TEXT-BOOK
OF THE
EMBRYOLOGY OF INVERTEBRATES.

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BY

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Vol. II.

PHORONIDEA, BRYOZOA ECTOPROCTA, BRACHIOPODA, ENTOPROCTA, CRUSTACEA, PALAEOSTRACA.

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PREFACE.

In presenting a second instalment of the translation of the *Lehrbuch der vergleichenden Entwicklungsgeschichte der wirbellosen Thiere* to students of Zoology, I feel that an apology is due to them for the long interval of time that has elapsed since the appearance of the first part. Professors Mark and Woodworth, the translators of Vol. I., found themselves unable to spare time to continue the translation, and others who subsequently undertook the work were for similar reasons obliged to relinquish it. Consequently the book came into the hands of the present translator and editor only last year; and although we have endeavoured to push the work forward as quickly as possible, the task of translating, printing, and editing has necessarily consumed a considerable time. The whole work, however, is now well in hand, and, in issuing Vol. II., we can confidently hope that no long period will elapse before the production of Vols. III. and IV., the former being already in the press.

It will be noticed that the order of the subject-matter has been changed. In its original form the Text-book is divided into three parts of unequal size. That already translated (Part I.) is much smaller than either of the remaining parts. We have consequently found it necessary to divide the second and third parts of the original into three. In doing so we were faced by a difficulty. If the original sequence of the chapters was to be retained, each part could not be made complete in itself unless the relative size of the volumes was left out of consideration. It was therefore thought preferable to alter slightly the original sequence of the chapters. Those dealing with the Phoronidea, the Bryozoa Ectoprocta and

Entoprocta, and the Brachiopoda have therefore been removed from the end of Part III. (Vol. IV. of the English edition), and placed at the commencement of Vol. II., which part contains, in addition, the Crustacea proper and the Palaeostraca. I do not think there can be any serious objection to this change, inasmuch as the four groups mentioned probably find a natural resting-place near to the Annelida, which were dealt with in Part I., while they have little, if any, relation to the Molluscan phylum treated in Part III. In all other respects the original text has been adhered to as closely as possible; but it has occasionally been found necessary to rewrite certain paragraphs which, when translated, appeared somewhat involved and obscure. In such cases the motive of the original has been adhered to as far as possible, the sentences, however, being entirely recast.

Additional notes have been added relating to the most important of the many fresh observations which have been made since the original work appeared. Such additional matter has been placed in footnotes, distinguished from the footnotes of the authors by being enclosed in square brackets. A considerable number of additional references have also been given; and these are placed with the Literature at the end of each chapter under the form of *Appendices*, and, as in Vol. I., numbered with Roman numerals. But even these additions could now be added to. For instance, since going to press a short note on the early development of *Phoronis* by E. Schultz* has appeared, which might with advantage have been incorporated in this work.

Although desirous, as far as possible, to use the same terminology as the translators of Vol. I., I have been compelled to differ from them in the rendering of the ever-recurring word "Anlage." This important term in Vol. I. is rendered by the word "fundament." Exception, with which I concur, has already

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* "Ueber Mesoderm-bildung bei Phoronis," *Otdyeln. Oppisk.*, *Tryd. imp. St. Petersburg*, *Obshch. estestv.*, T. xxviii., Vuip. 1. The author deals mainly with the formation of the mesoderm, and controverts all Caldwell's observations relating to the origin of this layer, which he maintains is a mesenchyme, and arises in the blastula and gastrula stages, most conspicuously in the latter, as proliferations from the entoderm. He could not find Caldwell's primitive groove. and thinks that this observer described as his posterior coelomic sacs the ventral invaginations which form the body-wall of the adult.

been taken to the use of this term,* on the ground that the word fundament implies the solid basis or foundation upon which a structure rests or is built, whereas an "Anlage" is essentially a changing, growing structure, which, though at one time the foundation, when only the foundation exists, eventually gives rise to, or rather itself becomes transformed into, the fully-formed organ.

Having thus decided against the continued use of this term, I found myself face to face with the responsibility of selecting one of the numerous terms which have at one time and another been put forward as the English equivalent of "Anlage," at the same time knowing full well that, whichever word was adopted, I should find a large number of biologists against me, as nearly every teacher of note has proposed at least one word which he believes to be the only correct rendering of "Anlage."

Realising, then, the impossibility of satisfying everyone, I thought it advisable to pass over all the numerous terms which have been recently suggested, none of which are really satisfactory, and to revert to that much-abused word rudiment. Most biologists will agree that the term rudiment, if it had not been misused by some of our most eminent zoologists, would undoubtedly be the best word by which we could render the German term "Anlage." Unfortunately, following the lead of Darwin and others, we have acquired the habit of applying the terms rudiment and rudimentary to certain structures present in the adult which, in consequence of their small size and frequent loss of function, have retained a somewhat embryonic stamp, thus preserving the outward appearance of a rudiment but losing its essential character, viz., its inherent tendency to further growth. These, then, are not rudiments, but arrested, reduced, vanishing, or vestigial structures, and should be spoken of as vestiges. Why, because Darwin unfortunately

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* See *Nature*, 1896, p. 361.

P. C. Mitchell, "Anlagen," *Nat. Sci.*, vol. v., 1894.

Dr. Willey (*Nature*, 1898, p. 390), who supports the use of the term *primordium*, objects to the word rudiment on the ground that the latter has been regarded as the first visible "Anlage" of an organ. But who is to decide when a growing structure is first visible to the eye?

Professor Wilder (*Science*, 1898, p. 793), in a reply to Willey, advocates the use of the term *proton;* but to define this term he has to make use of the word rudiment. Thus he states that proton was employed "to designate the primitive, undifferentiated mass or *rudiment* of a part."

misapplied the word rudimentary, should we necessarily regard this misuse as hallowed, and ever after refuse to use the word in its common sense? To such an extent has this misuse of the word been carried, that even encyclopaedic dictionaries, after defining the word rudiment in such a manner as to prove that it is the very word we are seeking, as a rendering of the idea expressed by "Anlage," give us, under the technical use of the word, "In Zoology, a part or organ, the development of which has been arrested (see Vestige)." It would require but little trouble on the part of teachers of Biology to reinvest the word rudiment with its proper meaning. By carefully insisting on the use of the words vestigium and vestigial, or their equivalents, for all abortive or reduced structures met with in the adult animal, and restricting the terms rudiment and rudimentary to all growing and developing tissues and organs, they could insure this result in a few years. We have by no means always rendered "Anlage" as rudiment, for we find that the German use of the term is not at all precise, and it was often possible to express the meaning better by another English word.

The extreme looseness with which some other terms, such as Vorderdarm, Mitteldarm, and Hinterdarm, are used in German was unfortunately not recognised until too late. These words are for the most part translated by the equally vague expressions fore-, mid-, and hind-gut. Throughout the Crustacea the fore-gut is co-extensive with the anterior ectodermal invagination, the stomodaeum, and the hind-gut is similarly related to the corresponding posterior invagination, the proctodaeum; the term mid-gut, however, is used in a more varied sense. While for the most part it is applied to the entire entodermal rudiment, it is at times used for the entodermal tube after the separation of the hepatic rudiment. As more precise terms, Professor E. Ray Lankester proposed the words enteron for the entodermal rudiment before the separation of the various entodermal derivatives, and metenteron for what is left of the enteric sac as the central element of the alimentary canal after the separation of the outgrowths,* and

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* See Preface to English translation of Gegenbaur's *Elements of Comparative Anatomy*, 1878.

these terms might well be adopted in the Crustacea for the three divisions of the alimentary canal. In the Phoronidea, Bryozoa, and Brachiopoda, it is impossible to be so precise in our terminology, for the origin and homology of the various divisions of the alimentary canal in these forms are more or less obscure. This is notably the case in the adult Bryozoon, where it is quite impossible at present to interpret the parts of the canal, all of which appear to arise from the ectoderm. The use of the terms fore-, mid-, and hind-gut must not, consequently, in this group be regarded as implying any morphological homology with the similarly-named parts in the Crustacea, but only an analogy with those parts.

All through this work the genital glands are spoken of as arising from, or in connection with, the mesoderm; and in places even the splanchnic or somatic layer of the mesoderm is specially mentioned as giving origin to the genital cells. These statements arose from the incompleteness of our knowledge, at the time when this work was published, concerning the early history of the genital rudiment. A number of observations have, however, since been made on this point in various groups of Invertebrata, especially in different orders of worms and Arthropoda, which tend to show that the primitive genital cells are separated from the somatic portion of the embryo at an extremely early period in the cleavage of the egg. In fact, in some cases, directly after the first cleavage plane has appeared, it can definitely be pointed out which of the two spheres will give rise to the genital rudiment, although this cell will also form certain other rudiments, the actual isolation of the genital cell taking place somewhat later (as early as the 32-celled stage in Cyclops, according to Hacker). All these observations lend support to the belief that the invisible genital rudiment is from the first quite distinct from the somatic rudiment; the former, at all events, attains a visible distinction at a much earlier period than is assigned to it in this work (see also Vol. i., p. 12, footnote).

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Chapter XIX. CRUSTACEA—*continued.*

CHAPTER XIX. CRUSTACEA—*continued.* PAGE

CORRIGENDA.

Page 10, line 2 from bottom—1897 change to 1867.
,, 57, in lettering of Fig. 28—*ma* change to *mg*.
,, 84, line 10—Denicker change to Deniker.
,, 209, line 5 from bottom—Sluier change to Sluiter.
,, 290, footnote *—enclose in square brackets.

CHAPTER XV.

PHORONIDEA.

Although investigators early drew attention to the many structural features in which the genus *Phoronis* resembles the Bryozoa, this form has nevertheless hitherto usually been classed with the Sipunculids. Recently, however, greater stress has been laid on its relationship to the Bryozoa and the Brachiopoda (Ray Lankester, Caldwell (No. 1), Cori (No. 4a)). It is chiefly in the anatomy of the adult that the resemblance between these groups is found, but the larval forms may also without difficulty be compared with one another.

I. Embryonic Development.

Our knowledge of the first ontogenetic stages of *Phoronis* is due to the researches of Kowalevsky (No. 6), Metschnikoff (No. 9), Foettinger (No. 5), Roule (No. 9a), and Caldwell (No. 2). The latter author, whose description we shall follow in all important points, arrived at results which frequently differ from those of earlier investigators, so that many points seem to require re-examination.

The eggs of *Phoronis*, according to Kowalevsky, are fertilised while still in the body-cavity of the parent.* They reach the exterior through the nephridial canals which open near the anus and function as genital ducts, and then, enveloped in a vitelline membrane, become attached to the tentacles of the parent, where the young develop up to the time of hatching.

Cleavage is total and unequal; the difference in size between the blastomeres of the animal and those of the vegetative pole is, however, inconsiderable. As early as the four-celled stage, two smaller blastomeres can be distinguished from two larger; the eight-celled stage shows four smaller and four larger cleavage-spheres symmetrically arranged In the further course of this very regular cleavage,

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* Cori considers this statement improbable, and thinks that fertilisation takes place outside the parent, in the water.

a small central cavity develops, and in this way a blastula forms which at first is spherical and then becomes elongated in the direction of the future longitudinal axis; in this blastula, a vegetative (entodermal) portion consisting of larger cells can be distinguished from a small-celled animal portion. The longitudinal axis coincides with the plane which divides the animal half from the vegetative half.

A true invagination-gastrula then develops (Fig. 1), the blastopore being originally oval (Fig. 1 *C*), but its posterior portion becomes slit-like and soon closes. The anterior part that has remained open persists as the oral aperture of the larva (or, more correctly, as the oesophageal aperture). The cells near the posterior closed part of the blastopore are found still later to be actively dividing, and, according to CALDWELL, they take part in the formation of the mesoderm, this being especially the case near a depression (Fig. 1 *D*, *g*) at the most posterior part of the blastopore. CALDWELL compares *Phoronis* in this respect to the Vertebrata, and calls the whole of this closed portion of the blastopore (Fig. 1 *D*) the *primitive streak*, and the depression appearing in the latter the *primitive groove.*

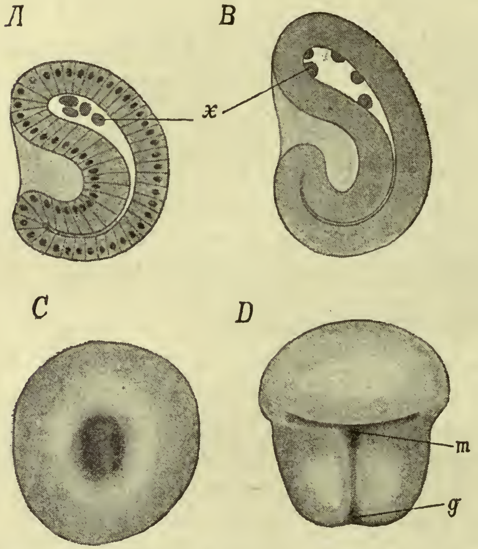

FIG. 1.—Gastrula stage of *Phoronis*. *A*, younger, *B*, older stage in optical section (after METSCHNIKOFF); *x*, protoplasmic bodies in the blastocoele (mesenchyme cells ?). *C* and *D*, ventral superficial aspects (after CALDWELL). *C*, stage with oval blastopore. *D*, stage with slit-like, partly closed blastopore; *m*, anterior open part of the same, from which the mouth of the larva is derived; *g*, posterior pit-like depression of the primitive groove; a pre-oral lobe is distinctly marked off at this stage.

Meanwhile, the embryo changes somewhat in shape. Its anterior part becomes swollen (Fig. 1 *D*) as the first indication of the future pre-oral lobe of the larva. The region of the primitive streak now lengthens greatly, so that the depression mentioned above shifts quite to the posterior end of the embryo. The surface upon which the blastopore is situated may be defined as the ventral surface and the opposite as the dorsal surface.

The mesoderm, according to CALDWELL (No. 2) forms in a very peculiar way. In the region corresponding to the most anterior part of the primitive streak, the entoderm-sac shows two lateral pocket-shaped outgrowths (Fig. 2 *A*, *d*), at the base of which mesodermal elements (*m′*) become detached through the proliferation of the entoderm-cells. When a considerable number of these mesodermal elements have been formed, they arrange themselves into a pair of sacs, each enclosing a coelomic cavity (Fig. 2 *B*, *m′*). This formation of paired coelomic sacs by the proliferation of cells from the lateral walls of the archenteron may, perhaps, be traced back to the type in which the enterocoeles arise through folding of the archenteron. Further back, single mesoderm-cells become separated from the primitive streak and pass into the space between the

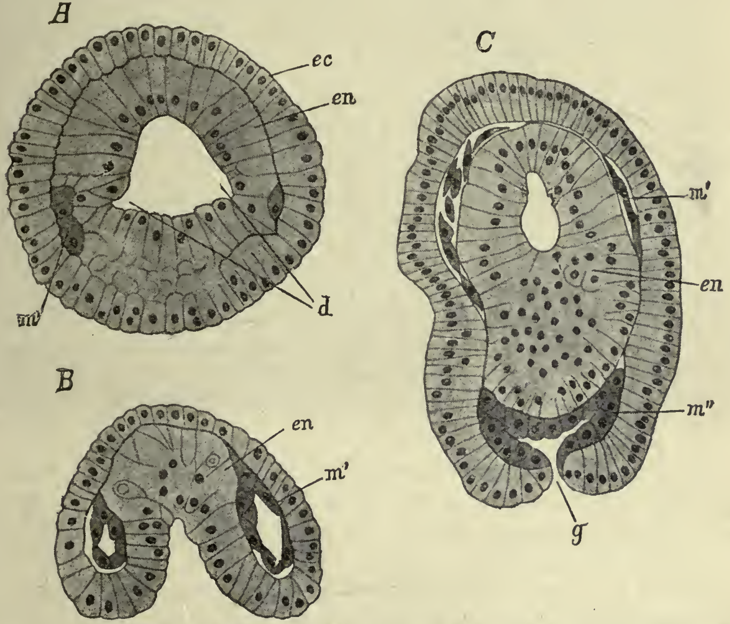

FIG. 2.—Formation of the mesoderm in *Phoronis* (after CALDWELL). *A*, transverse section through the anterior part of the embryo, showing the origin of the mesoderm. *B*, transverse section through the oral aperture of an older stage. *C*, horizontal section through an embryo, showing the formation of the posterior coelomic sacs (*m″*); only parts of the anterior sacs (*m′*) are cut through. *ec*, ectoderm; *en*, entoderm; *d*, paired archenteric diverticula; *g*, small pit at the posterior end of the primitive streak; *m′*, anterior, *m″*, posterior pair of coelomic sacs.

ectoderm and entoderm. At the most posterior part of the streak lies the small pit mentioned above (Fig. 1 *D*, *g*; Fig. 2 *C*, *g*); this depression soon gives rise to two lateral diverticula that extend anteriorly between the ectoderm and entoderm (Fig. 2 *C*, *m″*), and become the posterior coelomic sacs. The two pairs of coelomic sacs (*m′* and *m″*) that thus arise are connected together by the isolated mesoderm-cells which have arisen from the anterior part of the primitive streak. After the formation of the posterior pair of coelomic sacs, which may, perhaps, be in some way connected with the formation of the nephridia, a shallow ectodermal depression forms posteriorly and fuses with the wall of the archenteron, and here the anal aperture arises.

According to METSCHNIKOFF (No. 9) and FOETTINGER (No. 5), the mesoderm forms much earlier than is stated by CALDWELL, by a kind of mesenchyme-formation, single cells appearing in the cleavage-cavity of the blastula-stage (Fig. 1 *A*, *B*, *x*). These elements, according to the authors just named, are rather small, so that CALDWELL'S assumption that particles of protoplasm lying in the blastocoele have here been mistaken for mesoderm-cells appears somewhat probable. It is, however, possible that the formation of the coelomic sacs is preceded by the rise of a mesenchyme.

According to ROULE also (No. 9a), single mesenchyme-cells are found as early as the gastrula-stage in the primary body-cavity. Later, after the anal aperture has formed, the cells of the primary entoderm are said to increase in number at the sides of the anus, and in this way to produce two solid mesoderm-bands, while single cells that become detached mingle with the rest of the mesenchyme.

The anterior pair of coelomic sacs above described, which might be called cephalic cavities, now grow out anteriorly, and soon completely fill the interior of the pre-oral lobe. These sacs seem to yield only the lophophoral cavities (Fig. 5, *lh*) and the connected (?) cavity in the epistome (Fig. 5, *eh*) of the adult, which are separated by a transverse septum from the posterior part of the body-cavity.* This latter is yielded by the posterior pair of coelomic sacs, from which also is derived the median mesentery suspending the intestine (Fig. 5, *ms*) which is retained throughout life. Secondary, lateral mesenteries, however, are also found.

With the development of the pre-oral lobe, the principal sections of the alimentary canal and the coelomic sacs, the chief parts of the embryo are represented in rudiment, and now the whole surface becomes clothed with cilia. Thickening of the ectoderm now takes

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* [According to MASTERMAN (No. II.), there are three perfectly distinct coelomic cavities in the larva, viz.—a pre-oral or epistomal cavity, a collar- or lophophoral-cavity, and a trunk-cavity. Their origin is *not* described.—ED.]

place at two definite points. The anterior thickening which occurs at the apical end of the embryo (Figs. 3, 4 *B*) may be regarded as the homologue of the neural plate of other larvae, and yields the ganglion known as the brain,* which here, throughout life, retains its original epidermal connection. A second thickening of the ectoderm appears behind the mouth as a semicircular, ciliated swelling. From this, which may be regarded as the equivalent of the post-oral ciliated ring, the row of larval tentacles develops (Figs. 3, 4 *B*), and also the nerve-strand that runs along their points of insertion. The tentacles begin to appear early as outgrowths of the body-wall; they rapidly increase in number, fresh pairs being added dorsally (Figs. 3, 4 *B*). If this row of tentacles is to be traced back to a transformation of a post-oral ciliated ring, we may regard a strongly ciliated swelling appearing at the edge of the pre-oral lobe as the pre-oral ciliated ring. The posterior part of the body which carries the dorsally displaced anal aperture now grows out into a large cone, the end of which is surrounded by a circum-anal ciliated ring (Figs. 3, 4 *C* and *D*). Three body-regions can be distinguished in the larva, which must now be called the *Actinotrocha* (Figs. 3, 4 *B* and *C*)—(1) the pre-oral lobe; (2) the post-oral section which carries the crown of tentacles and covers the posterior part of the body like an apron; and (3) the posterior or anal section.

The changes just described, which lead to the development of the *Actinotrocha*, take place after the commencement of free larval life. The youngest larva, just hatched from the egg (Fig. 4 *A*), is still without the crown of tentacles, two small projections lying near the anus being the only indications of the tentacle-rudiments.†

II. Metamorphosis.

The *Phoronis* larva (Figs. 3 and 4 *B*), the shape of which has been described above, was discovered by Joh. Müller and described as *Actinotrocha branchiata*, and was afterwards more carefully examined by Wagener, Gegenbaur, and others. Krohn (No. 7) and Schneider (No. 10) investigated the metamorphosis which led to the production of a Gephyrean-like form, Kowalevsky (No. 6) being

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* The pre-oral lobe, together with the brain of the larva, is, as we shall see below, thrown off during metamorphosis. Since, however, these parts are regenerated later, we may still theoretically trace them back to the corresponding parts of the larva.

† [For the structure of the *Actinotrocha*, see Masterman's recent work (No. II.) on this larval form. These observations, if confirmed, would show that *Phoronis* is directly related to *Balanoglossus*, *Cephalodiscus*, and *Rhabdopleura*.—Ed.]

the first to prove that the *Actinotrocha* was the young form of the *Phoronis* discovered by Wright. Since that time, the metamorphosis of *Phoronis* has been more accurately investigated by Metschnikoff (No. 8), Wilson (No. 11), and Caldwell (No. 1).

The first changes that take place in the *Actinotrocha* consist of a simple increase in size through growth and a continual increase in number of the tentacles. At the same time, a sensory organ develops in front of the neural plate, four eye-spots being added to it in one species. The pigment-spots characteristic of the different species now also develop on the pre-oral lobe and on the tentacles.

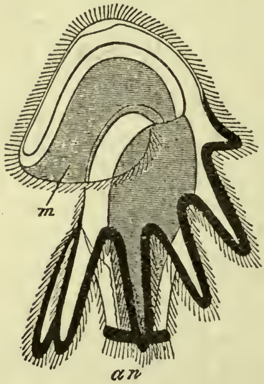

Fig. 3.—Larva of *Phoronis (Actinotrocha)*, after Metschnikoff, from Balfour's *Text-book*. *m*, mouth; *an*, anus.

Rudiments now appear of the definitive structures that are destined to replace the larval organs. Of these, the first to develop is an invagination of the body-wall on the ventral surface of the posterior region of the larval body (Fig. 4 *C*, *iv*), and in this the two layers of the body-wall (the ectoderm and the somatic mesoderm) can be distinguished. This invagination, which soon grows as a much-coiled tube into the larval body-cavity, represents, as we shall see, the rudiment of the greater part of the body-wall of the adult. Small truncated processes now develop at the base of the crown of tentacles, and from these are derived the adult tentacles (Fig. 4 *D*).

When these structures have appeared as rudiments, the *Actinotrocha* sinks to the bottom, the critical moment of the commencement of metamorphosis having arrived, the whole process being accomplished within a quarter of an hour. Metamorphosis is introduced by the evagination of the tube mentioned above (Fig. 4 *D*), this being protruded like the tentacle of a snail. Since the alimentary canal, together with its mesentery, is attached to the inner end of this tube, it soon has to follow the movement thus begun, and so comes to lie inside the completely evaginated tube (Fig. 4 *E*). During these changes the rest of the larval body loses its turgescence. The oral and anal apertures therefore come to lie remarkably near one another. The pre-oral lobe of the larva is now thrown off, and the same fate overtakes the larval tentacles and the circum-anal ciliated ring. The lost larval organs in the oral region consequently have to be replaced by extensive regeneration. It has already been mentioned that the rudiment of the permanent crown of tentacles which soon assumes the form of a horseshoe-shaped lophophore appears early.

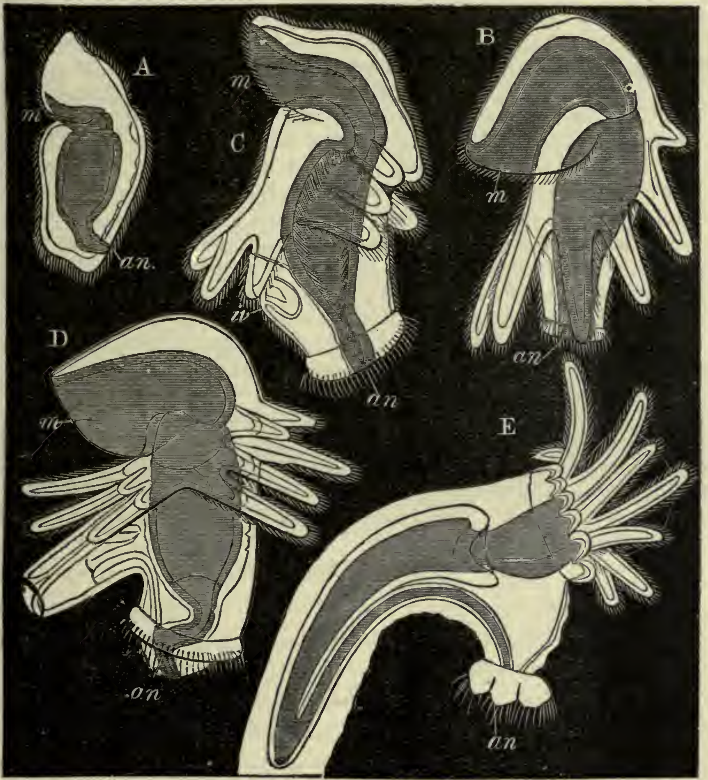

FIG. 4.—A series of stages in the metamorphosis of *Phoronis* from the *Actinotrocha* (after METSCHNIKOFF, from BALFOUR'S *Text-book*). *A*, young larva. *B*, larva after the development of the post-oral ring of tentacles. *C*, larva in which the invagination (*iv*) is commencing, from which is derived the greater part of the body of the *Phoronis*. *D*, invagination partially, and *E*, completely everted. *an*, anus ; *m*, mouth.

