Ray Lankester has kindly called my attention to some observations by Dr. J. Von Kennel,* who describes certain lagoons bordering the coast of Trinidad, which communicate at times with the sea, and so receive a number of marine inhabitants; and when subsequently the water of the lagoon becomes fresh, several of the marine forms, adapting themselves to the changed conditions, continue to live on, and amongst others thus persisting is a Medusa, which Dr. Kennel regards as different from *Limnocoedium*, without, however, specifically determining it.

Besides this repetition by Nature of Beudant's experiments, Dr. Kennel gives a very clear instance of the direct introduction of marine forms into a river—due probably to the transportation of free-swimming larvæ by tidal agency—thus, he mentions *Mytilacæ*, a small species of *Pholas*, and *Lumbriconereis*, as existing in the freshwater of the river Ortoire, eight miles above its mouth.

NOTE II.—The occurrence as freshwater forms of marine animals which inhabit floating timber is very suggestive from two points of view, for first it leads one to infer that, in such cases, means of transport being afforded, adaptation to freshwater conditions follows readily; and next, since such instances are rare, that to inhabit freshwater is only the first step towards becoming a characteristic freshwater organism; till the developmental history also becomes modified a wide distribution is not probable. Hence I would call special attention to Prof. E. Perceval Wright's remarks on this subject in a Paper describing a freshwater *Teredo* (*Nausitora Dunlopei*) in the waters of the river Hurreegonga a tributary of the Ganges.†

* Biologische u. faunistische Notizen aus Trinidad, Arb. d. Zool.-zoot. Instituts in Wurzburg; Bd. vi., 1883.

† On a new genus of *Teredininae*, by E. Perceval Wright, M.D., *Transactions Linnæan Society*, Vol. xxvii., p. 451 (1864).

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