By means of this remarkable metamorphosis, an animal is produced the body of which is derived for the greater part from a prolongation of the ventral side of the larva. The dorsal side, on the contrary, has undergone considerable abbreviation, and can be recognised in the short tract lying between the mouth and the anus.

There are a few points connected with the rise of the organs which must be described a little more in detail. The nephridia of *Phoronis* which have recently been carefully studied by Caldwell (No. 1) and Cori (Nos. 4 and 4a. and Ectoproc. Bryoz. Lit., No. 46) are, in the adult, paired, looped, ciliated canals opening externally near the anal aperture (Fig. 5, *n*). Each nephridium consists of a curved tube starting from the nephridiopore, passing outside the transverse septum, and opening through two ciliated funnels into the posterior part of the body-cavity. These organs thus belong essentially to the posterior section of the body. These nephridia, which in structure may be compared to the segmental organs of the Annelida, arise, according to Caldwell, through the metamorphosis of the larval nephridia discovered by him in the *Actinotrocha.* The latter, in their structure, recall rather the head-kidney of the Annelida. They are paired canals which open externally behind the transverse septum or diaphragm on either side of the invaginated ventral sac, the inner blind ends being connected with a number of excretory cells. These are star-shaped, a fine canal leading from each of them into the common duct. With regard to the origin of this larval kidney, Caldwell thinks that we may regard the paired ducts as the remains of the communication established between the posterior coelomic sacs and the surrounding medium by means of the pit-like depression mentioned above (Fig. 2 *C*, *g*). The excretory cells, on the other hand, would have an independent origin in the somatic mesoderm-cells.

Phoronis is specially distinguished by the possession of a closed blood-vascular system which ramifies on the intestine and in the tentacles, and in which a fluid containing red blood-corpuscles circulates. The details of the origin of this blood-vascular system are as yet not known, but it appears that the vessels originate by dehiscence in the splanchnic layer of the mesoderm. While, according to Cori, the vascular system of the adult is completely closed, there seems, in the larva, to be a communication between it and the cephalic part of the body-cavity. In the latter, the blood-corpuscles are said to arise in large agglomerations.

III. General Considerations.

The *Actinotrocha* may without difficulty be regarded as a somewhat modified *Trochophore.* Indications are found in it of a pre-oral and of a post-oral ciliated ring, the latter being transformed into a row of tentacles, and of the characteristic neural plate. The development of the mesoderm is of special importance. This is arranged as two pairs of coelomic sacs which, however, do not appear to be fully equivalent to one another, since, according to Caldwell, they differ in their origin. The anterior pair of coelomic sacs yields the cephalic cavity (lophophoral cavity),* the posterior pair the whole body-cavity of the adult trunk. A transverse diaphragm dividing the two parts of the body-cavity is found in the *Actinotrocha* on a level with the crown of tentacles. The nephridia belong to the posterior coelomic section.

We can thus distinguish, in the body of the *Actinotrocha*, as well

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* [In the light of Masterman's observations this point requires reinvestigation.—Ed.]

as in that of the adult *Phoronis*, a cephalic section and a trunk section. Further, the body is unsegmented, and there are no indications of the descent of *Phoronis* from a segmented ancestor.

The metamorphosis of *Phoronis* affords important data for the orientation and interpretation of the adult animal. We have seen that the principal parts of the body owe their origin to an excessive growth of the ventral side. The longitudinal axis of the adult therefore lies at right angles to that of the *Actinotrocha*. The dorsal surface is shortened, being restricted to the short tract lying between the mouth and the anus (Fig. 5, *m–a*). Although the larval organs are cast off, we may regard the organs that appear in their place as their full equivalents. We shall therefore have to derive the tentacle-crown of the adult from the post-oral ciliated ring of a *Trochophore*-like ancestor, and to regard the epistome as the transformed pre-oral lobe.

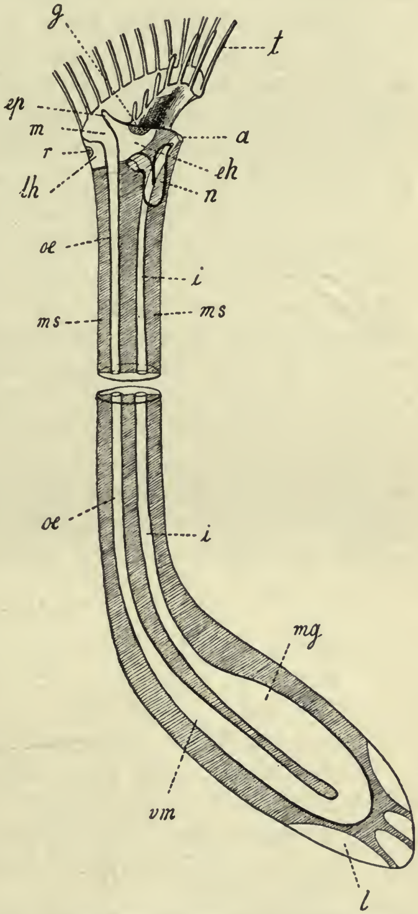

FIG. 5.—Diagram representing a median longitudinal section of *Phoronis* (constructed after CORI). *a*, anus; *eh*, epistomal cavity; *ep*, epistome; *g*, ganglion; *i*, intestine; *l*, fenestrae in the mesentery; *lh*, lophophoral cavity; *m*, mouth; *mg*, second stomach [intestine of BENHAM]; *ms*, dorso-ventral mesentery; *n*, nephridium; *oe*, oesophagus; *r*, circular nerve; *t*, tentacles; *vm*, first stomach.

The remarkable metamorphosis of *Phoronis* certainly does not correspond to any phylogenetic condition. We shall have to assume that a very gradual shifting of the anal aperture along the dorsal middle line took place in the worm-like ancestor of *Phoronis*, which perhaps lived in sand or even in a tube, a shifting similar to that which takes place in the *Sipunculidae* (Vol. i., p. 363).

The fact that, in the trunk region of the adult *Phoronis* the symmetrical arrangement of the body begins to be disturbed, is no doubt connected with the tubicolous manner of life. There is thus a longitudinal nerve-strand on the left side, and, according to Cori (No. 4), a new plane of symmetry, different from the original one, is evident in transverse sections in the grouping of the longitudinal muscles in *Phoronis psammophila.* Indeed, in the presence of secondary and tertiary mesenteries, which leave between them distinct intervals containing the groups of longitudinal muscles, there is a tendency to the development of the radial type.

It should here be pointed out that, in *Phoronis*, the cephalic region is often lost and again regenerated. According to Cori (No. 4a), not only the tentacle crown, but with it a part of the oesophagus, the epistome, the ganglion, the so-called lophophoral organs, the blood-vascular ring, and perhaps also the nephridia are lost. The spontaneous throwing off of the cephalic section is specially liable to occur when the animals are placed in unfavourable conditions of existence. This process closely resembles the throwing off of the head in *Pedicellina* and in the Tubularia; and the same process is found in the Ectoproctous Bryozoa, in the disintegration and subsequent regeneration of the polypide (p. 55).

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CHAPTER XVI.

BRYOZOA ECTOPROCTA.

Colonial Bryozoa with the anus outside the lophophore, with a well-developed introvert and a spacious coelom.

Systematic :—

A. PHYLACTOLAEMATA. Fresh-water forms, with horseshoe-shaped lophophore prolonged into two arms; with epistome overhanging the oral aperture (*Cristatella, Plumatella, Pectinatella, Fredericella*).

B. GYMNOLAEMATA. Mostly marine; with circular lophophore; without epistome.

I. Cyclostomata. Apertures of the zooecia terminal, circular and devoid of closing apparatus; without appendages (*Crisia, Diastopora, Hornera, Tubulipora, Frondipora*).

II. Ctenostomata. Apertures of the zooecia terminal, closable by means of tooth-like or seta-like projections of the tentacle-sheath.

1. Halcyonellea (*Alcyonidium, Pherusa, Flustrella*).

2. Stolonifera (*Vesicularia, Amathia, Bowerbankia, Farella, Hypophorella;* the fresh-water forms *Paludicella* and *Victorella* also belong here).

III. Chilostomata. Apertures of the zooecia not, as a rule, terminal, usually closable by a movable lid.

1. Stolonata (*Aetea, Eucratea*).
2. Radicellata.
    a. Cellularina (*Cellularia, Scrupocellaria, Bugula*).
    b. Flustrina (*Flustra, Membranipora*).
    c. Escharina (*Retepora, Microporella, Eschara, Lepralia, Schizoporella*).

I. Formation of the Egg, Fertilisation, Position of the Embryo.

The genital products of the Ectoproctous Bryozoa arise in cell-masses which originate as growths of the mesodermal parenchymatous tissue (marine Ectoprocta), or of the peritoneal epithelium corresponding to the latter (Phylactolaemata), on the inner side of the body-wall (*endocyst*), or else in strands of the so-called *funicular* tissue. The ovaries are very generally found on the neural wall (dorsal side) in the anterior or middle part of the body; the testes lie at the base of the zooecium (*i.e.*, in the proximal part). In the fresh-water Bryozoa, the genital rudiment frequently bears a relationship to that part of the mesenterial strand which is known as the *funiculus*. In *Paludicella*, for instance, the eggs lie on the body-wall near the point of insertion of the upper funiculus, while the spermatozoa arise on the basal portion of the lower funiculus. In the Phylactolaemata, on the contrary, the ovary lies on the oral body-wall, while the spermatozoa, as a rule, develop in aciniform masses at the upper part of the funiculus. In *Cristatella*, the spermatozoa arise on the mesodermal septa of the body-cavity.

The genital products pass into the body-cavity, where, in some forms, fertilisation takes place. Since the Bryozoa are, as a rule, hermaphrodite, and as it is difficult to state in what way foreign spermatozoa can reach the body-cavity, self-fertilisation has been assumed to occur. The fertilised eggs either pass through the whole of their embryonic development, up to the time when the ciliated larva is formed, within the body-cavity of the parent, or else, through the dehiscence of the body-wall, reach the tentacle-sheath (*Valkeria*, Joliet, No. 17; *Lepralia* and *Vesicularia*, Ostroumoff, No. 26), in the cavity of which they pass through the embryonic stages till the larva hatches, or else the eggs (as in many Chilostomata) are received into special outgrowths of the zooecium which serve as brood-cavities. These are the *ooecia* and *ovicells* which have been described as individuals of the polymorphous Bryozoan stock peculiarly metamorphosed for the care of the brood.*

In those cases in which the larvae pass through their earliest ontogenetic stages in the body-cavity of the mother, they escape either through the aperture of the zooecium, after the polypide to which they belong has undergone degeneration, or else there is a special aperture near the base of the tentacles for the passage of the

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* [In some Cyclostomata (*Crisia*) the ovicells are undoubtedly modified zooecia in which the polypide is rudimentary or degenerate.—Ed.]

embryos. Such an aperture was found in *Farella* by VAN BENEDEN, and in *Hypophorella* by EHLERS.

In a few Gymnolaemata (*Alcyonidium gelatinosum*, *Membranipora pilosa*) FARRE, SCHMIDT, and HINCKS found a flask-shaped ciliated canal (*nephridium* ?) connecting the body-cavity with the surrounding medium and opening out between the tentacles. PROUHO (No. 28a) recently observed in some species of *Alcyonidium*, that this *intertentacular organ* was connected with oviposition. In *Alcyonidium albidum*, the eggs probably undergo fertilisation within the body-cavity and become surrounded by a soft shell, being then ejected into the surrounding medium through the intertentacular organ while the parent polypide is extended, further development taking place in the water. More complicated conditions are found in *Alcyonidium duplex.* In this form, at the period of sexual maturity, the (male) polypide of a zooecium which is without an intertentacular organ develops spermatozoa. At the same time, on the aboral side of this zooecium, a second (female) polypide, provided with an ovary and an intertentacular organ, is developed; soon after fertilisation the male polypide degenerates.

The fertilised eggs, which are provided with a shell, probably reach the tentacular sheath through the intertentacular organ; here, each attached by a fine stalk, they pass through their further development. When the polypide is extended, the part of the tentacle-sheath carrying the eggs is evaginated. In this position the egg-shell bursts and the larva swims about freely.

Within the ovaries, which originally consist of small, indifferent cells, a few (2-5) young egg-cells soon appear, the remaining cells becoming grouped round these to form a follicular epithelium (VIGELIUS). Of these young egg-cells, two at first develop more than the others; but, as a rule, only one egg becomes fully mature. This egg remains at first connected with the ovary by means of a strand, while what remains of the ovary draws back to the body-wall so as to serve later as the place of origin of another egg. (On the conditions of the maturation of the egg and the ooecia of the Phylactolaemata, see below, p. 33.)

Remarkable conditions of embryogenesis were found by HARMER (No. 15) in *Crisia*, a form in which the ripe ovicells contain a large number of embryos.* Beside these is found a protoplasmic nucleated network which sends out finger-

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* [This condition is brought about by a fission of the primary sexually-produced embryos. As many as one hundred secondary embryos produced by budding are found in a single ovicell. HARMER, *Quart. Journ. Micro. Sci.*, Vols. xxxiv. and xxxix.—ED.]

shaped processes, from the free ends of which the embryos are developed like buds and eventually cut off. In quite young ovicells, on the contrary, a single egg-cell, surrounded by a follicle, is found; this appears to give rise to the finger-shaped budding organ mentioned above as producing the embryos. In *Crisia*, therefore, the number of embryos produced by the early division of the primary embryo is larger. The mature larvae swim out through the tubular aperture of the ovicell.

According to VAN BENEDEN and PERGENS, the maturation of the egg is connected in a certain regular way with the disintegration of the polypide* that produces it, and, in some forms (*Flustra truncata, Microporella malusii, Bugula simplex* and *turbinata*) with its later regeneration, so that, when the egg is fully mature, the polypide undergoes histolysis, and becomes changed into a brown body. While the ovary brings another egg to maturity, a new polypide forms. For details of these processes of regeneration see below, p. 55. Among these must also be reckoned the above observations of PROUHO on *Alcyonidium duplex*. In the Phylactolaemata also, as a rule, during the development of the embryos and the statoblasts, the polypide to which they belong degenerates, but, in this case, there is no subsequent regeneration.

II. Embryonic Development.

The mature, spherical, or ellipsoidal eggs are surrounded by a hyaline membrane called by PERGENS the *chorion*. In the ovum can be recognised a vesicular nucleus with spherical nuclear bodies, and a granular yolk often yellow or brown in colour. The two polar bodies, which are usually of unequal size, correspond in position to the animal pole of the egg.

The first ontogenetic processes in the egg of the marine Ectoprocta are best known in *Lepralia* (BARROIS, Nos. 6 and 7), in *Tendra zostericola* and *Bowerbankia* (REPIACHOFF, Nos. 32 and 34), in *Bugula calathus* (VIGELIUS, No. 39), and in *Microporella malusii* (PERGENS No. 27). In these eggs cleavage is total and almost equal (Fig. 6). The two-celled stage is attained by means of a meridional furrow, and the four-celled by means of another meridional furrow at right

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* The expressions "polypide" and "cystid" correspond to an older view, according to which the cystid forming the wall of a chamber represents an individual which gives rise asexually through budding to the polypide. Each chamber of the Bryozoan stock, consisting of a polypide and a cystid, would then represent a double individual or a miniature colony. This view was founded on the great independence of the polypides as shown in the processes of degeneration and of regeneration above-mentioned. Although we do not share this view, we still retain in use these expressions which have become established. The cystid, then, means to us the lower part of the body-wall, while the polypide represents the retractile anterior section of the body with the intestinal canal attached to it. These two are merely parts of one individual.

[Acting on the suggestion of Dr. HARMER, we have substituted the term "zooecium" for cystid in referring to the outer parts of the ordinary adult individual, as this term is of much more general use in English works on the Bryozoa.—ED.]

angles to the first; this stage, in consequence of an equatorial furrow, passes over into the regular eight-celled stage (Fig. 6 *A*). A small blastocoele can frequently be observed as early as this stage, and the animal pole can be distinguished from the vegetative pole by a difference of size—often only very slight—in their respective blastomeres. In the further segmentation there is a peculiarity worthy of note. The sixteen-celled stage is reached through the appearance of two

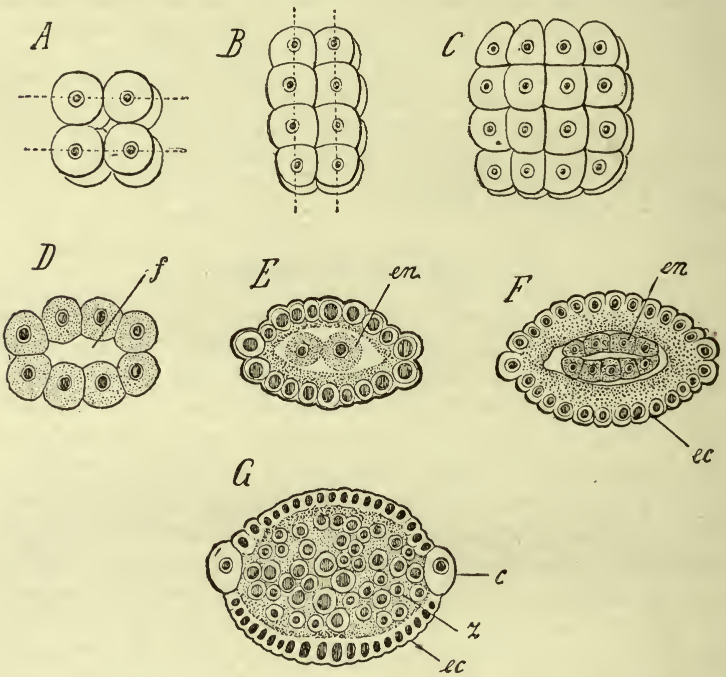

Fig. 6.—Cleavage and embryonic stages of *Bugula calathus* (after Vigelius). *A*, stage with eight blastomeres. *B*, stage with sixteen blastomeres. *C*, stage with thirty-two blastomeres. All seen from above. The dotted lines in *A* and *B* indicate the direction of the next cleavage planes. *D*, blastula-stage in vertical section. *E* and *F*, gastrula-stages. *G*, a later ontogenetic stage. *c*, corona-cells; *ec*, ectoderm; *en*, entoderm; *f*, cleavage-cavity; *z*, central tissue derived from the primary entoderm.

furrows lying on either side of the first meridional plane and running parallel to it. An embryo thus results, each half of which consists of eight cells (in two rows of four, Fig. 6 *B*). A similar division leads to the thirty-two-celled stage (Fig. 6 *C*), two furrows forming parallel to and at the sides of the second meridional plane. Each half of this embryo consists of four rows, each containing four cells. This stage is followed by less regular divisions and results in a blastula bearing a general resemblance to a biconvex lens (Fig. 6 *D*). A more active division of the cells of the animal (later aboral) pole can now be remarked, while, from the vegetative pole, four entoderm-cells wander into the blastocoele (Fig. 6 *E*). As soon as the entoderm-cells have shifted inwards, the surrounding ectoderm-cells seem to join together. This type of entoderm-formation may be traced back to polar ingrowth. A shallow depression in the region of the vegetative pole is often noticeable during these processes.

After the ectoderm has completely closed, the four entoderm-cells multiply, their derivatives becoming grouped so as to enclose a small slit-like cavity (archenteric cavity, Fig. 6 *F*). This cavity is usually obliterated later, the entoderm-cells multiply still more, and finally yield a mesenchyme or embryonic connective tissue (the inner mass, central tissue, "Füllgewebe," Fig. 6 *G*, *z*), which completely fills the blastocoele. This tissue, which seems to be of little importance in the later development, playing merely a passive rôle, soon assumes a reticular character (Fig. 9 *B*, *f*). While these processes have gone on within, two rows of cells at the edges of the biconvex embryo have become distinguished by their larger size (Fig. 6 *E* and *F*); one of these rows at a later stage becomes very conspicuous, forming the rudiment of the ciliated ring or girdle of the larva, and is known as the corona or velum (Fig. 6 *G*, *c*).

After the larva has attached itself, the central tissue gives rise to the mesodermal portion of the first sedentary individual (primary zooecium), *i.e.*, to the parietal mesoderm-layer on the inner side of the endocyst, and to the outer layer of the sac-like rudiment of the polypide (Fig. 12, *b*, p. 29). The rest of the central tissue unites with the cell-mass yielded by the degeneration of the larval organs to form a spherical mass (the so-called *brown body*), which is composed of remains of cells, particles of food-yolk and detritus, and which, when the first polypide develops, is used up as food material.

The central tissue is derived direct from the primary entoderm of the gastrula-stage. This germ-layer does not, as a rule, separate into mesoderm and definitive entoderm. Barrois (No. 7), indeed, maintains that such a separation does take place in *Lepralia unicornis*, the mesoderm there becoming arranged in paired mesoderm-bands. His observation, however, has received no further confirmation through researches made in connection with various other genera. In those few forms in which an alimentary canal is developed, there must of course be a separation of the mesoderm from the definitive entoderm. In quite early stages (corresponding to that in Fig. 6 *F*), a separation of the mesoderm from the entoderm was observed by Prouho (No. 28b) in the embryos of *Alcyonidium* and *Membranipora pilosa* (*Cyphonautes*), but no further details as to the rise of the mesoderm could be observed.

The embryo which originates in this manner (Fig. 6 *G*), in which two body-layers (ectoderm and central tissue = primary entoderm) can be distinguished, gives rise to the typical Ectoproctous larva by certain characteristic modifications of the ectoderm. The cells of the *corona* increase in size and become covered with cilia, giving rise to a transverse ciliated zone (Fig. 7, *c*), by means of which the body of the larva is divided into an upper aboral half (corresponding to the former animal pole) and a lower oral half. In the aboral half, a disc-like thickening beset at its edge with stiff setae develops (Fig. 7, *r*); this is the so-called *retractile* or *ciliated disc* (*calotte* of Barrois, *cap*), which has been regarded as the rudiment of the polypide that develops in the primary zooecium of the Bryozoan stock. At its periphery, this organ is encircled by a depression (Fig. 7, *p*, mantle-cavity Barrois). In the oral half, two organs develop first of all, the plane of symmetry of the larva being marked by their position. In the posterior portion of the oral side a deep ectodermal depression occurs; this originally has the form of an almost completely closed sac (Fig. 7, *s*), and from the fact that it serves as an attaching organ during the subsequent metamorphosis, it is called the *sucker* (*sac interne*, Barrois).* Further forward there is a median furrow beset with strong flagella, the so-called *anterior ectodermal furrow* (*oral furrow* of Nitsche, *fente* of Barrois, *dorsal organ* of Balfour); this is connected internally with a glandular tissue to which Barrois gave the name of *pyriform organ* (Fig. 7, *o*). In the space between the anterior ectodermal furrow and the sucker, the oral aperture (Fig. 7, *m*) is found in those larvae in which an alimentary canal develops.

III. Metamorphosis.

The metamorphosis of a Bryozoan larva comprises a more or less protracted free-swimming stage, during which no perceptible advance is made in the development of the animal, and further, the attachment of the larva, and the subsequent somewhat complicated changes which bring about its transformation into the first primary zooid of the young Bryozoan colony.

Although there is no difficulty in tracing back the larvae of the Ectoprocta to a common type resembling that indicated above, we find certain distinguishable larval types, which, for the sake of clearness, must be treated separately. The description of each larva

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* It should here be pointed out that the name "sucker" is calculated to convey a false impression as to the function of this ectodermal invagination, which is in reality merely the basal plate of the future primary zooecium in preparation and in an invaginated condition. Fixation does not occur through suction, but only after the evagination of this basal plate, as will be seen later.

will be followed by the account of its transformation into the attached form, as far as this latter is accurately known.

1. Type which develops an Alimentary Canal.

We shall commence our study of the Ectoproctous larvae with the consideration of a few isolated forms, which, in external structure, do not greatly differ from the typical larva (especially from that of the *Escharina*), but which in the higher differentiation of their internal organs show a more primitive condition. In the possession of a well-developed (though also to some extent functionless) alimentary canal especially, these larval forms afford important points of comparison with the larvae of other groups, whereas, in most other Ectoproctous larvae, the primary entoderm gives rise merely to a parenchyma (central tissue), which in many forms contains a yolk-mass.

a. Larva of Alcyonidium.

The larva of *Alcyonidium* (Fig. 7) has already been described and figured by Farre and others, and later by Barrois (No. 6), its internal structure having been specially investigated by Harmer (No. 13). This larva differs little externally from the type which we shall find retained in the *Escharina*. When viewed from above, it appears perfectly spherical; when seen from the side (Fig. 7 *A*) the oral surface is distinguished by its greater convexity from the flat aboral side. Almost the whole of the latter is occupied by the *retractile disc* (Fig. 7, *r*), bordered with stiff cilia, this organ being separated by a circular depression (*mantle-cavity*, *p*) from the ciliated *corona* (*c*) which is composed of large cells. On the oral surface, in the anterior region of the larva, we can recognise the *anterior ectodermal furrow* (*o*), at whose edge are cilia which, anteriorly, become grouped together to form a ciliated tuft (*plumet*). In the posterior part of the larva the sucker-invagination (*s*) is visible. Two pairs of flagella belonging to the posterior region of the oral surface should also be mentioned.

In a longitudinal section (Fig. 7 *B*), we recognise first the large cells of the ciliated ring (*c*), then, in the anterior part of the oral surface, the *pyriform organ* (*o*) lying at the base of the ectodermal groove, consisting of elongated ectodermal cells that possess a peculiar histological character. Between this organ and the aperture of the *sucker* (*s*), which lies further back, is the oral aperture (*m*) leading through a narrow oesophagus, which may have arisen as an ectodermal invagination, into a wide gastric cavity that ends blindly. A comparison with the larvae of *Tendra* and of *Cyphonautes* renders it probable that the part lying behind the aperture of the sucker corresponds to the anal region. This distinctly developed alimentary canal appears to be a vestigial organ, there being no indication that it actually functions. It degenerates in the further course of larval life.

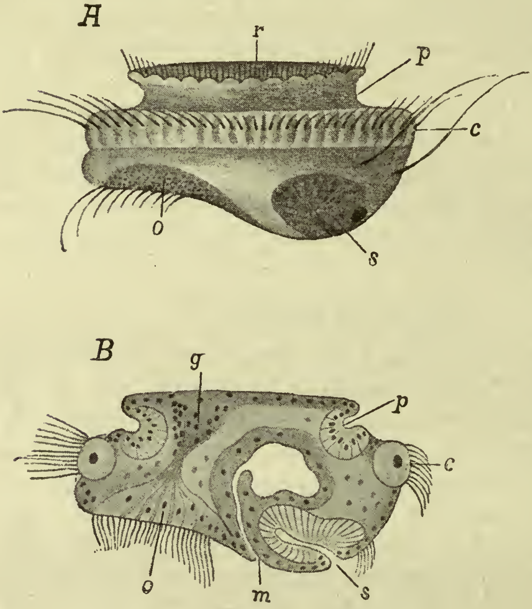

Fig. 7.—*A*, larva of *Alcyonidium mytili* (after J. Barrois). *B*, longitudinal vertical section through the larva of *Alcyonidium* (diagram constructed after the figures of Harmer). *c*, coronal cells; *g*, brain (?); *m*, oral aperture; *o*, pyriform organ; *p*, mantle-cavity; *r*, retractile disc; *s*, sucker.

The thickness of the epithelium which lines the mantle-cavity (*p*) is remarkable, and contrasts with the somewhat thin ectodermal layer of the retractile disc. Closely connected with the latter layer, in the anterior part of the larva, there is a cell-mass (Fig. 7 *B*, *g*) which Harmer (No. 13) regards as the brain. This author observed, arising within this cell-mass, fibrous strands, some of which are said to become connected with cells of the ectodermal furrow, while others can be followed into the neighbourhood of the large coronal cells. Should these statements be confirmed, we should appear justified in considering the pyriform organ as a sensory organ, whereas until now its histological constitution seemed to point to the conclusion that it functioned as a gland. The presence of a larval brain comparable in position to the neural plate would be of importance in tracing the Ectoproctous larvae back to the *Trochophore*. The statements of Harmer have recently been confirmed by the researches of Prouho (No. 28) in connection with *Flustrella*, but on account of the difficulty of investigating this point, we are unable as yet to accept with certainty the interpretation that these fibrous strands are nerves.

b. Larva of Tendra.

If we leave out of account *Cyphonautes*, to which reference will shortly be made, Repiachoff (No. 32) deserves the credit of having been the first to prove the existence of a well-developed alimentary canal in a typical Ectoproctous larva. This author found in the larva of *Tendra (Membranipora) zostericola*, which in other respects follows the type of the ordinary *Escharina* larva, and also resembles the *Alcyonidium* larva, an intestinal canal, the oral aperture of which lies in front of the sucker, while the anal aperture lies behind that organ. The *Tendra* larva would thus approximate to the larva of *Alcyonidium* in the topography of its internal organs.

c. Larva of Membranipora and Flustrella.

The larva of *Membranipora* has frequently been investigated. Ehrenberg placed it under the name of *Cyphonautes* among the Rotatoria; later, Joh. Müller compared it with the larva of *Mitraria*; and Semper, Leydig, and Claparède (No. 1) declared it to be a Lamellibranchiate larva, Schneider (No. 5) being the first to establish its true affinities as the young of *Membranipora*. Later observations were made by Allman, Metschnikoff (No. 19), Hatschek (No. 2), Barrois (No. 6), Repiachoff (No. 4), and Prouho (No. 28) as to the structure of *Cyphonautes*, while its attachment and transformation were investigated by both Schneider and Ostroumoff (No. 3). It appears from the statements made by these authors that *Cyphonautes* agrees closely in all important points with the typical Ectoproctous larva (*e.g.*, *Alcyonidium* larva), the apparent differences between them being of an unessential kind.

Cyphonautes (Fig. 8.) resembles in shape a laterally compressed bell. The lower surface is bordered by cilia. If we compare this with the corona of the *Alcyonidium* larva, we find that we must regard the external surface of the bell as the aboral side, and the under surface of the bell as the oral side partly invaginated to form a vestibule or atrium. The whole body is covered externally by two triangular shell-valves connected together along their anterior edges, which run parallel to the fibrous strand (Fig. 8, *f*). The two valves that come into contact along this hinge-line cover the laterally compressed body on the two sides. Their posterior edges, which run parallel to the mid-gut and the hind-gut (the intestinal edges), are sharply bent round towards the middle line of the body. The shell-valves meet at this point like pincers. Near the lower aperture (the entrance to the atrium) the valves gape. At the aboral pole, a prominence (*r*) covered with stiff cilia projects from the shell, but can be withdrawn into it. In this we recognise the homologue of the "retractile disc."

Some uncertainty still prevails as to the ciliated ring that runs round the edge of the bell. According to EHRENBERG and HATSCHEK, there is a single complicated ring, forming many coils, but CLAPARÈDE and SCHNEIDER, whose view has been adopted by PROUHO, think they can distinguish two distinct rings of cilia, an anterior ring in the neighbourhood of the pyriform organ (*o*) and a posterior, circum-anal ring, part of which sinks into the atrium.

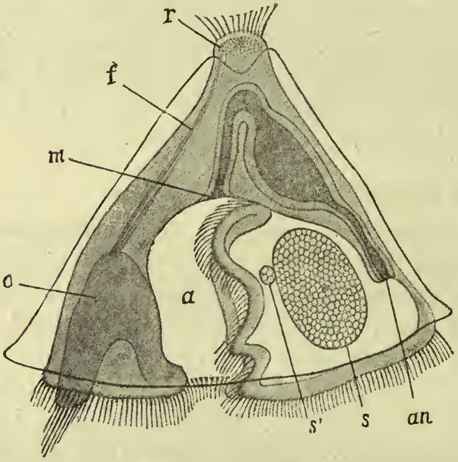

FIG. 8.—Larva of *Membranipora* = *Cyphonautes* (combined from the figures of CLAPARÈDE, SCHNEIDER, and HATSCHEK). *a*, atrium; *an*, anal aperture; *f*, fibres connecting the pyriform organ (*o*) and the retractile disc (*r*); *m*, mouth; *s*, glandular thickening (homologue of the sucker); *s'*, similar, smaller organ (shell-adductor muscle).*

On the oral invaginated surface we notice first, in the anterior angle, a cell-mass provided with a tuft of cilia; this is the *pyriform organ* (*o*). According to REPIACHOFF, two parts may be distinguished in it; an invaginated, sucker-like epithelial thickening surrounded by a ring of cilia (ectodermal furrow), and a cell-accumulation lying above this (the actual pyriform organ). As in *Alcyonidium*, this organ is connected with the retractile disc (*r*) by fibrous strands (*f*), some of which have been claimed as muscle-fibres and some as nerve-fibres (PROUHO).

Cyphonautes has a fully-developed and functional alimentary canal. The oral aperture (*m*) is found in the base of the atrium, and leads

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* [The organs *s* and *s'* are not isolated structures as represented in the figure, but are situated underneath the body-wall, which latter should be indicated as a line extending forwards from the anus below *s* and *s'* and joining the ciliated ring near the mouth.—ED.]

into a very expansible oesophagus, which ascends towards the aboral surface; here it bends sharply downwards and joins the dilated stomach which passes into the hind-gut. The anal aperture (*an*) opens into the atrium. In the space between the mouth and the anal aperture there is a paired glandular thickening (*s*). Near this kidney-shaped organ lies a similar smaller organ (*s*′). Ostroumoff has shown that when the larva begins to change into the sedentary form, fixation takes place by means of this paired disc and the cementing substance secreted by it, so that we may regard it as the homologue of the *sucker* of other Ectoproctous larvae.

The smaller organ seen near the sucker was assumed by Schneider and H. Prouho to be the transverse section of the adductor muscle of the shell.

It is evident from the above description that *Cyphonautes* agrees in all important points with the typical *Alcyonidium* larva, from which it is distinguished chiefly by the slighter development of the retractile disc and by the absence of a circular mantle-cavity surrounding that organ. In place of this cavity we find an extensive surface (mantle-surface) on the aboral half of the body, which secretes the two cuticular shell-valves. The oral surface does not here, as in *Alcyonidium*, bulge out downwards, but is withdrawn into the interior of the body, forming an atrium such as is also found in the Entoproctous genus *Pedicellina.*

Intermediate between the *Cyphonautes* and the *Alcyonidium* type we may place the larva of *Flustrella hispida,* known through the researches of Metschnikoff (No. 20), Barrois (No. 6), and Prouho (No. 28). In this larva, the rudiment of the alimentary canal appears in the embryonic stages, but degenerates later. In other respects, the development of the *Flustrella* larva agrees closely with that of the *Alcyonidium* larva. An embryo develops in which the central part of the aboral surface becomes marked off from the corona by a circular mantle-cavity. Only secondarily does the corona bend round downwards in the form of two lateral lobes, apparently enclosing the oral surface in an atrium, while the circular mantle-cavity disappears. Paired shell-valves then appear and cover the whole aboral surface with the exception of the very small retractile disc. A similar though less complete transformation in the same direction is found in the larva of *Eucratea chelata* (Barrois).

The researches of Prouho have led to interesting revelations as to the internal structure of the *Flustrella* larva. With regard to the presence of a nervous system, Prouho's researches agree essentially with those of Harmer. In the *Flustrella* larva, the retractile disc is connected, as in *Cyphonautes,* with the pyriform organ by a strand of muscle-fibres. Along this strand runs a bundle of nerve-fibres; these start from the retractile disc and can be followed as far as to the cells of the ectodermal furrow and of the corona. In their course, single fibres of this bundle become connected with ganglion-cells. Prouho thinks that he can trace back the elements regarded by Harmer as ganglion-cells to simple mesoderm-cells, and considers certain elements which are provided with large nuclei as the true ganglion-cells of this region.

When the complex organ connected with the ectodermal furrow is more carefully examined, an inner cell-complex (glandular organ, pyriform organ in a restricted sense) is found to be distinct from the ciliated cells of the ectodermal furrow. In this organ, which is evidently of glandular structure, three parts can be made out. The lateral parts show radially arranged cells opening into the ectodermal furrow, while the cells of the middle part run longitudinally and open into a small pit lying in front of the ciliated tuft of the ectodermal furrow (PROUHO).

Further, there is in this larva a highly developed musculature, consisting of lateral parietal and longitudinal muscles, and of a shell-adductor, already noticed by METSCHNIKOFF. A mesodermal cell-layer lying below the ectoderm plays an important part in metamorphosis, the mesoderm-layer of the developing polypide and of the primary zooecium being formed in it.

The transformation of the larva of this type into the sedentary form (primary zooid of the colony) takes place in the same way as in other Ectoprocta; the reader is therefore referred to the description of the metamorphosis of *Bugula* and *Lepralia*, given on p. 27. It need here only be mentioned that *Cyphonautes*, whose metamorphosis has been made known through the researches of SCHNEIDER and OSTROUMOFF, attaches itself by means of the paired, disc-like organ mentioned above on the oral side of the body, and on the degeneration (histolysis) of the internal organs, changes into a spherical mass covered by the shell-valves, this being the rudiment of the primary zooecium. While the ectocyst of the zooecium is secreted on the surface of this mass, the polypide of the first chamber is derived from the retractile disc through ontogenetic processes to be described later (SCHNEIDER and OSTROUMOFF).

With regard to the last point, the recent researches of PROUHO in connection with *Flustrella* have led to the remarkable discovery that the retractile disc, like all other larval organs, becomes invaginated and undergoes degeneration. During this process, a thickened disc forms out of the surrounding ectoderm, mesodermal elements joining it on its inner side. This bilaminar plate, which lies in the place of the degenerated retractile disc, now in its turn becomes invaginated, and thus gives rise to the sac-like rudiment of the polypide. Even though most other authors regard the polypide as derived directly from the retractile disc, it must be considered probable that the ontogenetic process here described in connection with *Flustrella* is the rule in the development of the polypides in all Ectoproctous larvae.

Pherusa tubulosa, which, according to PROUHO (No. 28a), is also distinguished by the possession of a bivalve shell, is allied to the above type, and the larva of *Hypophorella*, according to the same author (No. 28b), also approaches this type.

2. Type of the intestineless Chilostomatous Larva with slightly-developed corona.

The larvae of this type, in outward appearance, almost exactly resemble the *Alcyonidium* larva. They chiefly occur in the *Escharina* tribe, an example being found in *Lepralia Pallasiana*, which has been described in detail by Barrois (No. 9). Here also we find the oral and aboral surfaces separated by a corona of somewhat large ciliated cells. The aboral surface shows the well developed retractile disc surrounded by a circular mantle-cavity; on the oral surface, the ectodermal furrow with its ciliated tuft and the sucker-invagination are situated. Strong pigmentation is often found in the larvae of this and the following types, paired patches of pigment, like eye-spots, being found in individual cases. The most essential distinction between the larvae of this type and the *Alcyonidium* larva is the entire absence of the alimentary canal. We assume that the inside of this larva contains only the so-called central tissue. In the very imperfect state of our knowledge of the anatomy of these larvae, it must still be regarded possible that many of them may possess a well-developed alimentary canal. We are therefore unable at present to define exactly the distinctions between this type and the one last described.

The metamorphosis of the larvae of this type will be described together with that of the following type.

3. Type of the intestineless Chilostomatous Larva with highly-developed corona.

a. Structure of the Larva.

We shall take as type of this group the larva of one of the *Cellularina*, the *Bugula* larva (Fig. 9), which has become well known to us through the researches of Nitsche (No. 22), Claparède (No. 10), Salensky (No. 37), Barrois (No. 9), and Vigelius (Nos. 39 and 40). The intestinal canal here also is altogether wanting. The primary entoderm changes direct into the so-called central tissue (Fig. 9 *B*, *f*). The distribution of the ectodermal organs is the same as in the larvae of the *Alcyonidium* and the *Escharina* types; the whole form of the larva, however, is somewhat different, chiefly on account of the great growth of the coronal cells (*c*) in the direction of the principal axis. These cells lengthen greatly, the whole of their surface becoming covered with cilia, while in the larvae of the preceding types these cells usually bear only one row of cilia. This extension of the corona encroaches greatly on the aboral and oral surfaces. The retractile disc (*r*) is consequently smaller, and the ectodermal furrow (*e*) is so grown over by the increasing coronal cells that it at last appears enclosed by the coronal region. In this way a more or less spherical or rounded larva is produced, and in this the plane of symmetry is denoted by the position of the ectodermal furrow; the larva is thus peach-shaped.

For details of the structure of the *Bugula* larva we are indebted chiefly to VIGELIUS (No. 39). Taking first the organs of the oral surface, the sucker originates as an ectodermal invagination. In the later stages the aperture of the invagination appears to close, at least it was no longer visible. The upper part of the wall of the sucker becomes invaginated into the cavity of the organ itself, thus greatly compressing it. The whole rudiment in this way becomes cup-shaped. In the anterior part of the oral surface a second ectodermal invagination appears; this is found later between the cells of the corona, and is known as the ectodermal furrow (*e*). The ectodermal cells of this region are elongated, columnar, glandular cells. In direct connection with this modified glandular epithelium, there is a cell-mass which extends towards the interior of the larva and ends posteriorly in three processes. This is the pyriform organ (*o*). VIGELIUS is inclined to regard the ectodermal furrow and the pyriform organ as a common glandular complex derived from the ectoderm.

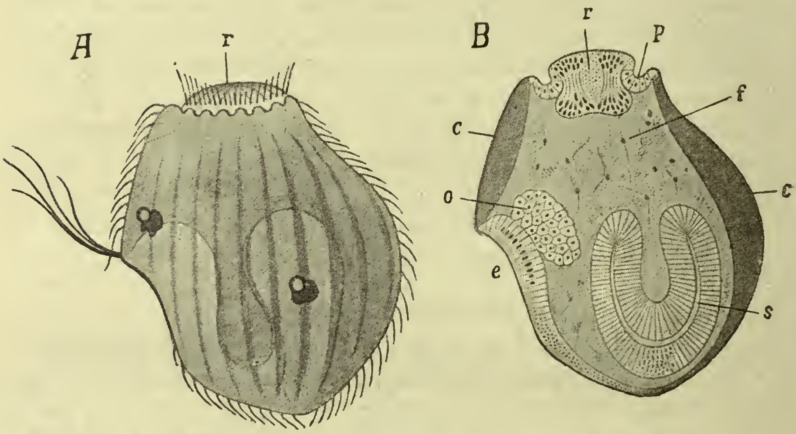

FIG. 9.—*A*, larva of *Bugula plumosa* (after J. BARROIS). *B*, median section through a *Bugula* larva (diagram constructed from figures by VIGELIUS). *c*, cells of the corona (a single cell of this kind on each side); *e*, ectodermal furrow; *f*, central tissue; *o*, pyriform organ; *p*, mantle-cavity; *r*, retractile disc; *s*, sucker.

The retractile disc (*r*) arises on the aboral surface as a simple ectodermal thickening, the cells of which lengthen greatly and become arranged in several layers. At the centre these elements seem to be wanting, while at the periphery of the organ they show a radial arrangement. This disc is protrusible beyond the surface of the larva. Its covering of stiff setae probably serves some sensory purpose, perhaps transmitting tactile impressions.

b. Metamorphosis.

The first indication that the larva is ready to attach itself is an alteration in its mode of progression. The larva now constantly moves in circles, with its retractile disc protruded to its utmost limit. By a sudden contraction of the body the sucker is shot out, and the fixation of the larva is accomplished by means of a sticky secretion from its lower surface. The evaginated sucker (Figs. 10 and 11, *s*) in *Bugula* shows at first on its under surface a circular furrow, which separates an outer broader part from a narrower central portion that projects downwards. At a later stage, the lower side of the sucker flattens into a broad cell-plate (*plaque adhésive*, BARROIS), from which is derived the basal surface of the endocyst of the primary zooecium.

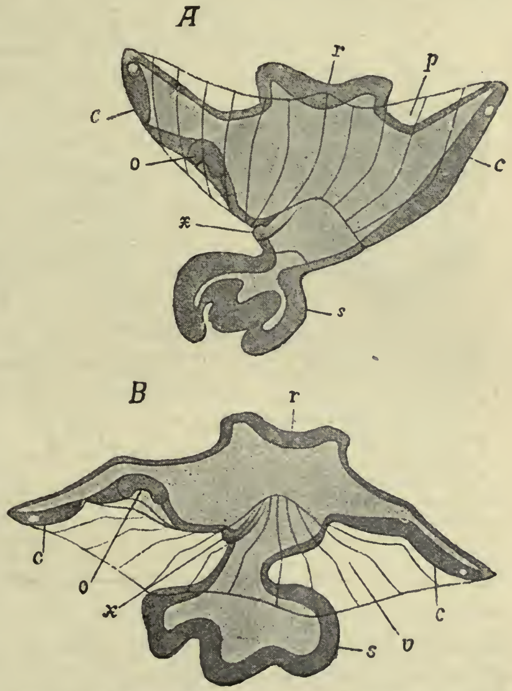

FIG. 10.—Metamorphosis of the larva of *Lepralia unicornis* (after J. BARROIS). *A*, first stage of metamorphosis. The sucker (*s*) is evaginated, the corona (*c*) is beginning to bend round. *B*, next (so-called umbrella) stage. The corona (*c*) is completely bent round. *c*, coronal cells; *o*, pyriform organ; *p*, mantle-cavity; *r*, retractile disc; *s*, protruded sucker; *v*, vestibulum; *x*, paired organ of doubtful significance (according to BARROIS, the mesodermal rudiment of the polypide).

The whole of the rest of the body-wall of the primary zooecium, *i.e.*, its upper part and its lateral walls, are yielded by the aboral portion which, in the larva, is comparatively small. This takes place chiefly by an extension of those parts of the ectoderm which previously formed the lining of the circular furrow (mantle-cavity, *p*), and which in the larva are distinguished by the great depth of their cells (Fig. 10, *A*). The mantle-cavity (*p*) is in this way completely obliterated, the circular fold that bordered it externally, and was called the mantle, bending over downwards (Fig. 10, *B*); its inner thus becomes its outer surface, and gives rise to the body-wall of the primary zooecium. The corona at the same time bends round or unfolds (Fig. 10, *B*). The lower ends of the coronal cells (*c*) retain their position, while the upper ends first shift outward (Fig. 10, *A*) and then downward (Fig. 10, *B*), so that each coronal cell at the end of this process has rotated through an angle at first of 90° and finally of 180° (Fig. 11 *c*). We thus have a stage to which Barrois has given the name of the *umbrella-shaped stage* (Fig. 10, *B*). The upper surface is formed by the future body-wall, the lower by the downwardly rotated coronal cells. The edges of the umbrella become applied to the adhesive plate of the sucker (*s*) and fuse with it, the body-wall thus completing itself (Fig. 11). The displaced coronal cells at the same time fuse with the upper surface of the sucker, and in this way a circular cavity arises (*vestibulum*, Barrois, Fig. 11 *v*), the walls of which soon become completely detached from the body-wall and undergo degeneration. This is the fate not only of the corona, but of the ectodermal furrow, the pyriform organ, and (where such is present) the larval intestine. There is then found inside the sac-like larva a cell-mass derived from the degeneration of the most important larval organs; this unites with the mass that resulted from the degeneration of the central tissue, and forms the so-called *brown body.*

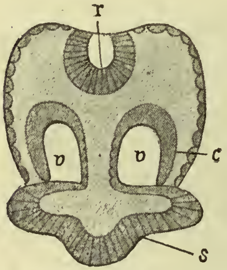

Fig. 11.—Longitudinal section of attached larva of *Bugula flabellata* (after J. Barrois). *c*, coronal cells; *r*, rudiment of the polypide (which has arisen by the invagination of the retractile organ); *s*, lower thickened surface of the evaginated sucker (adhesive plate); *v*, vestibulum.

The rudiment of the body-wall of the primary zooecium is formed in the way just described. Its surface soon becomes covered with a chitinous secretion (often impregnated with lime salts); this is the *ectocyst.*

During these ontogenetic processes, other changes can be seen to occur at the aboral pole which result in the development of the polypide of the primary individual. The retractile disc that lies here has changed into a plate formed of deep cells which becomes invaginated (Figs. 11, *r* and 12 *A*, *a*). The sac which thus arises soon becomes completely cut off from the body-wall (Fig. 12 *B*), and represents the rudiment of the ectodermal and also of the entodermal parts of the polypide. A second cell-layer (*b*) appears on the outer side of this sac, this being the mesodermal layer of the polypide. Various conjectures have been made as to the origin of this layer. According to Barrois (Nos. 7 and 9), there are, in *Lepralia*, two ectodermal thickenings at the sides of the anterior ectodermal furrow (Fig. 10, *x*); when the corona bends over, these reach the interior of the primary zooecium, and they alone are unaffected by the subsequent degeneration of the larval organs, and remain to form the mesodermal layer of the polypide. These statements have not been confirmed by later researches. Far more probable is the conjecture of Ostroumoff (Nos. 25 and 26) and Vigelius (No. 40), which has recently been confirmed by Prouho (No. 28), that this cell-layer is derived from the mesodermal larval tissue (central tissue). Of the remainder of this tissue, part seems to yield the somatic mesodermal layer (the so-called parenchymatous tissue), while another part joins with the granular masses which have arisen through degeneration in the formation of the so-called brown body. This body becomes connected with the stomach of the newly-formed polypide and is finally absorbed. These processes will be

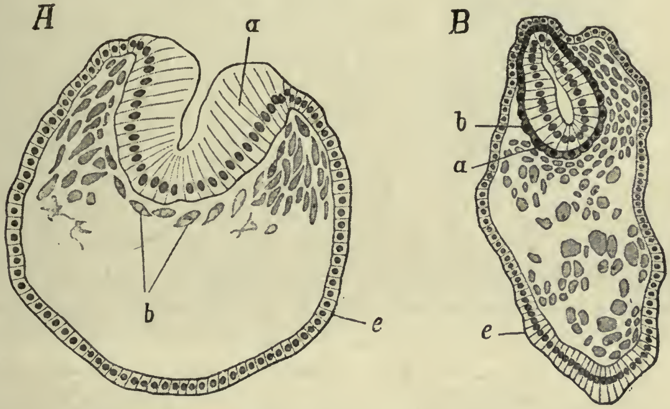

Fig. 12.—Two ontogenetic stages of the primary zooecium of *Bugula calathus* (after Vigelius). *A*, invagination of the retractile disc to form the rudiment of the polypide (*a*); *b*, cells of the external layer of the polypide; *e*, epithelium of ectocyst. *B*, a somewhat older stage. The invagination forming the rudiment of the polypide has closed. In *A* the degenerating mass derived from the larval organs is omitted.

more fully discussed in a special section on the further development of the rudiment of the polypide (pp. 43, 44, and 55).

In considering the metamorphosis of the *Bugula* larva, which is identical with that of the types hitherto described, we are at once struck by the fact that the larval intestine degenerates in all cases, and that the intestine of the primary individual is formed anew from an independent rudiment on the *aboral surface.* This fact, however, is explained by the capacity possessed by the Bryozoa in certain cases of degenerating and again regenerating the alimentary canal or even the whole polypide (see p. 55). We are therefore not obliged to regard the polypide of the primary individual as a second generation of the Bryozoan colony, derived by budding from the larva. The production of the primary individual from the larva rather comes under the category of metamorphosis, although this latter becomes very complicated in consequence of the far-reaching degeneration of the larval organs, and on account of the inconspicuous form assumed by the rudiments of the future parts of the permanent body in the larva, these rudiments being somewhat comparable to the imaginal discs of the Insecta.

With regard to these rudiments, that of the polypide is represented in the larva by the retractile disc. The rudiment of the endocyst of the primary zooecium lies partly in the mantle-cavity and partly in the sucker-invagination. The body-wall of the primary individual is thus present in the larva in an invaginated condition, so as to afford the corona, as the locomotory organ of the larva, more room for development.

While most of the parts of the primary zooecium are thus waiting in the larva in an invaginated and apparently functionless condition, it is a striking fact that the retractile disc, which has hitherto been regarded as the rudiment of the polypide, seems to be of functional importance to the larva (sensory organ ?). On this account, the observation of Prouho recorded above (p. 24) seems significant, according to which the retractile disc does not pass directly over into the rudiment of the polypide, but after its invagination undergoes a degeneration similar to that of the other larval organs, while, at the place formerly occupied by it, a new two-layered rudiment develops, viz., that of the polypide.

The bending over of the corona and the formation of the vestibule, in the wall of which are included the coronal cells, the pyriform organ, and a part of the sucker, there to undergo degeneration, will appear less remarkable if we consider how often larval parts which have become useless, instead of being thrown out, sink into the interior of the individual undergoing metamorphosis, there, after degenerating, to be utilised as food-material. Under this aspect, these processes appear comparable to the retrogression of the embryonic membranes and the formation of the so-called dorsal organ in Insect embryos.

4. Type of the Vesicularian Larva.

In the larvae of this type an excessive lengthening of the coronal cells is found (Fig. 13). The whole larva in this way becomes greatly elongated; the aboral and oral areas are exceedingly circumscribed, and the ectodermal furrow (*ec*), as in the previous types, is covered by the cells of the corona. Another characteristic of these larvae which was observed by Barrois in *Serialaria lendigera* (No. 9) and by Ostroumoff in *Vesicularia* (No. 26) is the small size of the retractile disc (*rs*) and the unusual depth of the mantle-cavity (*m*); posteriorly, *i.e.*, opposite to the ectodermal furrow, it is so deep as to extend beyond the middle of the body. Observers are not quite unanimous as to the sucker. According to Barrois, only a functionless vestige of this organ (*s*) is retained; Ostroumoff, on the other hand, found a well-developed though not very large sucker.

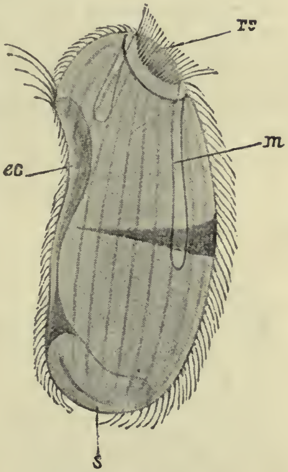

Fig. 13.—Larva of *Serialaria lendigera* (after Barrois). *rs*, retractile disc; *s*, vestige of sucker; *ec*, anterior ectodermal furrow; *m*, mantle-cavity.

In the same way, authorities differ as to the metamorphosis of the sucker, though in other respects metamorphosis here takes a similar course to that described for *Bugula*. Ostroumoff maintains that in this type also metamorphosis commences with the evagination of the sucker, while Barrois holds that fixation takes place by means of two lobes that grow out from the lower end of the ectodermal furrow and which belong to the corona. For details of the remarkable manner in which the corona is reversed, its long cells being rotated and bent round, we refer the reader to Barrois (Nos. 8 and 9). The polypide is here said to arise not by invagination, but through the separation from the retractile disc of a cell-plate which becomes invaginated later (Ostroumoff).

5. Type of the Cyclostomatous Larva.

The metamorphosis of the marine Cyclostomatous Bryozoa has been investigated chiefly by Metschnikoff (No. 21), Barrois (Nos. 6 and 9), and Ostroumoff (No 25). The larvae of this type (Fig. 14, *A*) are distinguished by the presence of a large sucker-invagination (*s*), and by the vestigial condition of the retractile disc (*r*), which is found as an inconspicuous cell-mass at the base of the large mantle-cavity (*p*). A further peculiarity is exhibited by the corona, which here does not consist of long cells extending from the oral to the aboral area, but is composed of numerous small elements. The ectodermal furrow is hardly perceptible, but Barrois (No. 9) was able to identify it.

This larva, in its metamorphosis, follows the usual course. Here also (Fig. 14, *B*) the first act of metamorphosis is the evagination of the sucker and its transformation into the basal plate (*a*) of the primary zooecium; the bending over of the mantle then takes place, and the fusion of its periphery with the edges of the basal plate, by means of which the annular vestibular space (*v*) is closed in. While subsequently this whole structure degenerates, the polypide forms, not by invagination, but by the separation of a cell-plate (*x*, Ostroumoff). This plate sinks in and becomes covered with mesoderm derived from the central tissue. Ostroumoff's observation of the appearance of a cavity lined with endothelium in the neighbourhood of the developing nutritive tube is worthy of mention. In this cavity, which degenerates later, we have perhaps a homologue of the body-cavity of the fresh-water Bryozoa.

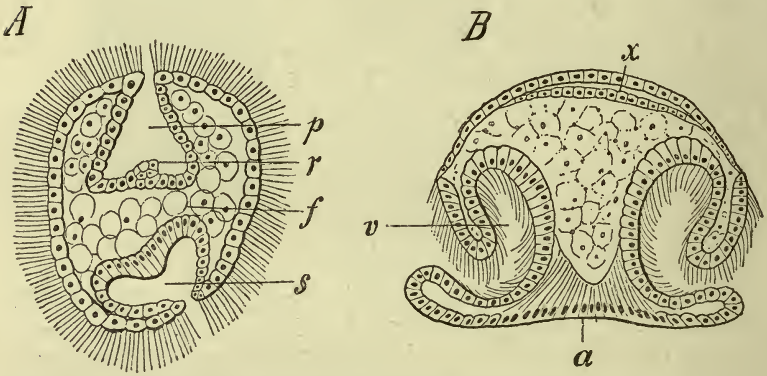

Fig. 14.—Longitudinal sections of two ontogenetic stages of a Cyclostomatous Bryozoon (after Ostroumoff). *A*, longitudinal section through the larva of *Frondipora*. *B*, metamorphosis of *Tubulipora serpens*. *a*, adhesive plate; *f*, central tissue; *p*, mantle-cavity; *r*, vestige of the retractile disc; *s*, sucker; *v*, vestibulum; *x*, cell-plate (rudiment of the polypide derived from the retractile disc).

6. Type of the Phylactolaematous Larva.

The embryonic development and the metamorphosis of the Phylactolaemata has been investigated by Metschnikoff (No. 20), Nitsche (No. 52), Reinhard (Nos. 54–56), Ostroumoff (No. 53), Korotneff

(No. 48), and Jullien (No. 47a), and more recently by Davenport (No. 46a), Kraepelin (No. 50), and Braem (No. 45a).*

The ovary (Fig. 15 *ov*) is an aciniform growth of the inner mesodermal layer of the body-wall, lying on the oral side of the polypide, immediately below the so-called duplicating bands (posterior parieto-vaginal muscles of Allman) and above the last daughter-bud. Single mesodermal cells increase in size, and become changed into young egg-cells, while other mesoderm-cells become grouped round them as the follicular epithelium. One embryo only develops in each individual (Reinhard, Kraepelin). Fertilisation and the commencement of cleavage take place within the egg follicle. Later, however, the young embryo passes into a peculiar brood-sac (*ooecium*, Fig. 15 *x*, 16 *o*), which functions as a uterus, and in which the further embryonic development takes place. The ooecium, when it first appears (Fig. 15 *x*), closely resembles a young polyp-bud, being a pocket-like invagination of the bilaminar body-wall. The outer or mesodermal layer of this bilaminar invagination is destined to envelop the embryo, while the inner ectodermal layer undergoes degeneration in the course of further development. It was formerly somewhat doubtful whether the ooecium was altogether distinct from the primary egg-follicle. According to Reinhard, it was derived directly from the epithelium of the ovary. Whereas, according to Metschnikoff, the egg passed out of the original follicle into the body-cavity, where the ooecium grew round it secondarily, according to Kraepelin and Braem, the rudiment of the ooecium presses closely on the egg while still in the ovary, and receives it from the egg-follicle.

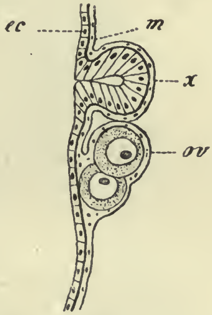

Fig. 15.—Section through a portion of the zooecial wall of *Plumatella fungosa* (after Braem). *ec*, ectoderm; *m*, mesoderm; *ov*, ovary; *x*, rudiment of the ooecium.

According to the statements of most authors, cleavage is quite regular. Kraepelin, however, thought that he found certain differences in the blastomeres in the first stages. A cleavage-cavity early appears within the embryo, and a coeloblastula (Fig. 16, *A*, *e*) develops, which, by a solid ingrowth of cells at one pole (Fig. 16, *B*), passes into the gastrula stage. The point of ingrowth, according to

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* [The form in which the development of the larva and of the polypide has been best worked out is *Plumatella* (*Alcyonella*) *fungosa* (= *P. polymorpha*, Kraepelin).—Ed.]

the statements of Davenport, Braem, and Kraepelin, invariably corresponds to that pole of the embryo which is turned towards the wall of the zooecium. At the same point, at a later time, the first rudiment of the polypide is said to develop, so that we have here an important contrast to the Gymnolaemata, in which, so far as we know, the primary rudiment of the polypide always develops at the aboral pole of the larva.

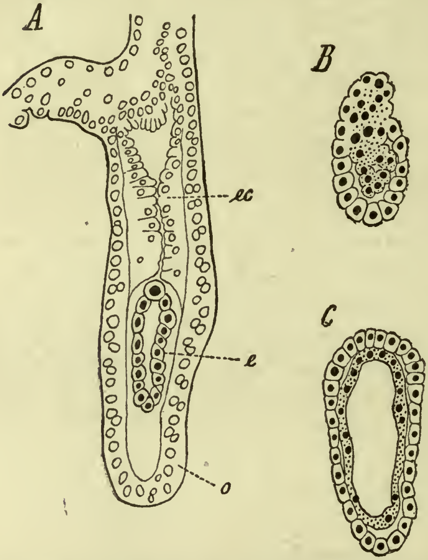

Fig. 16.—Three stages in the embryonic development of *Plumatella* (after Kraepelin). *A*, blastula stage in the ooecium. *B*, stage of ingrowth of the mesoderm. *C*, bilaminar stage. *e*, embryo in the blastula stage; ec, invaginated ectodermal part of the ooecium (*cf.* Fig. 15); *o*, ooecium.

While the ingrowing cell-mass more and more fills the blastocoele, a new cavity develops within the former; analogy with other animals might incline us to consider this cavity as the primary enteric cavity, but we are led by the study of the further course of development to regard it as the body-cavity. The ingrowing cell-mass represents the mesoderm, and the cavity that develops within it the coelom. We thus find here a gastrulation in which the entoderm proper is apparently wanting. As the coelomic cavity increases in size, the mesodermal epithelial layer becomes closely pressed against the ectoderm, and in this way a bilaminar, vesicular embryo develops (Fig. 16, *C*).

We shall only be able to interpret this stage correctly if we compare it with the stage that follows the gastrula in most marine Ectoprocta (Fig. 6, *G*, *p*). The primary entoderm there yields the so-called central tissue which represents the enteric rudiment of the larva, out of which, however, important mesodermal organs of the primary zooecium are also derived. In the embryo of the Phylactolaemata this tissue is represented by the inner epithelial layer. We must here assume that the larval intestine has undergone excessive reduction, so that not a vestige of it can be seen, and, taking into consideration the further development, we must regard this inner layer as mesoderm, and the central cavity enclosed by it as the coelom.

We shall have to call the external cell-layer of the embryo the ectoderm, but it must not be forgotten that this layer contains indifferent embryonic material from which will be produced the future rudiment of the polypide, including the entodermal organs.

The next ontogenetic phenomenon is the development of the rudiment of the first polypide. The larvae of some fresh-water Bryozoa (*Plumatella*) at the free-swimming stage contain two well-developed polypides (Fig. 19 *A*), one of which, however, always seems to develop as the older primary polypide, and the other as a precocious daughter bud. The larva of *Plumatella fruticosa*, on the contrary, contains, according to Allman, only one primary polypide, and in *Cristatella* also, the second polypide does not seem to develop so early as in the above-named form. The polypides (Fig. 17, *p*) arise as simple invaginations of the bilaminar wall of the embryo. Their further development will be described more in detail below (p. 37). The first indications of the polypide-invagination are found in the form of a simple thickening of the body-wall. Davenport states that, in *Plumatella*, the rudiment of the second polypide appears from the first independent of the primary polypide.

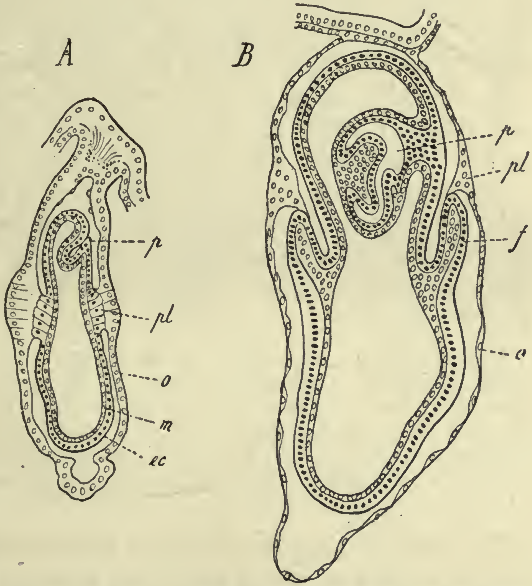

Fig. 17.—Two later ontogenetic stages of the embryo of *Plumatella* (after Kraepelin). *ec*, ectoderm of the embryo; *f*, mantle-fold; *m*, mesodermal layer; *o*, ooecium; *p*, polypide-rudiment; *pl*, placenta.

The conditions in *Cristatella* are, according to Davenport, somewhat different. We shall see below (p. 47) that in this form every new bud is intimately connected at its commencement with an older bud, and that the inner budding zone of the polypide is derived from a layer of embryonic tissue capable of growth, lying below the ectodermal epithelium. The ectodermal layer of the polypide-rudiment in the embryo also is overgrown by the surrounding ectoderm. The ectoderm at this part is therefore bilaminar. The inner layer represents the tissue capable of producing buds, from which the inner layer of the polypide-rudiment is derived. From this tissue is developed the inner layer of the first polypide-rudiment, and soon after, by its side, the invagination of the second polypide, which thus, in *Cristatella*, is directly connected with the primary polypide.

While the polypide-rudiments are developing, we find, in *Plumatella*, a zone of ectodermal cells encircling the middle of the embryo and fusing with the wall of the ooecium (Fig. 17, *pl*). This is the girdle-shaped placenta already recognised by KOROTNEFF, by means of which the embryo is suspended in the uterus-sac and nourished. In *Cristatella* this is wanting; nourishment here takes place through the ectodermal cell-plug which closes the neck of the ooecium, and which is in close juxtaposition to the anterior pole of the embryo.

In the later stages a circular fold of the body-wall develops (Fig. 17 *B*, *f*), which surrounds the anterior half of the body, and may be regarded as the equivalent of the mantle-fold of other Bryozoan larvae. An ectodermal thickening, including the posterior pole (Fig. 18 *A*, *x*), was regarded by OSTROUMOFF as a vestigial sucker, while the anterior swollen part of the body in which the polypide-rudiments appear may be considered as the equivalent of the retractile disc.

Although, in this way, the larvae of the Phylactolaemata may, without undue forcing, be compared with those of the marine forms, a difficulty arises from the above-mentioned circumstance that the primitive gastrula-ingrowth here occurs at the anterior pole, which has been regarded as the equivalent of the retractile disc. We are unable at present to overcome this obstacle in the way of comparing the larvae of the Phylactolaemata with those of the Gymnolaemata.

The embryo, after developing in the manner described above, becomes covered externally with cilia, and, escaping from the parent, swims about freely. According to KRAEPELIN, it emerges through the aperture of a degenerated polypide (usually that of the parent). BRAEM, on the contrary, holds that the cavity of the ooecium opens directly upon the exterior in order to allow of the passage of the embryo. At this stage the larva is oval (Figs. 18 *A* and 19 *A*), and the whole surface of its body is ciliated. At the anterior pole there is an aperture leading into the large mantle-cavity, from the base of which the two polypide-rudiments project.

The attachment of the larva takes place at first by means of modified glandular ectodermal cells at the posterior pole (Fig. 18 *A*, *x*)—sucker-rudiment of Ostroumoff. The projection which carries the polypides is evaginated from the mantle-cavity, the mantle-fold (*f*) at the same time bending back (Figs. 18 *B* and 19 *B*). The posterior pole of the body now becomes detached from the substratum, the edges of the mantle-fold (*f*) approach each other till they fuse (Fig. 18 *C*), and in this way a closed sac forms in which is included the greater part of the external ciliated surface of the larva, which then undergoes degeneration.

The essential distinction between the metamorphosis here described and that of the marine forms consists in the absence of the sucker. In consequence of this a basal adhesive plate does not develop. The whole wall of the young colony is derived exclusively from that part of the body-wall which, in the larva, lined the mantle-cavity. The condition of the mantle-fold consequently here resembles that in the marine forms.

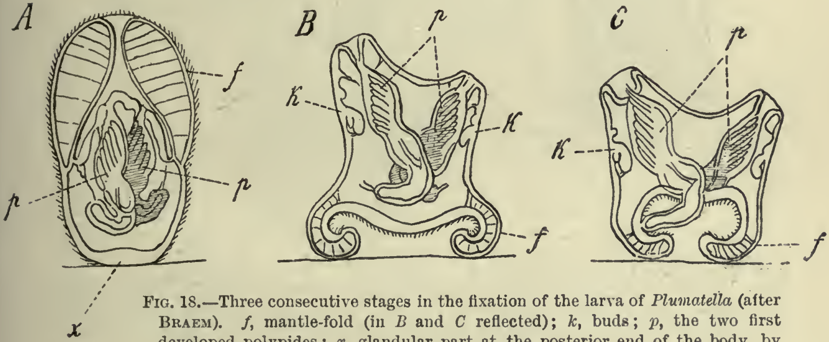

Fig. 18.—Three consecutive stages in the fixation of the larva of *Plumatella* (after Braem). *f*, mantle-fold (in *B* and *C* reflected); *k*, buds; *p*, the two first developed polypides; *x*, glandular part at the posterior end of the body, by means of which the first attachment takes place.

IV. Development of the Polypide.

We must now describe more in detail the development of the polypide, *i.e.*, of the retractile cephalic section of the animal plus the intestinal canal appended to it. For our knowledge of the metamorphosis of the larva and the development of the polypide in the primary zooecium, we are indebted chiefly to the observations of Repiachoff (No. 29) on *Tendra*, of Barrois (No. 9) on *Lepralia*, and of Prouho (No. 28) on *Flustrella*. The development of this primary polypide takes place in exactly the same manner as that of the polypides in the buds, which develop later in the colony, or in those zooecia in which the alimentary canal and polypide, as already mentioned (p. 15), have undergone degeneration, the polypide having therefore to be regenerated. In the forms mentioned above the regeneration of the polypide has repeatedly been investigated; notably by NITSCHE (Nos. 23 and 52), REPIACHOFF (No. 30), JOLIET (No. 17), HADDON (No. 12), OSTROUMOFF (No. 26), and more recently by SEELIGER (No. 37a), DAVENPORT (Nos. 11 and 46a), BRAEM (No. 45a), OKA (No. 52a), and KRAEPELIN (No. 50).* The way in which the polypide develops in the statoblasts has been specially described by BRAEM (No. 45a) and OKA (No. 52a).

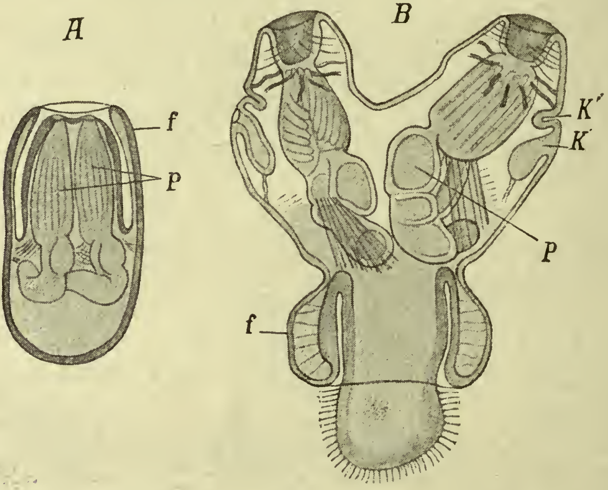

FIG. 19.—Two ontogenetic stages of *Plumatella fungosa* (after NITSCHE). *A*, an advanced embryo. *B*, larva with two polypides in the act of attaching itself; the mantle-fold (*f*) is already reflected, the apertures of evagination have moved far apart and the polypides are retracted. *p*, the two first formed polypides; *k*, *k′*, buds of future polypides; *f*, mantle-fold.

We have already seen the rudiment of the polypide arising in the primary zooecium of *Bugula* (Fig. 12, *B*, p. 29) in the form of a double-walled sac, the inner cell-layer of which is said to be derived through invagination from the retractile disc (see, however, the statements of PROUHO, p. 24), while the outer layer has probably arisen from the cells of the central tissue. In the same way the first rudiment of the polypides in the buds (*k*, *k′*, Fig. 19), in the regenerated individuals, and in the statoblasts are bilaminar sacs, which arise through invagination at one point of the bilaminar body-wall (endocyst). In the marine Bryozoa and in *Plumatella*, such an invagination has, from the first, a lumen which passes direct

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* *Cf.* HARMER, *Quart. Journ. Micro. Sci.*, Vol. xxxiii., p. 123.

over into the lumen of the polypide-sac. In other cases, *e.g.*, in *Paludicella* (Davenport), we find at first a solid ingrowth within which a lumen forms secondarily. The bilaminar sac always remains connected by a longer or shorter strand with that part of the body-wall at which the invagination occurred. This strand (only a portion of which is represented in Fig. 20, *A* and *B*), is derived from the neck of the primitive polypide invagination, becomes hollow again at a later stage, and then represents the aperture of the tentacular sheath (Fig. 20, *C*, *ts*).

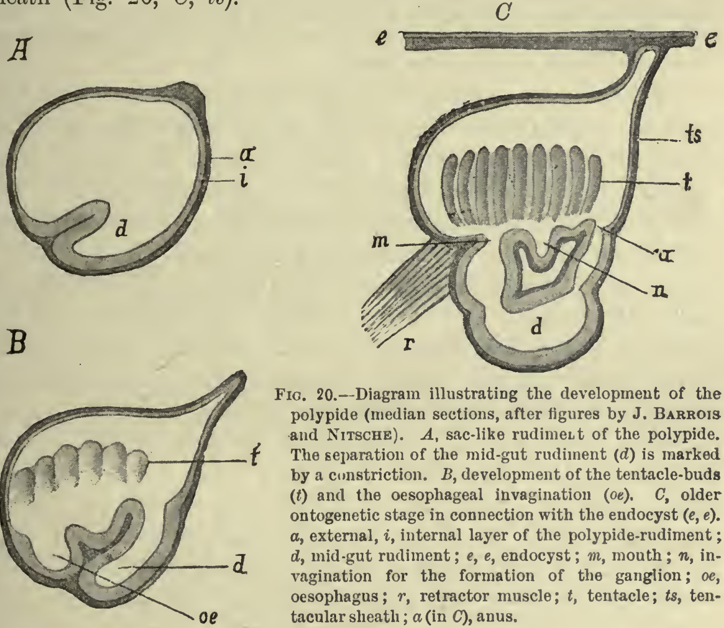

Fig. 20.—Diagram illustrating the development of the polypide (median sections, after figures by J. Barrois and Nitsche). *A*, sac-like rudiment of the polypide. The separation of the mid-gut rudiment (*d*) is marked by a constriction. *B*, development of the tentacle-buds (*t*) and the oesophageal invagination (*oe*). *C*, older ontogenetic stage in connection with the endocyst (*e*, *e*). *a*, external, *i*, internal layer of the polypide-rudiment; *d*, mid-gut rudiment; *e*, *e*, endocyst; *m*, mouth; *n*, invagination for the formation of the ganglion; *oe*, oesophagus; *r*, retractor muscle; *t*, tentacle; *ts*, tentacular sheath; *a* (in *C*), anus.

The outer layer of the polypide-sac (Fig. 20, *A*, *a*) is continuous with the mesodermal layer of the body-wall (endocyst), and yields the mesodermal part of the polypide (the lining of the body-cavity, and the larger groups of muscles, &c.). The inner layer (Fig. 20, *A*, *i*) is derived from the primitive ectoderm, and yields the ectodermal epithelium of the whole polypide and of the tentacle sheath, the nervous system, and the lining epithelium of the whole of the digestive tract. We should be justified in calling this layer the ectoderm of the polypide, did not the mid-gut epithelium also originate from it.*

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* [Braem, in a recent work on the development of *Plumatella* (*Bibl. Zool.*, H. 23, 1897), states that entodermal tissue can be made out in the embryo.—Ed.]

According to the more recent researches of SEELIGER, DAVENPORT, KRAEPELIN, BRAEM, and OKA on the development of the buds, there can be no doubt that the inner layer of the bilaminar sac is to be derived by invagination from the ectodermal layer of the parent, the outer layer, on the contrary, owing its origin to the mesoderm of the latter. Some of the earlier observers had derived the whole bud from the ectoderm of the parent (NITSCHE, EHLERS, and CLAPARÈDE), while HADDON held that all the three germ-layers of the parent take part in the formation of the bud. According to JOLIET (No. 17), on the contrary, the first rudiment of the polypide in *Eucratea* is derived exclusively from the funicular tissue (endosarc), *i.e.*, from a layer which we regard as belonging to the mesoderm. The first rudiment of the polypide is said here to consist of a mass of similar cells, which become arranged only secondarily into two layers, the inner cells acquiring an epithelial character and surrounding a central cavity, while the superficial cells yield the outer layer.

The first change which can be remarked in the bilaminar polypide-sac consists in the formation of a diverticulum (Fig. 20 *A*, *d*; 23 *B*, *d*), which represents the first rudiment of the enteric canal, especially that of the stomach and hind-gut. The origin of this diverticulum can be traced to a constriction or infolding of the wall of the primitive sac taking place from each side. In consequence of this, the lumen of the enteric rudiment at first remains connected along its whole length through a narrow slit with the lumen of the rest of the sac. As the intestine becomes more differentiated this slit becomes narrower, but never completely closed, for it persists as the anal aperture (Fig. 20 *C*, *a*). In the following stages a second diverticulum develops at the opposite (oral) side of the polypide-sac (Fig. 20 *B*, *oe*); this diverticulum, which represents the rudiment of the oesophagus, grows out towards the blind end of the first diverticulum and fuses with it (Fig. 20 *C*). After communication has been established at the point where the two diverticula come into contact, the intestinal canal is essentially complete, the so-called stomach-caecum developing at a later period.

The description here given of the development of the enteric canal is founded upon the statements of BARROIS (No. 9), PROUHO (No. 28), BRAEM (No. 45a), DAVENPORT (Nos. 11 and 46a), and KRAEPELIN (No. 50). A modification of this process was described by NITSCHE (No. 23) in *Plumatella* and *Flustra membranacea*, and more recently by OSTROUMOFF (No. 26), the formation of the intestine taking place through two ingrowths which extend into the interior of the sac-like polypide-rudiment, from right and left, meeting and fusing in the median plane. The apertures left in front of and behind this fusion become the oral and anal apertures. "This process resembles what takes place if we hold an indiarubber ball with a double wall in our two hands and press it on each side with a finger until the finger-tips are separated only by the four-fold wall of the ball." The oesophagus in this case would not have an independent origin. SEELIGER observed a similar origin for the alimentary canal in the buds of *Bugula*. It should here be pointed out that the two different types of development of the intestine are not fundamentally opposed to one another; in both cases a constriction pressing in from each side brings about the separation of the enteric canal from the atrium. Whether the rudiment of the oesophagus is completed at the same time is of comparatively little importance, and we may well imagine, even in nearly related forms, that in some cases the first and, in others, the second type of bud-development may be found.

In *Pectinella*, on the contrary (OKA, No. 52a), in the statoblasts as well as in the buds, the diverticulum that forms first is said to represent the common rudiment of the oesophagus and the stomach, so that here the oral aperture seems to form first. The intestine is said here to grow out as a caecum from the stomach and to open towards the atrium (the upper cavity), the anal aperture seeming to form in this way.

The ganglion can be traced back to an invagination which forms at the base of the upper cavity or atrium between the oral and the anal apertures (Fig. 20 *C*, *n*). The lumen of this invagination gives rise to the future brain-cavity. After the rudiment of the ganglion has been completely cut off from the surface layer, an ear-shaped diverticulum forms on each side of it (BRAEM); these diverticula represent the rudiments of the lophophoral nerves. Each grows out as two nerves, one of which runs posteriorly into the corresponding arm of the lophophore, while the other runs forward and spreads out upon the oesophagus.

The portion of the primary sac which remains after the intestine has been separated from it is known as the atrium (Fig. 23 *B*, *at*) or the cavity of the tentacular sheath. The greater part of its wall becomes modified into the tentacular sheath. The rudiments of the lophophore and of the tentacles (Fig. 23 *B*, *at*) develop early in the base of this cavity. The first rudiment of the *lophophore* takes the form of a swelling projecting into the atrium, and forming a semicircular border to the oral aperture. In the Gymnolaemata, this swelling closes in front of the anal aperture to form a ring, encircling the mouth, which carries the tentacles. Corresponding to the inwardly projecting swelling of the lophophore, there is, on the outer side of the polypide-sac, a groove which soon changes into a closed canal. This is the so-called circular canal, which must be regarded as part of the body-cavity. The tentacles arise as outgrowths of the lophophore resembling the fingers of a glove. In the Gymnolaemata they are situated in a row on either side of the body (DAVENPORT, PROUHO). Only later do these two rows become connected through the development of the tentacle-buds in front of the mouth, while the last tentacles to arise close the ring on the anal side.

In the Phylactolaemata the posterior ends of the semicircular rudiment of the lophophore grow out as large finger-like structures (Fig. 23, *C*, *l*), projecting into the atrium. These are the rudiments of the two arms of the lophophore. The cavities within these processes (lophophore-cavities) are to be regarded as a part of the body-cavity. They communicate with one another through the semicircular canal that encircles the oesophagus. On the anal side, according to Braem, they are connected by the so-called *forked canal*, so that here also the system of lophophore-cavities forms a ring surrounding the oesophagus. Another significance has been attributed to this forked canal by Cori (p. 56). In the Phylactolaemata the outer tentacles make their appearance before those on the inner side of the lophophore. The former appear first in the neighbourhood of the mouth and gradually fresh tentacles are added, each new one being nearer the free end of the lophophore, those at the apex forming last. The tentacles of the inner row develop in the reverse order, *i.e.*, those nearest the apex arise first, whilst those near the epistome and above the forked canal are the last to appear.

The epistome arises as a projecting fold on the anal side of the oral aperture, and into it is continued an outgrowth of the body-cavity—the epistomal cavity. It should be mentioned that several authors (Seeliger and others) maintain that a rudimentary epistome is to be found in the Gymnolaemata.

The outer or mesodermal layer of the polypide-rudiment gives rise to the following parts: the peritoneal covering of the enteric canal, the muscle-layer of the intestine, and some of the body-muscles, especially the retractors. The development of the latter has been studied chiefly by Braem and Davenport. Groups of mesoderm-cells become detached at the neck of the bud, and become inserted at one end upon the polypide and at the other on the zooecial wall. These rudiments of the retractor muscles are originally inserted at a point on the zooecial wall quite near the neck of the bud, and only at a later stage, as the wall develops, do the points of insertion shift further from the aperture of the polypide-rudiment.

In the Phylactolaemata, the outer mesoderm-layer of the polypide-bud also takes an important part in the development of the funiculus, which will be dealt with later (p. 50). The nephridia of the Phylactolaemata also, the existence of which has been maintained by Verworn and Cori, and recently confirmed by Blochmann, although denied by Braem and Kraepelin, are probably to be traced back to this layer.*

It is thus evident that the inner layer of the bilaminar polypide-rudiment yields the ectodermal epithelial layer of the polypide, and also the epithelial lining of the enteric canal and those parts which we have been accustomed to attribute to the entoderm. From the outer layer of the polypide-rudiment are derived the mesodermal structures (the splanchnic layer of the mesoderm, the retractor-muscles, the lining of the tentacle-cavities, etc.).

When the rudiments of the organs described above have fully developed, the atrial cavity of the polypide-rudiment becomes connected with the exterior, and through the aperture so formed the anterior portion of the polypide with its crown of tentacles, the introvert, can be protruded and extended.

It must strike the reader as very remarkable that, according to the above statements, the whole lining epithelium of the alimentary canal (both the part usually derived from the ectoderm and the entodermal part) is derived from one and the same rudiment, the inner layer of the sac-like polypide-rudiment. In the primary zooecium of *Bugula* it was possible to trace this layer back to an invagination of the ectoderm of the larva; and in the same way, in the polypide-rudiment of the buds and of the regenerating individuals it may be traced back to the ectoderm of the zooecia. If these observations are correct, we should be forced to assume that the whole enteric canal here originates from the ectoderm.

Several attempts have in consequence been made to find some other origin for the middle (entodermal) part of the alimentary canal. A suggestion of a distinct origin for the enteron is yielded by the constant connection discovered by Repiachoff (No. 30), at later stages, between the enteric rudiment of the polypide and the so-called *brown body*. In the primary zooecium, the brown body contains the mass which has arisen by the degeneration of the larval organs and of the central tissue, while the brown bodies found in the degenerated zooecia of the adult colony enclosed in cellular envelopes of their own must be regarded as remains of the degenerated parent-polypide. The rudiment of the intestine, which in the bud of the newly-forming polypide is originally connected with the brown body through strands of funicular tissue, at a later stage comes into contact with it, and is said finally to grow round it and to receive it into the interior of the enteric cavity. The last remains of the brown body are then said to be expelled through the anal aperture of the newly-formed polypide. During this circumcrescence, according to Ostroumoff (No. 26), the epithelial layer of the stomach-caecum is yielded by the cells

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* [Oka, *Jour. Sci. Coll. Japan*, Vol. viii., p. 339, states that the Ectoproctous Polyzoa have no nephridia. He does not regard the ciliated portions of the coelomic epithelium, which apparently open by a pore under the median tentacle, as nephridia. He states that the excretory function is carried on by free mesodermal cells, which leave the body through the above-mentioned pore, their passage to the exterior being facilitated by the presence of cilia on the cells of the peritoneal epithelium adjacent to the pore. The tube-like character of these modified peritoneal areas is due to the presence in the Phylactolaemata of an epistome-lophophoral partition.—Ed.]

of the brown body. A certain difficulty attends this assumption, in consequence of the development of the intestine in the young buds, in which there is no brown body. Ostroumoff, however, tries to escape these difficulties by pointing out the relations established by the funicular tissue between the parent-zooecium and the bud, as well as by assuming that in this way entodermal cell-masses pass from the parent into the bud. In this respect the views of Ostroumoff have something in common with those of Haddon, who held that all the three germ-layers of the parent-zooecium took part in the formation of the bud. According to Joliet (No. 17), the alimentary canal of the developing polypide does not originate from the inner layer of the bilaminar sac-like polypide-rudiment, but from a distinct cell-mass derived from the outer layer of that rudiment. The inner layer of the polypide-rudiment would then yield only the ectodermal parts of the polypide, while the outer layer would contain the mesodermal and entodermal parts. In any case, according to Joliet, the enteric canal (mid-gut) has an origin distinct from that of the ectodermal rudiment. The most recent researches, however, confirm the view that the whole intestine of the polypide originates from the inner layer of the double-walled sac, *i.e.*, from the ectoderm, but Prouho differs to some extent from the description given above and founded on the statements of more recent authors, for he regards a small mass of irregularly-arranged cells, lying at the end of the diverticulum *d* in Fig. 20, as the rudiment of the mid-gut, while the hind-gut arises exclusively from the diverticulum itself. According to Prouho, indeed, this cell-mass is to be derived from this same diverticulum; but it cannot be denied that this statement is likely to strengthen the doubt that has long been felt as to the common origin of the fore-, mid-, and hind-guts.

V. Asexual Reproduction of the Ectoprocta.

A. Budding.

In the Bryozoa, the colonies are produced by the continuous budding of the primary individual. The nature of this budding has been carefully studied by Nitsche (Nos. 23 and 52), and more recently by Braem (No. 45a) and Davenport (Nos. 11 and 46a).* Two kinds of buds may usually be distinguished, according to the direction of their growth:—(1) those that continue to grow in the same direction as the parent-zooecium, such buds serving for the direct prolongation of the branch or branchlet to which the parent-zooid belongs; and (2) those that, in growing out from the parent-zooecium, take a new direction and thus give rise to new branches. In many cases the new branches grow out laterally. The buds of the second kind are then *lateral buds*, while the *median buds* provide for the continuation of the branches, such individuals usually continuing in the same axial direction as the parent. It should, however, be mentioned, that in many cases median buds may also give rise to new branches, since, while retaining the same plane as the mother, they may take a new direction.

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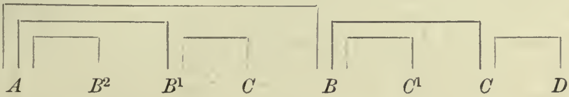
* [For the development of the colony in the Gymnolaemata, see important papers by Harmer on *Lichenopora*, *Crisia*, and *Tubulipora*. *Quart. Journ. Micro. Sci.*, Vols. xxix., xxxii., and xli.—Ed.]

The development of the buds and the branching of the stock thereby determined takes place in the different forms of Bryozoa according to definite laws which were long since reduced to certain written formulae. For the laws of growth of the colonies, which cannot here be entered upon in detail, we refer the reader chiefly to DAVENPORT's treatise (No. 11). BRAEM, for *Plumatella*, has composed a formula which also applies to the other Phylactolaemata.



In this, the parent and offspring are always connected by a bracket ┌─┐ thus. This formula will be explained by comparing it with Fig. 21. The primary individual *A* has given rise by budding to the individuals *B*, B^1, B^2; *B*, on its side, has produced *C* and C^1, and so on. The individuals *A*, *B*, *C*, *D*, *i.e.*, the so-called principal buds resulting from the first division, serve for the continuation of the principal stem in a centrifugal direction, while the intermediate buds B^1, B^2, B^3, etc., become intercalated between the oldest bud and the mother *A*, and lead to secondary branching of the stem. The order of succession in the two cases is reversed. Of the principal buds, the distal individual which denotes the tip of the branch (in this case *G*) is the youngest, while of the intermediate buds B^1, B^2, B^3, the last-formed individual (B^3) lies nearest to the mother-individual *A*.

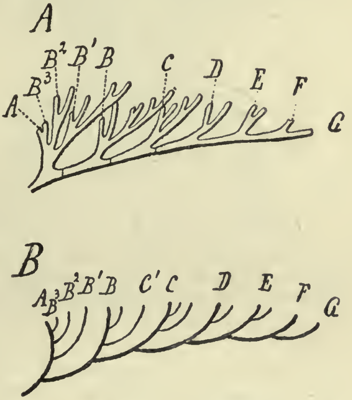


FIG. 21.—*A*, branch of *Plumatella fruticosa* (after BRAEM). *B*, diagram illustrating the branching of this form.

The number of buds that each individual is capable of producing is often limited. In *Cristatella*, for instance, only two buds are, as a rule, produced, the elder being a lateral bud and the younger a median bud. In *Paludicella*, on the contrary, each individual is able to produce a median bud and two lateral buds, and so on.

The variations in the appearance of the Bryozoan stocks are caused by the constitution of the zooecial wall, which through stronger chitinisation or impregnation with lime salts may become stiffened, or, on the other hand, may be soft (*Cristatella*) or even gelatinous (*Alcyonidium*, *Flustrella*), and by the more or less close juxtaposition of the single branches. When the latter retain their independence, moss-like colonies with serrated branches are formed. When the separate branches lie so close to one another in the same plane that the neighbouring branches fuse together, leaf-like, fan-shaped, or encrusting colonies are produced, while close crowding of the branches in various planes leads to the development of fungoid forms (*Plumatella fungosa*). The fusion of the separate zooecia has gone furthest in *Cristatella*, in which the originally distinct character of the branches is indicated only by the mesodermal septa growing in from the edge of the colony.

The youngest buds lie, as a rule, at the apex of the branch. In encrusting colonies, the edge of the colony thus represents the budding zone, from which the further growth of the colony proceeds. In the same way, in *Cristatella*, the youngest individuals, those in the act of forming, are at the edge of the colony (Fig. 22 *kz*), while the oldest (*dp*) lie at its centre.

Braem has pointed out an important distinction between the relations of the bud to the parent in the Phylactolaemata and in the Gymnolaemata. The colony in the Phylactolaemata arises in such a way that the oral side of each individual is directed towards the distal end of the branch to which it belongs. The younger individuals therefore bud out on the oral side of the older (Fig. 22). In the Gymnolaemata, on the contrary, the individuals are placed in the opposite way, each new bud arising on the anal side of the parent (*cf.* Fig. 24). A similar distinction between the two groups is found in the position of the separate individuals with respect to the substratum. In the Phylactolaemata the individuals, in a withdrawn condition, turn the oral side to the substratum, while in the Gymnolaemata the anal side is thus turned. The attempts made by Braem and Davenport to trace back these different relative positions of the bud and the mother in the Gymnolaemata and the Phylactolaemata to a common type do not seem to us altogether successful.

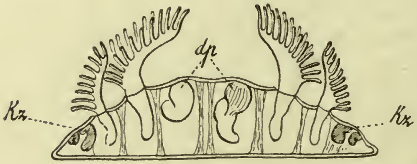


Fig. 22.—Transverse section through a colony of *Cristatella* (after Braem). *dp*, eldest polypide of the colony, in the act of degenerating; *kz*, budding zone.

Braem presupposes, in the Gymnolaemata, a degenerate primary individual which corresponds to the distal end (apex) of the stem. Through this assumption he makes the principal buds of the Gymnolaemata agree with the intermediate buds of the Phylactolaemata. According to Davenport, on the other hand, in both groups, each bud turns its anal side to the budding zone from which it has originated. In the Gymnolaemata, this zone lies at the apex of the stem, *i.e.*, distally, but in the Phylactolaemata it lies proximally. To us it appears that in this very point of the position of the budding zone there is no essential distinction between the Gymnolaemata and the Phylactolaemata, since, in both cases, the youngest buds appear distally, that is, at the edge of the colony. Consequently the budding zone must, in both cases, have the same position.

It has already been pointed out by Nitsche (No. 52) that two distinct types of budding occur in the Ectoprocta, the Gymnolaemata being in this way opposed to the Phylactolaemata. In the first of these groups the type of budding in which the zooecium forms first is common. In this case the zooecium of the bud arises first as an outgrowth or diverticulum of the parent-zooecium (Fig. 24), and only after this has attained a certain size and independence does the first rudiment of the polypide (*p*) appear in it as a bilaminar invagination of the zooecial wall. In the Phylactolaemata, on the contrary, the polypide of the bud appears first, in close proximity to the parent-polypide, as the direct descendant of the latter (Fig. 23). Only later does it shift further from the parent-polypide, newly-formed parts of the zooecial wall being interposed between them. This latter is the type of budding in which the polypide forms first.

The zooecium of the bud is not always a direct outgrowth of the parent-zooecium, for budding may be brought about by special basal extensions (stolons) as, for instance, in the Cyclostomatous Bryozoa (**Ostroumoff**, No. 25), and in some of the Ctenostomata (the group of the Stolonifera).

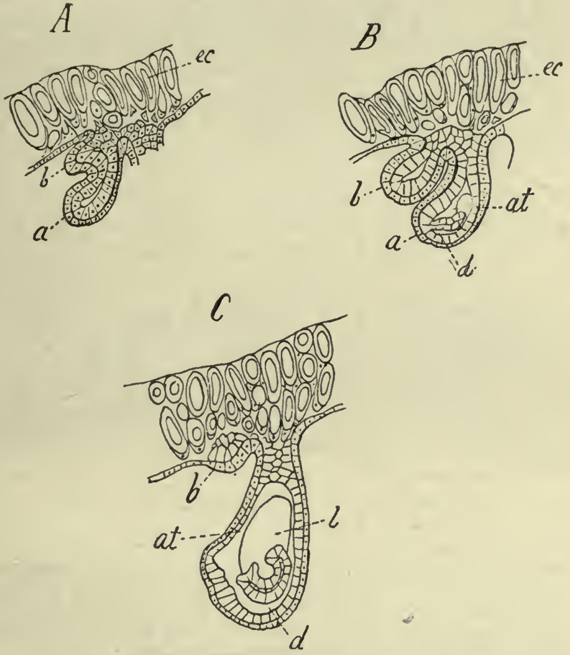


Fig. 23.—*A* and *B*, two ontogenetic stages of the lateral buds of *Cristatella*. *C*, development of the median buds of the same form (after **Braem**). *a*, developing polypide; *b*, the bud developing on it; *at*, atrium; *d*, rudiment of the intestine; *ec*, ectoderm; *l*, rudiment of the lophophore.

It appears that in all Bryozoa budding takes place only at definite parts of the parent in which the original capacity for regeneration has been retained. In the Phylactolaemata, in which asexual reproduction according to the type in which the polypide precedes the zooecium is retained, the rise of a new polypide-rudiment is, as first shown by **Hatschek**, and more recently by **Braem** and **Davenport**, always connected with an already developing polypide-rudiment (Fig. 23). While the parent-polypide, which was originally a bilaminar invagination of the body-wall, develops in the way described above (Fig. 23 *A*, *a*), there is often found at the neck of this invagination, on its oral side, an outgrowth; this is the rudiment of the daughter-bud (*b*). As the two rudiments develop further, they become more distinctly marked off from one another (Fig. 23 *B*), and finally shift quite apart, a portion of the tissue of the neck of the bud being used for the development of the adjacent parts of the zooecial wall (Braem). Nitsche had already observed this form of origin of one polypide-rudiment from another, and defined such forms as double buds. In *Plumatella*, as well as in *Cristatella*, the first bud to develop in each polypide (*B*, *C* in the diagram, Fig. 21) forms after the type of the double bud. The buds that develop later (B^1, B^2, C^1, etc., in the diagram) form after another type which, however, is not essentially different. The rudiment of the bud here arises (Fig. 23 *C*, *b*) in the zooecial wall itself on the oral side of the parent polypide-rudiment; the young bud-rudiment is, however, from the first, in direct connection with the germinating tissue of the parent-rudiment, so that here also we can recognise the connection of each new rudiment with an older one. We can see here very clearly that budding is to be traced back to a process of division. Each newly arising individual becomes cut off from an older individual already present, so that finally all the individuals of a colony can be derived from the first individual produced from the larva.

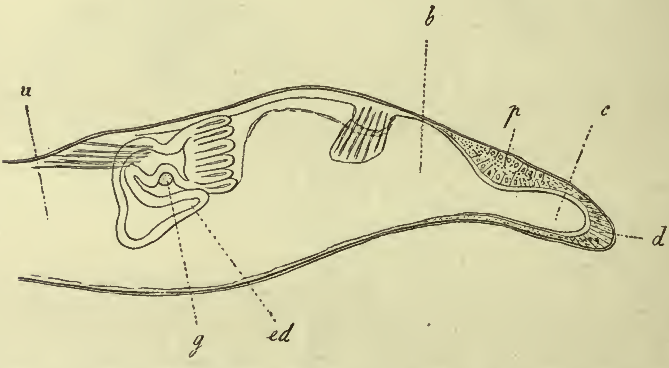


Fig. 24.—Budding in *Paludicella Ehrenbergii* (after Davenport). Median section through the growing apex of a branch. *a*, *b*, region of the branch belonging to most distal of the polypides as yet developed; *b*, *c*, region belonging to the polypide-bud (*p*) that is beginning to develop; *c*, *d*, region of the growing tissue at the tip of the branch; *d*, growing tissue; *ed*, hind-gut of the polypide; *g*, ganglion; *p*, young polypide-bud.

Authors still differ as to the development of the zooecial wall in the Phylactolaemata. Braem is inclined to derive it exclusively from the germ-tissue of the neck of the bud, but Davenport maintains that the zooecial wall grows independently in *Cristatella*, at least at the marginal parts of the colony.

Another method of budding, in which the rudiment of the polypide has from the first a certain independence, forms the transition to the type of budding in which the zooecium develops first, a type common in the Gymnolaemata. Fig. 24 illustrates the rise of new individuals at the apex of a branch of *Paludicella* (Davenport). The apex of the branch is here occupied by actively growing tissue (*d*), which gives rise first of all to the zooecium of the new individual. While the wall of this new zooecium undergoes the general histological transformation by means of which it attains the special character of the adult form, the tissue, at one definite point, retains its embryonic character and its capacity for regenerating, and at this point the polypide-rudiment arises (*p*). Two islands of germinating tissue which persist at the two sides of this rudiment represent those parts of the zooecial wall which, later, form the starting point of the lateral buds.

It was pointed out by Nitsche (No. 23), and more recently by Pergens (No. 27), that the oldest individuals of the Bryozoan colony, and above all the primary zooecium derived from the larva, may, in many cases, be distinguished from the other normal zooecia of the colony by their shape and size as well as by their method of budding. For example, Nitsche found that the primary zooecium in *Flustra membranacea* is remarkably similar to that of *Membranipora*, and with respect to budding agrees with *Membranipora pilosa* as described by Schneider (No. 5), *i.e.*, a number of buds here appear, whereas the secondary zoöecia of *Flustra membranacea*, as a rule, produce only one bud each at the distal end. Pergens also found that the primary zooecium of *Microporella* passed through a Membraniporan stage, while the buds produced from it grew into zooecia of normal shape.

Heteromorphous development of single individuals often occurs in the Ectoprocta. Thus in the polymorphous stock there may be found, besides the usual individuals, root-processes, and specialised organs known as *ooecia*, *ovicells*, *avicularia*, and *vibracula* which are regarded as polypides modified in adaptation to a special function.

B. The development of Statoblasts.

A special kind of asexual multiplication is brought about in the Phylactolaemata by the production of peculiar reproductive bodies, the so-called *statoblasts*. This form of development may be traced back to budding. The recent researches of Kraepelin and Braem prove that the statoblasts are undoubtedly *encysted persistent buds*, intended to secure the continuance and distribution of the fresh-water Bryozoa during the winter months.

The lenticular statoblasts or winter eggs (Fig. 27 *B*) consist of a mass of cells, the germ-body, enclosed in a thick cuticular envelope (*c*), the latter is usually provided with a ring of air-cells which serve as a float (*sr*). In the germ-body we can distinguish a superficial epithelium, discovered by Reinhard (Fig. 27 *A*, *ec*), and a granular cellular mass rich in yolk (*d*). The structure of the germ-body can therefore be compared to that of the Ectoproctous embryo described above (p. 15), if we regard the superficial epithelium as the ectoderm and the granular inner mass as the equivalent of the central tissue.

The statoblasts arise in connection with a mesodermal strand known as the *funiculus,* which runs from the end of the stomach-caecum to the zooecial wall (Fig. 28, *f*). Along this strand they are arranged in a chain, the youngest visible rudiment of a statoblast appearing at the end of the funiculus nearest to the zooecial wall, while the most developed are found near the stomach-caecum.

To obtain a clear view of the origin and significance of the statoblasts, we must, following Braem, examine the earliest stages in the development of the funiculus. This strand first arises as a fold-like prominence in the outer (mesodermal) layer on the oral side of the neck in the young polypide-rudiment. In the further course of development, this fold separates from the neck of the polypide-rudiment (Fig. 25 *A*), so that it assumes the form of a short strand (*f*), this being inserted at its upper end into the zooecial wall, and at its lower into the polypide-rudiment. Through the further growth of the zooecial wall, the upper point of insertion of the funiculus shifts further and further from the aperture of the polypide, and may finally reach the basal surface of the zooecium.

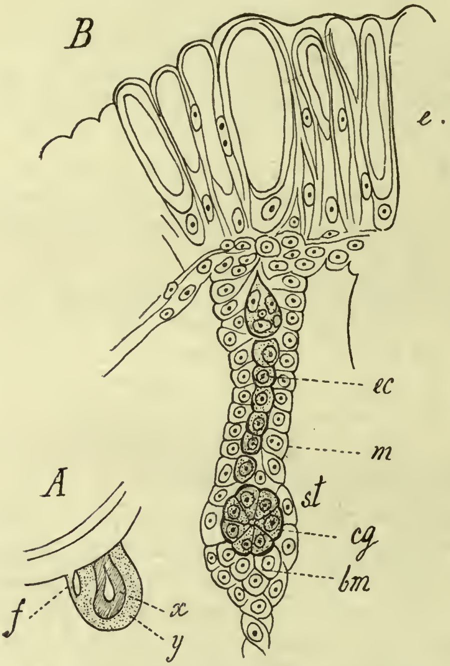


Fig. 25.—*A*, young polypide-bud of *Plumatella* with the rudiment of the funiculus (*f*) (after Braem). *x*, inner (ectodermal), *y*, outer (mesodermal) budding layer. *B*, longitudinal section through a funiculus of *Cristatella* (after Braem). *bm*, "formative mass"; *cg*, "cystigen part" of the statoblast rudiment (*st*); *e*, ectoderm; *ec*, inner (ectodermal) layer of the funiculus; *m*, outer (mesodermal) layer of the funiculus.

The funiculus, in its origin, is, as we have seen, purely mesodermal. Very soon, however, a conical mass of ectoderm-cells, capable of further growth by division (Fig. 25 *B*, *ec*), grows out from the zooecial wall into the funiculus, which in this way becomes bilaminar, consisting of an inner core of ectoderm and an outer layer of mesoderm. At the lower end of this cone the first statoblast-rudiments form, a group of ectoderm-cells (*cg*) becoming detached from the central core and arranged round a small cavity, thus forming a vesicle. This part of the statoblast-rudiment has been named by NITSCHE the "cystigen half," as from it are formed the cysts of the statoblasts. A second part of the rudiment, the so-called "formative mass" (*bm*), arises from the outer mesodermal layer of the funiculus. It represents the rudiment of the inner mesodermal mass which, filled with particles of food-yolk, is found in the statoblasts, while the "cystigen half" yields not only the cell-layer which secretes the cyst but, as REINHARD has proved, the ectodermal layer of the statoblast-germ (Fig. 26 *A*, *a* and *b*).

According to DAVENPORT (No. 46a) the funiculus is to be traced back not so much to a fold as to an active independent wandering of its component mesoderm-cells. KRAEPELIN (No. 50) has stated that the inner layer of the funiculus does not grow in from the zooecial wall, but from the internal lining of the stomach-caecum at the opposite end of the strand. If we follow the statements by BRAEM given above, the essential agreement between the rudiment of the funiculus and that of a polypide-bud is very clear, so that we are justified in regarding the statoblasts as internal buds. A view formerly held by VERWORN (No. 57) derived the cystigen half and the formative mass from a single cell, which underwent a process of cleavage. VERWORN was therefore inclined to regard the statoblasts as parthenogenetic winter eggs.

As the statoblasts develop further, the complete circumcrescence of the "formative mass" (Fig. 26, *b*) by the vesicular "cystigen half" (*a*) takes place. The point last affected by this circumcrescence (*p*), where for some time an aperture can be seen, corresponds to the middle point of the lower surface of the lens-shaped statoblast, which is usually somewhat more convex than the other. The "formative mass" is in this way enveloped by two layers of the "cystigen half" (*a′* and *a″*). The inner layer (*a″*) corresponds to the ectoderm of the statoblast, while the outer layer (*a′*) is concerned in the formation of the shell (*c*). The cells of this outer layer first secrete on their inner ends, *i.e.*, on the side next to the ectoderm of the statoblast, a cuticular cyst (*c*) which surrounds the statoblast. In the substance of this cyst, a slit or line of demarcation soon appears, corresponding to the equator of the cyst; this indicates the division of the cyst into the two watch-glass-like halves which separate later to allow of the escape of the young colony. After this chitinous envelope has been secreted, the marginal cells of the secreting layer elongate and form a fold round the statoblast. These cells now form the annular float, the whole surface of each of them becoming cuticularised. The protoplasmic body remaining within the cuticular cells then completely disappears. When the annular float is completed, it is grown over from above and below by the margins of the central caps of the chitinous secreting layer, which then secretes an external enveloping chitinous layer (Fig. 27, *ud* and *od*).

In *Cristatella*, the equator of the developing statoblasts is at right angles to the longitudinal axis of the funiculus. In *Plumatella*, on the contrary, it lies parallel to that structure. The elongated form of the statoblasts of *Plumatella* is explained in this way. The most complicated conditions are found in the annular float of *Cristatella*. For an account of these we must refer the reader to VERWORN and BRAEM.

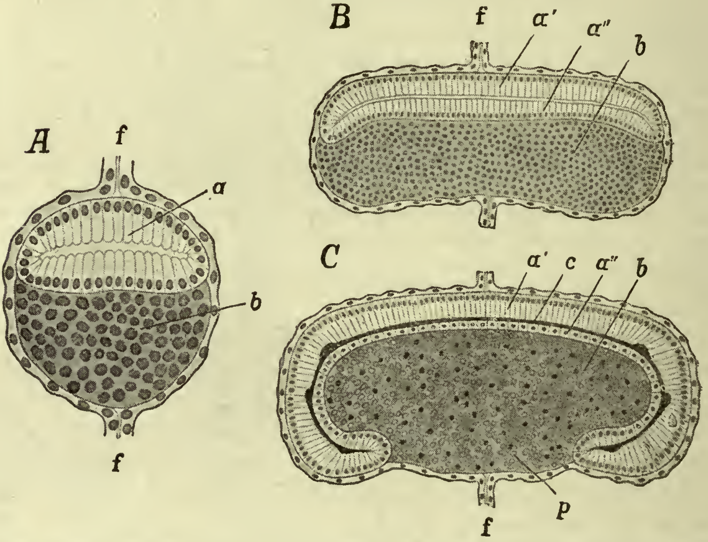


FIG. 26.—Three ontogenetic stages of the statoblasts of *Cristatella* (after VERWORN). *a*, cystigen half; *a′*, external layer; *a″*, inner layer of the cystigen half; *b*, formative mass; *c*, cuticular envelope; *p*, point where during circumcrescence a pore forms; *f*, funiculus.

The germ-body proper consists of the ectodermal layer (Fig. 26 *C*, *a″*) and of the formative mass (*b*) which this surrounds. In proportion as the cells of the latter become filled with food-yolk the boundaries between them disappear. But not all the cells of the formative mass undergo this transformation. Some of them which are in close contact with the ectodermal layer remain unchanged. It appears that these cells, which BRAEM found to be specially plentiful in *Cristatella*, where they often form a continuous layer under the ectoderm, are of importance in the development of the mesoderm-layer (Fig. 27 *A*, *m*) of the young colony.

The completely formed statoblasts which, after the disintegration of the parent colony, become free, are not at once capable of regeneration. The capacity for further development, as a rule, appears only after they have been frozen, or after a long period of rest when air has been excluded (Braem). A higher temperature or contact with air stimulates the statoblasts, which are then capable of germinating, to further development.

A transformation of the cells of the inner yolk-mass first takes place. Those of the superficial layer assume the appearance of ordinary embryonic cells and become applied to the ectoderm (Fig. 27, *ec*), thus thickening the layer of mesodermal elements (*m*) mentioned above as lying below the ectoderm. This mesodermal layer consequently soon becomes a continuous epithelium. The first rudiment of the primary polypide consists of a rounded ectodermal thickening (germ-disc, Fig. 27 *A*, *p*) which develops in the middle of that side of the statoblast which, when floating, is turned downwards, *i.e.*, at the point at which the circumcrescence

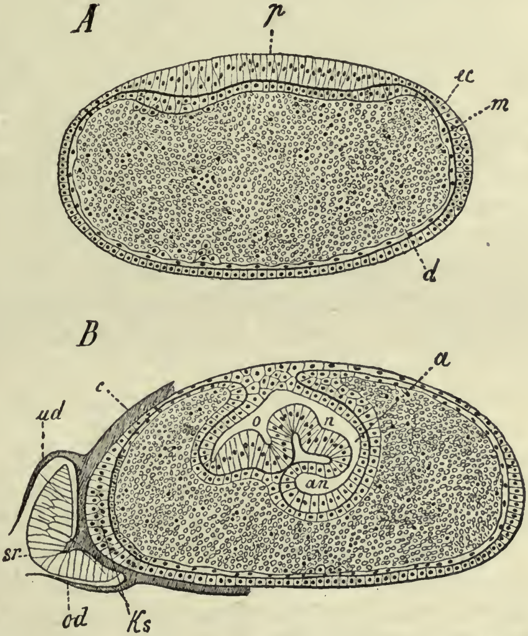


Fig. 27.—Two ontogenetic stages of the germinating statoblasts of *Cristatella mucedo* (after Braem). *A*, on the lower side of the statoblast (that turned upwards in the figure) the polypide-rudiment (*p*) can be seen in the form of a germ-disc. *B*, the polypide-rudiment in a more developed condition. *a*, anus; *an*, intestinal rudiment; *c*, cuticular shell (disc); *d*, yolk substance with nuclei; *ec*, ectoderm; *ks*, budding zone of the future polypide; *m*, mesoderm-layer; *n*, ganglionic invagination; *o*, rudiment of the oesophagus; *p*, germ-disc; *od*, upper spines; *sr*, float; *ud*, lower spine.

of the formative by the cystigen half was concluded (Fig. 26 *C*, *p*). The germ-disc, in which must also be included the adjacent lower mesodermal layer, now becomes invaginated into the yolk-mass. The closing of the aperture of this invagination gives the polypide-rudiment the form of a bilaminar sac, which develops further according to the type described above (p. 37 and Fig. 27 *B*). The only difference in this case is that the body-cavity and all its derivatives (the lophophore-cavity, the circular canal, etc.) are originally completely filled with food-yolk (*d*), which disappears only gradually through the absorption that takes place during further development.

The rudiments of the future buds are early to be recognised as epithelial thickenings (Fig. 27 *B*, *ks*) at the margin of the statoblast (corresponding to the oral side of the primary polypide), from which, by invagination, the second and then the third polypide-rudiments are formed. These, from the time of their first development, are thus independent of the germ-disc. In a similar way, according to DAVENPORT, in the embryos of *Plumatella*, the rudiment of the second polypide appears independently of the first. All the buds that develop later, on the contrary, arise in connection with an older polypide-rudiment, as was described above, for the type of budding in which the polypide develops first.

C. Winter Buds (Hibernacula).

In the fresh-water Gymnolaemata, *Victorella* and *Paludicella*, statoblasts do not develop. In *Paludicella*, isolated individuals (zooecia with rudimentary polypides) persist in an encysted condition. These individuals, which are enclosed in strong, highly calcified, chitinous envelopes (ectocysts), are known as winter buds (*hibernacula*, VAN BENEDEN). In the spring the envelope bursts, and there emerges from it an individual covered with a delicate chitinous cuticle, which by budding gives rise to a new colony; the budding may occur while still in the hibernaculum. The winter buds here represent merely the resting condition of the adult form. Their development in the spring is essentially reducible to a process of ecdysis.

In a similar way, in *Victorella*, short stolons with closely crowded knob-like rudiments of individuals persist through the winter, and give rise in the spring to the first cylindrical cells of new colonies (KRAEPELIN).

VI. Regeneration.

It has long been known that, in the marine Gymnolaemata, the polypides in the older individuals of a colony are constantly regenerated, the zooecium remaining unaffected by the processes of degeneration. The remains of the degenerated polypide are found as the so-called brown body suspended by strands of the funicular tissue in the body-cavity. The regeneration of the polypide takes place from the zoöecial wall and, in the Chilostomata, in most cases (according to Ostroumoff and Davenport, No. 11) on the operculum. Harmer found recently that the first rudiment of the polypide is paired and appears on the lateral margins of the operculum, the two parts only uniting later to form an unpaired invagination. This explains the abnormal cases in which, during regeneration, two polypides are formed in one zooecium. By the invagination of the two layers of the body-wall that now takes place, a new polypide is produced in the way described above. It has long been known that, during this process of regeneration, the wall of the stomach of the new polypide comes into close contact with the brown body. According to Haddon, the latter even passes through the wall into the stomach of the newly-formed polypide, and Ostroumoff held that during these processes entoderm-elements pass out of the brown body into the wall of the stomach of the polypide, to take part in the development of the latter (pp. 43 and 44). These statements, however, have not been confirmed by Davenport's more recent researches. According to Harmer, indeed, in *Flustra*, the brown body is actually taken into the newly-formed alimentary canal, although in *Bugula* this is not the case.

We are still without any explanation of the significance of these regenerative processes, which recall the regeneration of the head in *Phoronis*, *Pedicellina*, and the Tubularia, and which may be compared with similar processes in the Tunicata. We should, however, mention Ostroumoff's view that, together with the brown body, certain excreta are received into the intestine, which are afterwards ejected through the anal aperture with the remains of the brown body. Harmer's researches (No. 16) seem to some degree to support this view.

VII. General Considerations.

Recent anatomical researches, especially those of Caldwell and Cori, show that there is a great agreement between the structure of *Phoronis* and that of the Ectoproctous Bryozoa. This similarity is specially marked in the Phylactolaematous Bryozoa (Fig. 28), on account of the horse-shoe-shaped lophophore, the presence of the epistome (*ep*), and the similarity in the arrangement of the body-cavity. Thus in the latter, we find a septum separating the lophophore-cavity from the rest of the coelom, and having the nephridial funnels* sunk in it, and an epistomal cavity distinct (?) from the lophophore-cavity (*cf.* Fig. 5, p. 9). The recognition of these points of agreement throws a new light upon the Bryozoa. It shows that the Phylactolaemata represent by far the most primitive type, while the Gymnolaemata, with regard to the segmentation of the lophophore, have undergone simplification, the condition of the body-cavity also showing degeneration.

Further, through a comparison with *Phoronis*, the remarkable form of the Bryozoan larva is to some extent explained, and the task of tracing back the Bryozoan larva to the Trochophoran type is rendered easier. The comparison of the Bryozoan larvae to the *Actinotrocha* has been made chiefly by HARMER (Entoprocta, Lit., No. 4) and OSTROUMOFF (No. 24).

The forms of Bryozoan larvae in which the larval intestine is retained will be treated first, as the most primitive. Among these forms, *Cyphonautes*, by the possession of shell-valves and an atrium, shows a secondarily modified condition, the larvae of *Tendra* and *Alcyonidium* being most suited for comparison with the larvae of other groups of animals. The most striking organ of the larva is the massive equatorial corona, the locomotory organ. We should be tempted to see in this the homologue of the pre-oral ciliated ring of the *Trochophore*, but for the difficulty presented by the fact that the circular mantle-cavity which is destined to form the greater part of the body-wall lies in front of the corona. In any case, we are led, by a comparison with the *Actinotrocha*, to consider the retractile disc, on account of the similarity of its position, as the equivalent of the apical plate. This view, which is

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* The investigations made so far on this point are not conclusive. The nephridia of the Phylactolaemata (see diagram, Fig. 28, *n*) were first seen by VERWORN, and later were described more in detail by CORI (No. 46), but their occurrence has recently been disputed by BRAEM and KRAEPELIN [also by OKA]. BRAEM connects the structures referred to with his "forked canal" (p. 42). It is, however, not impossible that these organs exist side by side. CORI's statements have, on the other hand, been supported by BLOCHMANN (Brachiopoda, Lit. No. 4).

HARMER (No. 16) was unable to convince himself of the presence of special excretory organs in the Gymnolaemata, but we may well feel inclined to regard as a nephridium the intertentacular organ observed in some forms by FARRE, SMITT, HINCKS, and more recently by PROUHO (see p. 14).

supported by the utilisation of this structure as larval tactile organ, obtains further confirmation from the statements of Harmer and Prouho quoted above (p. 20). Both these authors were able to observe that the larval brain is connected with the retractile disc, and Prouho was able to add the information that the latter organ underwent, during metamorphosis, a degeneration similar to that which takes place in all other larval organs (p. 24).

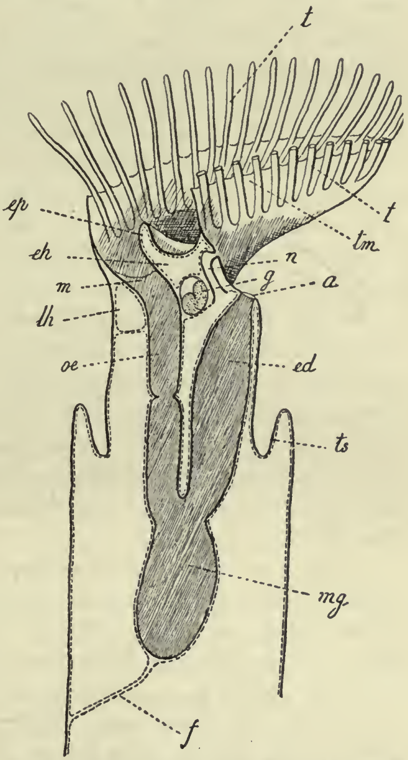

Fig. 28.—Diagrammatic median section through a Phylactolaematous Bryozoan (constructed after Cori). This should be compared with the diagrams of *Phoronis* (Fig. 5, p. 9) and *Terebratula* (Fig. 41, p. 80). *a*, anus; *ed*, hind-gut; *eh*, epistomal cavity; *ep*, epistome; *f*, funiculus; *g*, ganglion; *lh*, lophophore-cavity, here termed the circular canal; *m*, mouth; *ma*, stomach; *n*, nephridium; *oe*, oesophagus; *t*, tentacle; *tm*, tentacular membrane; *ts*, tentacle-sheath.

Of the larval organs lying on the oral side, the so-called sucker is evidently the homologue of the invagination which lies on the ventral side of the *Actinotrocha*, between the mouth and the anus (Fig. 4 *C*, *iv*, p. 7)* In the Bryozoa also, during metamorphosis, this invagination gives rise to a part of the body-wall, though it here produces only the adhesive plate which lies altogether at the base of the primary zooecium. The structures known as the ectodermal furrow and the pyriform organ, on the contrary, seem to be provisional organs peculiar to the Bryozoan larvae, for which no homologue can be found in the *Actinotrocha* or the *Trochophore* stage of other groups.

We may thus, perhaps, recognise in the Ectoproctous larvae a somewhat modified *Trochophore* stage, which in the possession of a ventral sucker may be connected with the *Actinotrocha*. Recently, however,

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* In position this organ agrees closely with the rudiment of the foot in Molluscan larvae, with which it has repeatedly been homologised.

obstacles to such a view have arisen from the study of the ontogeny of the Phylactolaemata. While most authors are agreed in assuming that, in the Gymnolaematous larva, the retractile disc belongs to the aboral region, more recent investigators are of the opinion that, in the Phylactolaemata, the point at which the polypide-rudiments appear (and which corresponds to the retractile disc) occupies the position of the vanished blastopore. We are not, at the present moment, in a position satisfactorily to solve these difficulties, which are due to the incompleteness of our knowledge of the ontogeny of the Bryozoa, and must await further investigations.

In the Bryozoa, as in *Phoronis*, metamorphosis begins with the evagination of the sucker-like organ. This is followed by fixation and extensive disintegration of the larval organs. In *Phoronis*, only a few larval organs are thrown off, and these are replaced by permanent organs (*e.g.*, pre-oral lobe, tentacle-crown, circum-anal ciliated ring), but, in the Bryozoa, the intestinal canal and the whole of the body-wall of the larva undergo degeneration. The latter are not simply thrown off (as are the provisional organs of *Phoronis*), but sink by invagination into the interior of the body (through the formation of the vestibulum), and are there transformed into the so-called brown body. This degeneration affects not only the larval integument, but all the provisional organs which lie in it—the corona, the ectodermal furrow, and (according to Prouho) the retractile disc.

By means of these transformations, the larva reaches an attached sac-like stage, and already shows on its surface the future ectoderm of the primary zooecium. Within it are found the remains of the original central tissue and the brown body, described above, which is formed of the degenerated larval organs. A primary zooecium, at this stage of development, strongly recalls those individuals of the Bryozoan colony in which, as is often the case, the polypide degenerates. These also consist of a zooecium closed on all sides, and have within them, besides strands of the funicular tissue, a brown body derived through the degeneration of former polypides

After the attachment of the Bryozoan larva, the primary polypide very soon commences to form, while the disintegration of the larval organs is still going on. Its rudiment is found at the upper or distal pole of the primary zooecium, having been produced either, as has till now been believed, by the invagination of the retractile disc, or, as Prouho holds, not directly from this, but from a new structure which appears at this point, as to the origin of which nothing is known. We have further seen above (p. 37) that this polypide develops in the primary zooecium exactly as the polypides regenerate in those zooecia of the colony in which a previous polypide has degenerated.

In both cases, as it appears to us, the continuity of the individual is retained by means of the persistent zooecium. We shall therefore have to regard the rise of the primary zooecium from the larva merely as metamorphosis, and to consider the newly-formed polypide as a part of the same individual which is represented by the larva. The cephalic section has been, if we may so express it, regenerated in the attached larva. It would be theoretically inaccurate to regard the rise of the polypide in the primary zooecium as the budding of a new individual. We must here bear in mind that in the Phoronid larva also it is chiefly the organs of the cephalic region that are thrown off and regenerated during metamorphosis.

The metamorphosis of the Ectoprocta is, indeed, connected with so far-reaching a disintegration of the larval organs that it is not possible to institute a direct comparison between the position of the organs in the larva and in the adult. There is a gap here which may be filled up by an examination of the metamorphosis of *Phoronis*. We may in consequence assume for the adult individuals of the Bryozoan colonies also, that the short line between mouth and anus is the dorsal middle line, and that the ganglion lying at this part represents the supra-oesophageal ganglion which is derived from the neural plate.

A few remarks as to the Bryozoan larvae in general have still to be added. A comparison with the *Actinotrocha* is here specially instructive. The *Actinotrocha* leaves the egg when only slightly developed; it feeds and grows considerably, and during larval life develops the rudiments of many important organs (and this is also the case in *Cyphonautes*). The *Actinotrocha* thus passes through important processes of growth and development, and at the same time seeks out a suitable point for fixation, and facilitates the distribution of the individuals over a large area. The swarming stage of most Bryozoa, on the contrary, serves, as a rule, merely for the last purpose. The larva does not feed, and consequently, the alimentary canal degenerates. Its one office is to seek out a suitable point of attachment, and for this purpose it is provided with a highly-developed locomotory apparatus and sensory organs. So as to facilitate locomotion as much as possible, the rudiments of the future parts of the body are present in an invaginated condition only (pallial cavity, sucker). The internal organs, furthermore, are packed into the smallest space possible. We shall therefore not be surprised at the absence of the coelom in the larva, although, from a comparison with the *Actinotrocha*, we should have expected it to be present. The coelom, even in adult forms of marine Ectoprocta, is, in a certain sense, degenerate (the peritoneal epithelium being wanting); the cause of its excessive degeneration in the larva, however, is to be sought in the conditions just mentioned. A similar temporary obliteration of the interior of the larva is to be found, for instance, in the *Planula*-larva of the Cnidaria.

If we now consider the Phylactolaematous larva in the light of what has been said above, we shall find that the central cavity within it, taking into account its further development, must be assumed to be the coelom. In this respect, then, the embryo of the Phylactolaemata, as compared with that of the Gymnolaemata, recalls more primitive conditions. We must not, however, forget that, in other respects, this larva has undergone the most far-reaching degenerations. The development of a large central cavity inside the ciliated larva may be connected with its life in a specifically lighter medium (fresh water). We find, for instance, that the larva of *Spongilla* is distinguished from somewhat similar marine Sponge larvae by the possession of a larger cavity.

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CHAPTER XVII.

BRACHIOPODA.

Our knowledge of the ontogeny of the Brachiopoda is still somewhat incomplete, especially with regard to certain important points. The anatomy of the adult forms is better known, but the close crowding of the organs between the shell-valves in the larva renders it difficult to ascertain their relative positions. This very crowding has no doubt been the cause of many of the changes that have taken place in the original type of organisation. All that is known of the ontogeny of the Brachiopoda, however, points to the conclusion that they are closely related to the two groups which have just been considered—the *Phoronidae* and the Ectoproctous Bryozoa. This view is founded upon the presence of a tentacle-bearing lophophore, originally horse-shoe-shaped, and of an integumental fold (epistome) above the mouth, and, further, on the agreement that prevails in the three groups with respect to the body-cavity and the nephridial system. The characteristic pelagic larvae of the Brachiopoda also, can without difficulty be brought into agreement with those of the Ectoprocta.

In our description of the Brachiopoda we shall treat of the Testicardines and the Ecardines separately, beginning with the first of these groups, the ontogeny of which has been more fully investigated.

1. Testicardines.

A. Embryonic Development.

The first ontogenetic stages of this group have been investigated by Lacaze-Duthiers (No. 10 in *Thecidium*), Morse (Nos. 11 and 12 in *Terebratulina*), and especially by Kowalevsky (No. 8 in *Argiope*, *Thecidium*, *Terebratula*, and *Terebratulina*). The more recent researches of Shipley (No. 16) have, in all essential points, confirmed the statements of Kowalevsky.

With respect to the first ontogenetic processes, the *Testicardines* may be divided into two groups, the one including the genera *Argiope*, *Terebratula* and *Terebratulina*, and the other being represented by *Thecidium*. The distinctions between these two groups, however, are only in points of secondary importance, and can be explained by the crowding of the blastomeres in *Thecidium*.

In *Argiope*, the mature eggs pass first into the body-cavity and thence into the nephridial canals that function as oviducts. The latter open into brood-pouches* lying on either side of the body; these are to be regarded as invaginations of the body-wall, and in them the eggs pass through the first stages of their development. The embryos are attached to the wall of the brood-sac by a tough filament at their anterior ends. It has not yet been definitely ascertained where fertilisation takes place, but it is probable that it occurs after the egg has reached the brood-sac. Cleavage is total and almost equal, and leads to the development of a regular coeloblastula which is followed by a gastrula-stage resulting from invagination. During this stage, the plane of symmetry of the body seems already to be defined. The last point at which the blastopore closes seems to correspond to the anterior part of the ventral side, perhaps to the position of the future oral aperture (*cf.* similar conditions in *Phoronis*, p. 2). While the blastopore is closing, two lateral coelom-sacs become separated from the archenteron by ingrowths of its walls (Fig. 29 *A*); this abstriction takes place in such a way that the last vestige of communication between the three cavities is retained in the most anterior part of the body. In this last point only is there a distinction between this process and that by which mesodermal folds arise in *Sagitta* (Vol. i., p. 367); in other respects the two processes are somewhat alike.

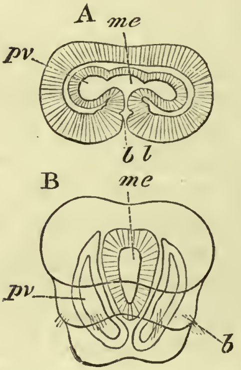

FIG. 29.—Two ontogenetic stages of *Argiope* (after KOWALEVSKY, from BALFOUR'S *Text-book*). *A*, late gastrula stage showing the origin of the coelomic sacs (*pv*). *B*, stage after the separation of the three regions of the body. *b*, provisional setae; *bl*, blastopore; *me*, mid-gut; *pv*, coelomic sacs.

After these coelomic sacs have become completely cut off, we find in the now lengthening embryo an archenteron closed on all

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* In certain fossil forms, the embryos seem to pass through the whole of their development within these brood-sacs, or at least within the mantle-cavity of the parent, as is indicated by the discovery by SUESS of quite young shells enclosed in a *Stringocephalus* (*cf.* ZITTEL, No. 17).

sides (rudiment of the mid-gut), which soon grows out posteriorly as the rudiment of the intestine, and two lateral coelomic sacs (rudiments of the middle germ-layer and the body-cavity)—Fig. 29 *B*. During the whole of larval life the alimentary canal remains closed, the rudiments of the mouth and anus being wanting. The coelomic sacs grow completely round the mid-gut, the walls of the two sacs becoming applied later to form a dorsal and ventral mesentery.

The embryo now grows somewhat in length and becomes marked off into two parts by a circular furrow. The anterior part of the body is soon cut up by another circular furrow into two regions, so that the animal now consists of three parts not quite of equal size (Fig. 29 *B*).* These three parts have repeatedly been called segments, but we shall see that they are in no way true segments, and we shall therefore name them the *cephalic*, the *thoracic*, and the *pedal regions*. The latter, defined by KOWALEVSKY as the caudal segment, contains only the posterior prolongations of the coelomic sacs (Fig. 29 *B*), the mid-gut belonging to the two anterior regions.

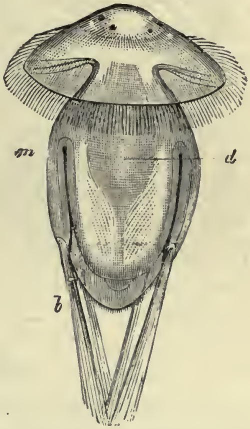

FIG. 30.—Free-swimming larva of *Argiope* (after KOWALEVSKY, from GEGENBAUR). *b*, setae; *m*, mid-gut; *m*, mantle.

The cephalic region gives rise later to the umbrella-like cephalic section of the body which is surrounded by a ring of cilia (Fig. 30), and carries at its apex four symmetrically placed eye-spots, the dorsal pair of which appears first. In the thoracic region, a fold is soon found growing out posteriorly (*m*); this fold, which at first is circular and then becomes divided up into a dorsal and a ventral lobe, must be regarded as the rudiment of the two mantle-lobes, and will here be called the *mantle-fold*. It carries ventrally two pairs of provisional tufts of setae (*b*), and almost completely encircles the pedal region

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* Authors differ with regard to the origin of the middle region of the body. According to HOYER (No. 7), it becomes cut off from the anterior section of the embryo when the latter consists of two sections. This is confirmed by SHIPLEY's statements in connection with *Argiope*, and LACAZE-DUTHIERS' in connection with *Thecidium*. OEHLERT and DENIKER (No. 9), on the contrary, agree with KOWALEVSKY in the view that "Le segment médian s'est probablement formé par la division du segment caudal." It cannot be denied that this is a point of some importance.

of the larva. The latter region gives rise to the peduncle of the adult.

The eggs of *Thecidium*, which are distinguished by their comparatively large size, after leaving the oviduct, pass into a brood-sac which develops as a median invagination of the ventral mantle-lobe, into which two of the cirri of the ring of tentacles hang down. To these the eggs are attached by means of fine filaments (*cf. Phoronis*). Cleavage here also is total and equal, but the cleavage-cavity is from the first small. An invagination of the blastoderm does not here take place, but the second embryonic layer arises "through the simple and irregular formation of its cells from the cells of the blastoderm," and thus probably by polar ingression. The whole of the cleavage-cavity is soon filled with cells of the primary entoderm, which become arranged into three masses, in each of which a cavity soon appears. The part that lies between the other two becomes the mid-gut, and the lateral parts represent the coelomic sacs, so that we now have a stage equivalent to that described above for *Argiope*. The further development of the two forms also agrees. The embryo first lengthens and becomes divided up into transverse regions. According to LACAZE-DUTHIERS, the middle region here arises by abstriction from the anterior half. The most anterior part of the cephalic region becomes marked off later by a circular furrow, so that the ciliated larva is finally composed of four distinct regions separated from each other by circular furrows.

B. Metamorphosis.

Our knowledge of the metamorphosis of the Brachiopoda we owe principally to the investigations of MORSE in *Terebratulina*, and KOWALEVSKY in *Argiope* and *Thecidium*, but these investigations are far from complete. The attachment of the larva, the form of which has been briefly described above, is brought about by means of a cement secreted by the posterior pole of the body (pedal region). The mantle-fold now bends anteriorly (Figs. 31 *F–K*, 32 *A*), so that it soon completely envelops the cephalic segment. The former external surface of the mantle-lobes now becomes the inner surface and *vice versâ*. In this way the points of insertion of the four larval tufts of setae come to lie on the inner surface of the mantle (Fig. 32). The setae now soon fall off (Fig. 33), and, in those forms which, in the adult condition, possess setae on the margin of the mantle, are replaced by the permanent setae. In

Argiope, these latter are wanting. The two shell-valves now soon form on the outer surface of the mantle-lobes as cuticular secretions. The pedal region of the larva becomes the peduncle of the adult, and two large groups of muscles which can be recognised even in the larva (Fig. 32 *B*) become changed into the ventral peduncular muscles. In *Liothyrina* and *Terebratulina* there is also a pair of dorsal peduncular muscles in the larva. The two pairs of muscles which end at the bundles of setae become the shell-adductors. The pair of muscles which, in Fig. 32 *B*, lies on either side of the posterior end of the digestive tract, represents the rudiment of the divaricators. This pair divides later into a pair of dorsal and a pair of ventral divaricators.

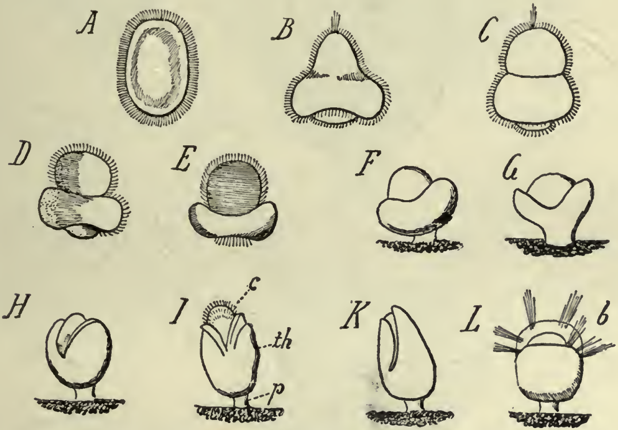

Fig. 31.—Stages in the attachment and metamorphosis of the larva of *Terebratulina* (after Morse). *b*, tufts of provisional setae; *c*, cephalic region; *th*, thoracic region; *p*, peduncular region of the body.

The metamorphosis of the cephalic region of the larva is the most obscure. In comparing this larva with that of *Phoronis*, we should expect that this section would give rise merely to the integumental fold above the mouth (epistome) and to the supra-oesophageal ganglion (see diagram, Fig. 34). According to Kowalevsky, however, it appears, on the contrary, that the rudiment of the oesophagus (Fig. 33 *A*, *oe*) develops as an ectodermal invagination in the region of the cephalic lobe, and the latter, with its eye-spots, is for some time longer recognisable within the attached larva (Fig. 33 *B*). If this is the case, we should have to attribute to the ciliated ring, which runs round the cephalic lobe of the larva, a postoral position.

It is, however, not impossible, indeed, taking into account the dorsal position of the lophophore-rudiment, it is probable that even before the oesophageal invagination appears in the cephalic lobe of the attached larva, certain displacements have taken place which alter the primitive conditions (*cf.* Fig. 34).

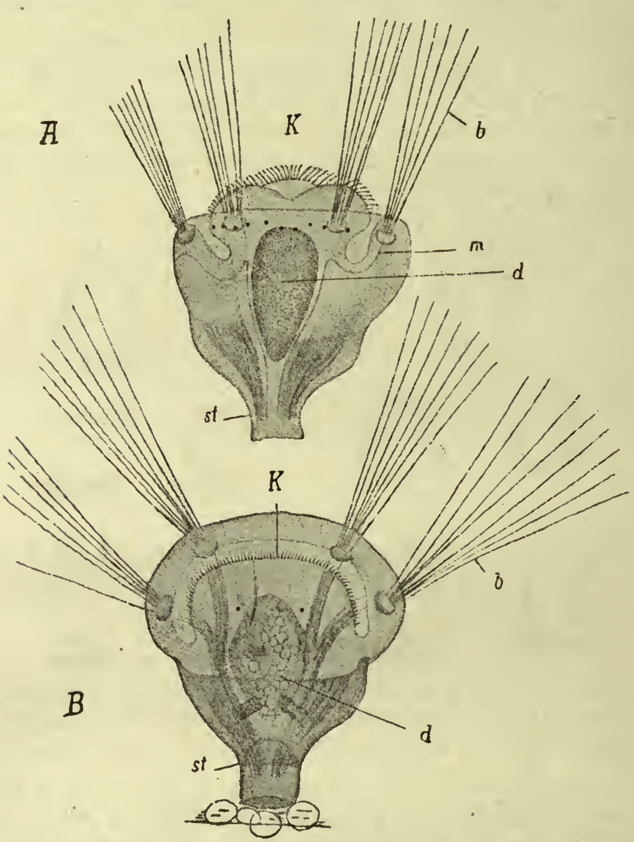

FIG. 32.—Two stages in the metamorphosis of *Argiope* (after KOWALEVSKY). *b*, provisional setae; *d*, rudiment of the mid-gut; *k*, cephalic lobe; *m*, mantle-fold; *st*, peduncle.

The rudiment of the lophophore (Fig. 33 *A*, *t*) arises in the form of an almost circular thickening on the inner surface of the dorsal mantle-lobe. As the mouth is later encircled by the lophophore, this circular thickening of the cephalic lobe must extend ventrally. The first tentacle-rudiments (*t*) are soon seen in the form of four swellings. At a later stage these develop into hollow tubular outgrowths

(Fig. 33 *B*), their number being increased by the addition of new rudiments, the point at which the budding of tentacles first takes place being the most anterior or distal part of the lophophore, which later becomes its dorsal part.

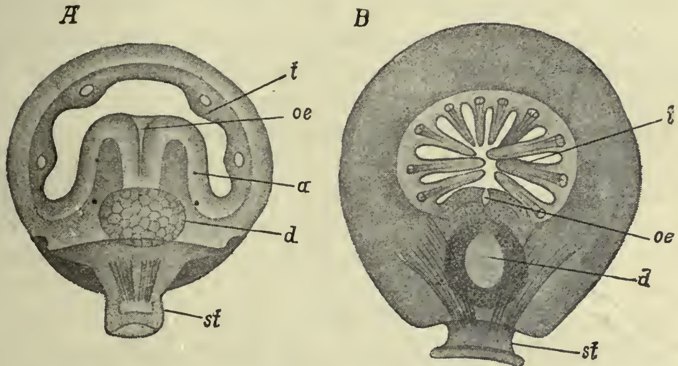

FIG. 33.—Two older ontogenetic stages of *Argiope* (after KOWALEVSKY). *a*, eye-spots; *d*, mid-gut; *oe*, oesophagus; *st*, peduncle; *t*, tentacle-rudiments.

It may at first sight appear remarkable that the tentacles grow out on the inner side of the mantle-lobe. But if we consider the free-swimming larva, in which this inner side still functions as the outer side of the thoracic section, we shall see that the crown of tentacles here has a similar post-oral position as in the *Actinotrocha* (*cf.* diagram Fig. 34, *t*).

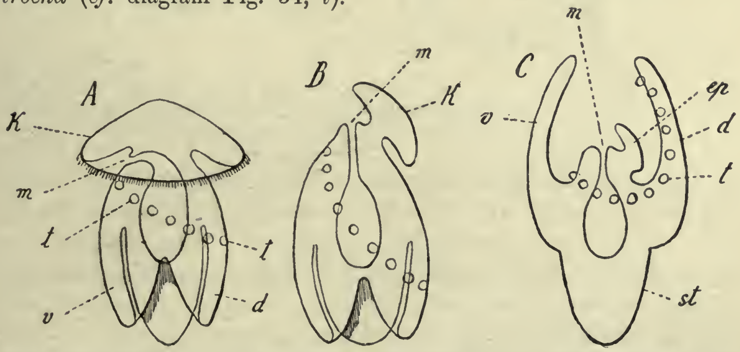

FIG. 34.—Hypothetical scheme of the metamorphosis of the Brachiopoda for comparison with the *Actinotrocha*. *A*, free-swimming larva. The oral aperture (*m*) is depicted, although not actually present at this stage. The position in which it here appears, below the cephalic lobe (*k*), is not in accordance with KOWALEVSKY's statements. The tentacle-buds also are not actually present at this stage. *B*, an imaginary transition stage. *C*, younger Brachiopod after the reversal of the two mantle-lobes. The epistome has arisen from the cephalic lobe (*k*). The row of tentacle-buds (*t*) belongs for the most part to the dorsal lobe of the mantle. *d*, dorsal lobe of the mantle; *ep*, epistome; *k*, cephalic lobe; *m*, mouth; *st*, peduncle; *t*, tentacle-buds; *v*, ventral lobe of the mantle.

The later transformations in the lophophore have been investigated in *Terebratulina* by Morse. The lophophore here is originally circular, but, later, the anterior edge becomes indented. In this indentation, close to the median line, new tentacles form. The tentacular apparatus, which in this way has become horseshoe-shaped (Fig. 35), resembles the similar organ in *Phoronis* and the Phylactolaemata, this resemblance being heightened by the fact that here also a dorsal fold, the lip (*e*), can be seen over the mouth; this must be regarded as the epistome which, in later stages, is continued along the whole length of the row of tentacles. The mouth (*m*) lies in a ciliated furrow, the buccal groove, between the ventral row of tentacles and this fold, this furrow being continued on to the arms as the brachial groove. The two processes of the horseshoe-shaped lophophore develop into the large lateral arms of the adult, while the little, spirally-coiled, inner arms (*b*) grow out only later in the dorsal indentation. The details of the development of the lophophore in later stages must vary on account of the varying shape of the adult organ in the different forms; but on this point we are still without accurate information.

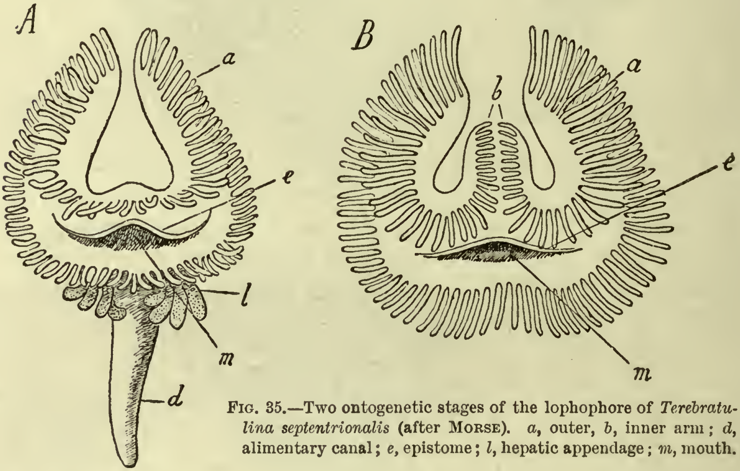

Fig. 35.—Two ontogenetic stages of the lophophore of *Terebratulina septentrionalis* (after Morse). *a*, outer, *b*, inner arm; *d*, alimentary canal; *e*, epistome; *l*, hepatic appendage; *m*, mouth.

In *Argiope*, the lophophore retains the simple original horseshoe-shape throughout life. Both this form and *Thecidium* show a primitive condition, inasmuch as the connection of the arms with the dorsal mantle-fold is permanently retained.

With regard to the external alteration of form in the attached larva, it should further be mentioned that, according to Morse, the youngest stage of *Terebratulina septentrionalis* strongly recalls the shape of the shell in *Megerlia* and *Argiope*. Later, a stage develops which, on account of the long, flattened shell-valves and the long peduncle, strikingly recalls *Lingula*, and this leads finally to the adult form.

The only details known as to the development of the inner organs are such as are easily understood. The division of the intestine into separate sections and the development of the hepatic tubes as lateral diverticula of the anterior section of the intestine (Fig. 35 *A*, *l*) are among these, as also the rise of the nervous system from thickenings of the ectoderm. The original connection of the central nervous system with the ectoderm in various forms of the Brachiopoda is, as in *Phoronis*, retained throughout life.

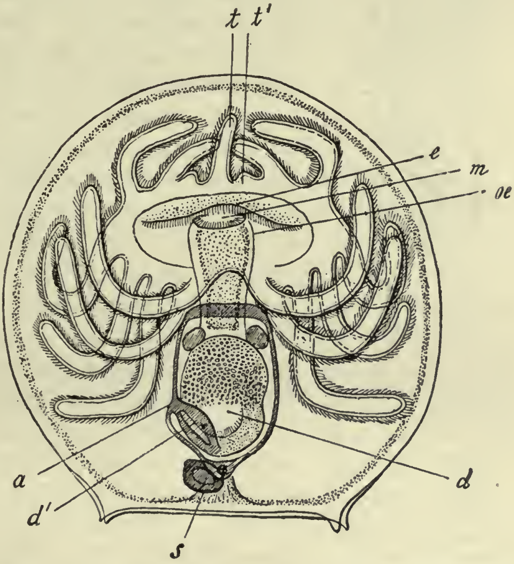

FIG. 36.—*Lingula* larva (after BROOKS). *a*, anus; *d*, dilated anterior section of the intestine; *d'*, narrowed terminal section of the same; *e*, epistome; *m*, mouth; *oe*, oesophagus; *s*, rudiment of peduncle; *t*, unpaired tentacle; *t'*, youngest tentacle-buds.

II. Ecardines.

The embryonic development of the Ecardines is up to the present unknown. Only the pelagic larvae and the youngest attached forms are known, the metamorphosis, briefly noticed by F. MÜLLER and McCRADY, having been chiefly investigated by BROOKS in *Lingula* (No. 5). The most striking feature in the metamorphosis of this group is, that the pelagic larvae are at a very advanced stage of development which, in the Testicardines, is reached only after attachment.

The youngest larva of *Lingula* observed by BROOKS was already enclosed in two flat, discoidal shell-valves, not articulating with one another, but covering the animal dorsally and ventrally, their edges being free all round (Fig. 37, *s* and *t*). The anterior part of the mantle-cavity is occupied by the disc-like lophophore beset with tentacles (Figs. 36 and 37), in the centre of which can be recognised the oral aperture (Fig. 36, *m*) and an epistomal fold (*e*) overhanging it. In the lophophore, a striking feature is the presence of a dorsal, unpaired tentacle (*t*), at the sides of which the youngest tentacle-rudiments grow out (Fig. 36, *t'*). The actual body of the animal is small, and contains a body-cavity which is not spacious, an alimentary canal, and a few groups of muscles. Among these latter, we notice first a pair running near the oesophagus (*oe*) and an unpaired bundle extending from shell to shell. The alimentary canal at first appears divided into the bent oesophagus (*oe*), a dilated stomach (*d*), in connection with which can soon be seen the hepatic diverticula and a posterior intestinal outgrowth (*d'*), which bends round anteriorly and fuses with the body-wall on the right side, at which point the future anal aperture soon arises (Fig. 36, *a*).

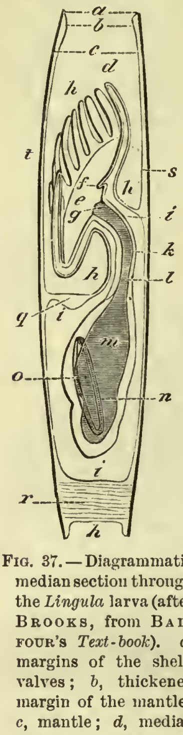

FIG. 37.—Diagrammatic median section through the *Lingula* larva (after BROOKS, from BALFOUR'S *Text-book*). *a*, margins of the shell-valves; *b*, thickened margin of the mantle; *c*, mantle; *d*, median dorsal tentacle; *e*, lophophore; *f*, epistome; *g*, mouth; *h*, mantle-cavity; *i*, body-cavity; *k*, wall of the oesophagus; *l*, oesophagus; *m*, hepatic chamber of the stomach; *n*, intestinal chamber of the stomach; *o*, hind-gut; *q*, ventral ganglion; *r*, posterior muscle; *s*, dorsal, *t*, ventral shell-valve.

Other features to be noted in the youngest *Lingula* larva are the complete absence of the rudiment of the peduncle and the presence of a remarkable semicircular skeletal plate, which lies below the dorsal shell-valve and is connected with that valve. In the larva described by F. MÜLLER (Fig. 38), which perhaps belongs to *Crania*, five pairs of strong provisional setae could be seen, the larva creeping by the help of these and the lateral movements of the shell-valves. In swimming, the shell-valves are opened and the lophophore is extended far beyond the shell, the swimming movements being brought about by the cilia covering the tentacles.

The rudiment of the nervous system can be recognised in the form of a ring surrounding the oesophagus; in this ring are found a ventral ganglionic thickening, two lateral ganglia and two dorsal otocysts. In FRANZ MÜLLER's larva (Fig. 38), paired eye-spots (*a*) and auditory vesicles (*o*) were also observed. These sensory organs degenerate in the course of further development.

The rudiment of the peduncle now arises at the posterior end of the body, and soon grows to a considerable length; by means of this the attachment of the larva takes place. In the further course of metamorphosis the lophophore assumes its final shape; characteristic changes occur in the form of the shell-valves, and the mantle-sinuses arise as horn-shaped diverticula growing out from the body-cavity, while the rows of setae found in the adult appear on the margin of the mantle.

III. Changes in the shape of the Shell.

Certain transformations undergone by the shell of *Terebratulina* in the course of ontogenetic development were pointed out by MORSE, who drew attention to the fact that the shell in this form, during its development, passes through stages in which it resembles the shells of *Megerlia* or *Argiope* (*cf.* p. 73). These developmental changes of the shell have recently been investigated by BEECHER (No. 1), who proposes to name the first rudiment of the shell of a newly metamorphosed larva, which consists of a horny, chitinous, or cuticular secretion, the *protegulum*. The most primitive and the most widely distributed form of protegulum is a semi-circular or semi-elliptical plate (Fig. 39, *p*) with a straight hinge-line which, in length, corresponds to the greatest breadth of the plate. The shape of the protegulum may be modified in individual cases, the future form of the shell then exercising an influence. Only in rare cases does the shell, after increasing in size by the formation of new layers, retain the original shape of the protegulum, the zones of growth here running parallel with the periphery. An example of this is afforded by *Paterina* (*Obolus*) *labradorica*. Other forms (*e.g.*, *Orbiculoidea*) pass through a *Paterina*-like stage in their ontogeny (Fig. 39 *A*).

The phases through which the shell-valves pass in later stages are connected with the relative length of the peduncle, with the angle formed by the longitudinal axis of the animal and the substratum, and with the consequent greater or slighter mobility of the body. The manner of insertion of the peduncle is also of significance in connection with the transformations in the form of the shell. In *Lingula*, for instance, the peduncle projects as a prolongation of the longitudinal axis of the body between the posterior ends of the shell-valves, which consequently are of somewhat the same shape. In most other forms, the peduncle is inserted more in the region of the ventral valve, the consequence being that, as it shortens, the two valves come into close but dissimilar relation to the substratum. Here we may perhaps find the reason for the valves having become more and more heteromorphous.

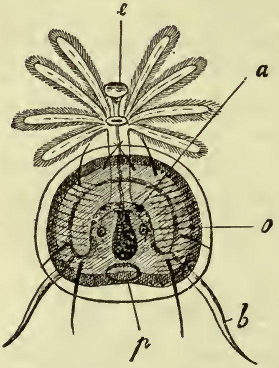

FIG. 38.—Pelagic Brachiopodan larva of *Desterro*, swimming by means of the extended lophophore (after F. MÜLLER). *a*, eye-spots; *b*, provisional setae; *e*, epistome; *o*, otocyst; *p*, internal skeletal plate.

As a rule, forms in which the peduncle is long and the body comparatively movable, have long and posteriorly pointed shells with a short hinge-line (*Terebratulina*). A shortening of the peduncle brings the posterior end of the body into contact with the substratum, and this leads to the development of broad forms with lengthened hinge-line (*e.g.*, *Argiope*, *Terebratella*). When, as in the *Discinidae*, the position of the body is strictly horizontal, the ventral valve resting on the substratum, and the peduncle emerging from an aperture near its centre, the shell resembles a circular disc (Fig. 39 *B*). Here, as in *Anomia*, among the Lamellibranchiata, there is a tendency to the development of a radial type of shell as a consequence of the attached manner of life. In the Oyster-like forms that fuse with the substratum (*Thecidium*, *Crania*), the divergence in the shape of the two valves reaches its highest limit. In one member of the *Productidae* (*Proboscidella*), the ventral shell-valve becomes lengthened by the growth of its frontal and lateral edges in such a way as to form a calcareous tube resembling that of *Aspergillum*. This form of shell may perhaps have arisen in adaptation to a boring or digging habit.

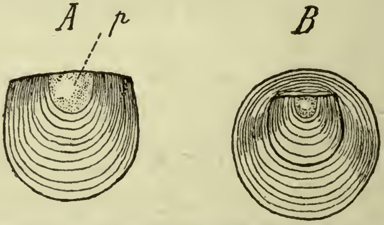

FIG. 39.—Two ontogenetic stages of the shell of *Orbiculoidea minuta* (after BEECHER). *A*, *Paterina*-stage. *B*, older stage. *p*, proteguIum.

With regard to the passage of the peduncle out of the shell, BEECHER has distinguished four different types:

I. **Atremata.** The peduncle passes out simply between the posterior edges of the two valves, retaining the direction of the axis of the body. *Lingula*, *Obolus*, *Paterina*.

II. **Neotremata.** The peduncle arises from the ventral shell-valve and stands at right angles to the axis of the body. It lies either in an incision of the ventral valve (*Schizocrania*), or becomes surrounded by the ventral valve as it grows, so that it then emerges from a subcentral orifice in the valve. *Orbiculoidea*, *Discina*, *Acrothele*. This group is perhaps nearly related to the *Craniidae*.

III. **Protremata.** The peduncle arises from a triangular deltidial slit in front of the beak of the large shell, which may either be open (*Orthis*, *Tropidoleptus*) or closed by a pseudodeltidium (*Orthisina*, *Leptaena*, *Strophomena*, *Chonetes*, *Strophaeodonta*). The *Thecidiidae* also belong here.

IV. **Telotremata.** The peduncle arises from a foramen perforating the beak of the ventral valve. The orifice from which it emerges is, as a rule, surrounded by a paired deltidium (*Spiriferidae*, *Atrypidae*, *Rhynchonellidae*, *Stringocephalidae*, and *Terebratulidae*). In these groups a calcareous brachial skeleton develops.

With regard to the development of the closing pieces of the beak-orifice known as *pseudodeltidium* and *deltidium*, little has been discovered. BEECHER, following up KOWALEVSKY's observations on *Thecidium*, traces back the pseudodeltidium to a skeletal secretion of the peduncle. During the metamorphosis of the attached larva, the two folds of the mantle are reflexed anteriorly (Fig. 40 *A*) and yield the first rudiment of the shell (the protegulum, *ds* and *vs*, p. 78), the line at which the reflexion of the valves took place indicates the hinge-line (*s*) of the protegulum. In *Thecidium*, the dorsal side of the peduncle-rudiment now also becomes covered with a skeletal secretion (*p*), which in later stages fuses with the growing beak of the ventral valve (Fig. 40 *B* and *C*) and becomes the pseudodeltidium. The true deltidium of the *Rhynchonellidae* and the *Terebratulidae*, on the contrary, is probably to be derived from the reflected parts of the mantle of the ventral shell-valve itself.

The two shell-valves, when they first appear, are completely separated from one another by the peduncle that emerges between them. They come into contact first at the outermost ends of the straight hinge-line (Fig. 36, p. 73), and at this point the first rudiments of the hinge-teeth develop. These already occupy the position they retain throughout life, lying at either side of the original hinge-aperture, and thus, later, near the deltidium. When the hinge-line, at a later stage, lengthens out laterally over the teeth, as is specially the case in *Orthis*, *Spirifer*, and *Strophomena*, this is a consequence of secondary processes of growth.

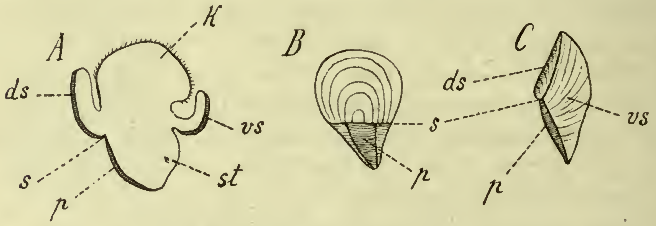

Fig. 40.—Development of the pseudodeltidium in *Thecidium mediterraneum* (after Beecher). *A*, metamorphosed larva of *Thecidium* with the first rudiments of the shell (after Kowalevsky). *B*, adult *Thecidium*, seen from the dorsal side. *C*, the same, seen in profile. *ds*, dorsal shell-valve; *k*, cephalic section; *p*, pseudodeltidium; *s*, hinge-line; *st*, peduncle; *vs*, ventral shell-valve.

IV. General Considerations.

A serious obstacle to our comprehension of the pelagic Brachiopodan larva, as represented typically by the *Argiope* larva, is to be found in the circumstance that the oral and anal apertures are here wanting, their absence making the orientation of the body-surfaces and segments extremely difficult and uncertain. We are inclined to homologise the ciliated ring at the edge of the cephalic section with the pre-oral ciliated band of the Annelidan *Trochophore*, although Kowalevsky's observation as to the rise of the oesophagus (p. 69) seems to contradict this view. The position of the neural plate would be indicated by the eye-spots (and in *Terebratulina*, Fig. 31 *B* and *C*, by a long ciliated tuft) on the cephalic pole of the larva. The anterior section of the body would thus possess characters in common with the *Trochophore*, and would be comparable to the cephalic lobe of the *Actinotrocha*.

In considering the significance of the posterior section of the body, we must institute comparisons with the larvae of the Bryozoa and of *Phoronis*. There can be no doubt that the point at which attachment takes place is identical in the Bryozoa and Brachiopoda, and corresponds to the posterior end of the body in the adult *Phoronis*. The fixation of the body is accomplished by means of the posterior pole of the body in the Brachiopodan larva; the pedal section passes over into the peduncle of the adult. Consequently, the cavity which is surrounded by the posteriorly projecting mantle-fold of the Brachiopodan larva is to be homologised only with the cavity within the so-called sucker of the Bryozoan larva. In the Bryozoa, also, that point of the sucker at which fixation first takes place forms a conical invagination in the main mass of the sucker (*cf.* the larva of *Bugula*, Fig. 9 *B*, p. 26). This conical portion would thus directly correspond to the pedal region of the Brachiopodan larva. This whole structure is evidently the equivalent of the invaginated ventral tube of the *Actinotrocha.* The aperture of this tube in the larva of *Phoronis* would be comparable to the aperture of the mantle-cavity in the *Argiope* larva. We can therefore without difficulty compare the Brachiopodan larva with an *Actinotrocha* in the later stages, in which the above tube-like invagination has already formed. The principal distinction between the two is the complete absence of the anal region in the Brachiopodan larva.

Here also metamorphosis commences (as in *Phoronis* and the Bryozoa) by the evagination of the formerly inturned part of the body through which fixation takes place.

We thus find that a comparison of larval forms leads us to regard the Brachiopoda as nearly related to *Phoronis* and to the Bryozoa, and that a comparison of the anatomy of the adult Brachiopoda with that of adults belonging to the two other groups gives a general confirmation to this view. The agreement between these groups is specially clear if we compare the tentacle-bearing lophophore in *Phoronis*, the Phylactolaemata, and the Brachiopoda. In the latter also, the lophophore is originally horseshoe-shaped, there is an integumental fold known as the epistome (Fig. 41, *ep*) above the mouth (brachial fold), and a lophophore-cavity not in any way communicating (?) with the rest of the body-cavity. We shall have to regard the so-called small brachial sinus (Fig. 41, *a*) of the Brachiopoda as the equivalent of the lophophore-cavity proper of the Phylactolaemata (circular canal of the Gymnolaemata) while the large brachial sinus (*b*) perhaps corresponds to the epistomal cavity.* Certain differences between the cavity in the lophophore

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* In comparing the large brachial sinus with the epistomal cavity of the Phylactolaemata, we shall have to bear in mind that the large arm-sinus, as has recently been pointed out by BLOCHMANN in *Crania*, is a paired structure, continuous in the median plane above the oesophagus. The median section (Fig. 41 *B*) represents the condition of the spiral arms laterally to the median plane. If we bear in mind the above-mentioned reservations, however, we shall be able to recognise in this diagram the agreement of the large brachial sinus with the epistomal cavity.

of the Brachiopoda and that of the Phylactolaematous Bryozoa have been pointed out by BLOCHMANN (No. 4). The chief of these is that, in consequence of the extension of the epistomal cavity (larger brachial sinus) in the Brachiopoda, the lophophoral cavity is so circumscribed as to be reduced to a canal running below the row of tentacles (smaller brachial sinus); this canal then appears to be cut through twice in transverse sections (*a*, *a′*) through the lophophore-arms, as also does the epistomal fold (brachial fold *ep*, *ep′*). These differences are, indeed, very easily explained through the higher differentiation which has arisen from the simpler type retained in the Phylactolaemata.

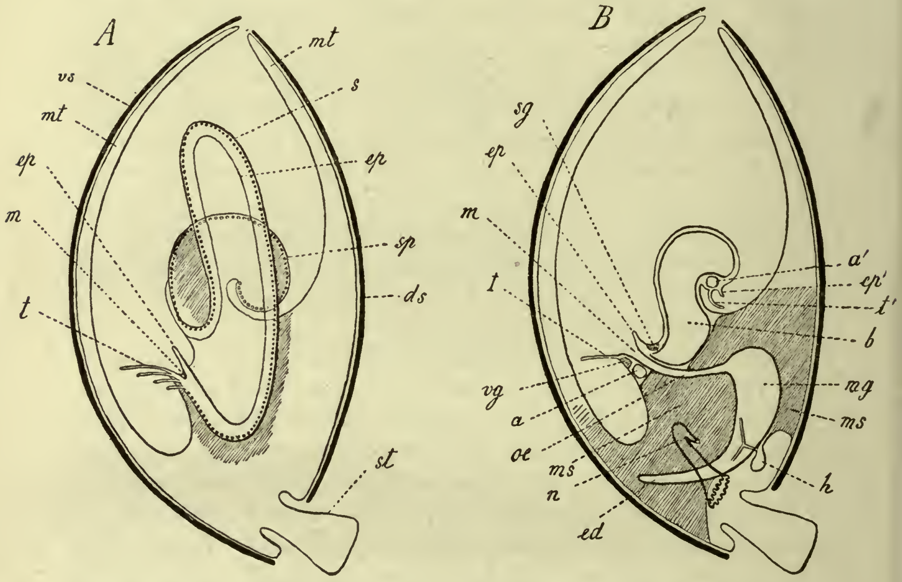

FIG. 41.—Diagram illustrating the structure of a Brachiopod (after preparations of *Terebratella corianica; cf.* Figs. 5, p. 9, and 28, p. 57). *A*, lateral view of the lophophore. Most of the tentacles are supposed to have been cut away. *B*, median section. The spiral arms are cut somewhat laterally to show the large brachial sinus. *a*, smaller brachial sinus; *a′*, the same in dorsal transverse section; *b*, larger brachial sinus (epistomal cavity); *ds*, dorsal shell-valve; *ed*, hind-gut; *ep*, epistome (brachial fold); *ep′*, the same in dorsal transverse section; *h*, heart; *m*, mouth; *mg*, stomach; *ms*, mesentery; *mt*, mantle-fold; *n*, nephridium; *oe*, oesophagus; *s*, lateral arm; *sg*, supra-oesophageal ganglion; *sp*, spiral arm; *st*, peduncle; *t*, ventral tentacle; *t′*, dorsal tentacle; *vg*, ventral ganglion; *vs*, ventral shell-valve.

From the condition of the lophophore and the position of the epistome it follows that the shell-valve, known as the *dorsal* valve, corresponds in position to the anal side of the body in the Bryozoa, although we should not be able to conclude this from the flexure of the alimentary canal (Fig. 41 *B*). We must here briefly return to the position of the anal aperture in the Ecardines. In *Lingula* and *Discina* the anus lies on the right side of the body, in *Crania*, as JOUBIN and BLOCHMANN have proved, in the median plane at the posterior end of the body. BLOCHMANN is inclined to regard this as a primitive condition. Since we, however, with CALDWELL, regard the posterior end of the body in the Brachiopoda (in view of the conditions prevailing in *Phoronis*) as in reality belonging to the ventral side of the body, we must consider the position of the anus in *Crania* also as secondarily modified. As a rule, in the Brachiopoda, the intestine is bent in the direction opposite to that which it assumes in the Bryozoa (*cf.* Fig. 41 *B*, with Fig. 28, p. 57). The external apertures of the nephridia also appear to have undergone shifting in the ventral direction. Such changes in the position of individual organs may, however, easily be explained by the crowding of the body between the two shell-valves. Although these displacements are a certain obstacle in the way of comparing the Brachiopoda with the Phylactolaemata and *Phoronis*, the general agreement between these forms (which is specially marked in the body-cavity and the nephridial system) is so great, that we can hardly doubt their close affinity. On this subject we refer the reader to the statements of BLOCHMANN.

Since STEENSTRUP and others first pointed out that the Brachiopoda are in no way related to the bivalved Mollusca (Lamellibranchiata), repeated attempts have been made to ally them more nearly to the Annelida, by laying undue weight on the agreement that exists between the two groups with respect to the condition of the body-cavity, genital organs, and nephridia in the Brachiopoda, and to regard them, when possible, as Annelida adapted to a sedentary manner of life. MORSE thus calls them "ancient cephalized Annelids," distinguishing them in this way from the sedentary Polychaetes (*e.g.*, *Serpula*), which he names "modern cephalized Annelids." We must therefore refer briefly to those characters which have been claimed as evidences of segmentation.

The division of the body of the larva into three or four regions is purely external, and, as far as is yet known, does not affect the coelomic sacs. BALFOUR pointed out that the order of appearance of the segments in the Brachiopodan larva differs from that prevailing in the Annelida. In the latter, the first segments to form are cut off from the posterior end of the body, while in the Brachiopoda the first segments become abstricted from the anterior part of the body. A consideration brought forward by CALDWELL seems of still greater importance. It is evident that in *Actinotrocha* the principal axis of the larva differs from that of the adult. In the larva, this axis runs from the neural plate to the anal aperture, and corresponds to that of the *Trochophore* and of the Annelid that develops from the *Trochophore*. In *Phoronis*, after metamorphosis, on the contrary, a secondary principal axis is met with at right angles to the primary axis of the *Actinotrocha*. The principal axis of the Brachiopodan larva, however, corresponds to the secondary axis of *Phoronis*, and runs from the neural plate to the point of attachment, which must be imagined as lying in the middle of the ventral side proper. When, therefore, segmentation takes place in a direction transverse to this principal axis, this cannot be compared to the segmentation of the Annelida, because the position of the latter is determined by the direction of another principal axis (the primary axis of an *Actinotrocha*). This example shows that the comparison with the *Actinotrocha* is of great utility in forming conclusions as to the Brachiopoda.

If we believe in the comparison of the Brachiopoda with *Phoronis* and the Bryozoa, in which two groups the short line lying between the mouth and the anus is to be recognised as the dorsal middle line, we shall be in agreement with CALDWELL, who considers that the two shell-valves in the Brachiopoda strictly speaking belong to the ventral side, and that here also attachment takes place at the middle of the ventral side.

We have seen that in the Brachiopodan larva there is no true segmentation, and this is also the case with the adult. The presence of two pairs of segmental organs in *Rhynchonella* is the strongest evidence that can be brought forward in favour of segmentation. Yet we know that in the Annelida more than one pair of segmental organs may occur in a segment, so that too great stress should not be laid on this feature alone. In the same way two pairs of nephridia also appear in *Phoronis australis* (BENHAM).*

There are many reasons for believing that the Ecardines must be regarded as the most primitive forms of the Brachiopoda. In this division a lateral anal aperture is retained in *Lingula*, and one lying posteriorly in the median plane in *Crania*. The peduncle in *Lingula*

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* [While pointing out that each of the two nephridia has a double opening into the body-cavity, BENHAM never commits himself to the assertion that there are two pairs of nephridia. He considers *Phoronis* as more closely allied to the Gephyrea than to the Bryozoa.—ED.]

is said often to be unattached and sunk into a sand-tube, so that in respect to this habit there is a marked similarity to *Phoronis.*

It should here be mentioned that a few zoologists have assumed a near relationship to exist between the Chaetognatha and the Brachiopoda, chief among these is van Bemmelen (No. 2), and the view has also been advocated by Bütschli,* O. and R. Hertwig (coelom-theory). These assumptions are based upon the agreement in the first stages of development, the rise of the coelom by folding, the development of three body-segments, and on those anatomical features common in the two groups as a consequence of the similar origin and nature of the enterocoele. The adult forms differ altogether in manner of life, and show essential differences of structure, the cephalic section especially being developed in an altogether different way in the two groups. Further, the Brachiopoda, in consequence of the agreement of the larva with the *Actinotrocha*, seem to be allied to the *Trochophore* type, while no such affinity has as yet been propounded for the Chaetognatha. The establishment of relationships between these two groups seems therefore to be still very doubtful, and their structural resemblances appear to be mere analogies. In any case it would only be possible to admit some very remote connection between the two.

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APPENDIX TO LITERATURE OF BRACHIOPODA.

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General Considerations on the Molluscoida.

As early as 1844, Henri Milne-Edwards (No. 11) pointed out the relationship existing between the Bryozoa and the Brachiopoda, and grouped them, with the Tunicata, as the "Molluscoida." In 1882, the true nature of the Tunicata having become known, Claus (No. 2) restricted the term Molluscoida to the Bryozoa and Brachiopoda. The near affinity between *Phoronis* and the Phylactolaemata was established chiefly by Caldwell (No. 1) and Ray Lankester

(No. 8). These two authors are inclined to claim for the *Sipunculidae* also affinity to these groups. A similar view has recently been adopted by EHLERS (No. 3) and ROULE (No. 12), the latter regarding the Brachiopoda, the Bryozoa, and the *Phoronidae* as a sub-group of the "Trochozoaires monomériques," and suggesting distant relationship to the *Sipunculidae*, the Molluscs, and the Rotifera. ROULE lays special stress on the Trochophoran characters of the Molluscoid larva. We ourselves have adopted the view of HATSCHEK (No. 6), who groups together the *Phoronidae*, the Bryozoa, and the Brachiopoda as Molluscoida, but excludes the *Sipunculidae* from the group. From all that is as yet known about the Entoprocta, we would, with HATSCHEK, separate them also from the Bryozoa and the Molluscoida generally. Further, according to the more recent researches made by McINTOSH, HARMER (No. 10), SPENGEL (No. 13), and EHLERS (No. 3) in connection with *Cephalodiscus*, and by FOWLER (No. 4) in connection with *Rhabdopleura*, these forms also must be removed from the group of the Molluscoida and probably grouped, as sedentary Enteropneusta, with *Balanoglossus.**

The union of the *Phoronidae*, the Bryozoa, and the Brachiopoda to form a sub-group rests chiefly on the structural resemblance of the adult forms. We have already repeatedly pointed out anatomical features possessed in common by these forms, and refer the reader to the diagrams given in Figs. 5 (p. 9), 28 (p. 57), and 41 (p. 80), which, when compared, reveal so uniform a fundamental type that we can only refer the agreement in structure found here to homology. The Molluscoida are provided with a true coelom, a body-cavity lined with a flattened epithelium which is often ciliated, and in which the intestine is suspended by mesenteries (these, in the Phylactolaemata, being replaced by the funiculus). Only in the Gymnolaemata is the lining of the body-cavity no longer epithelial, while strands of connective tissue traverse the so-called funicular tissue of the body-cavity. The dorsal region of the body appears shortened, the oral and anal apertures of the looped alimentary canal are consequently approximated, as is so often the case in tubicolous animals or those leading

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* [MASTERMAN's interpretation of *Actinotrocha*, if correct, shows that *Phoronis* must for the future be associated with *Cephalodiscus* and *Rhabdopleura*. It is now fairly well established that these genera are closely related with *Balanoglossus* to the primitive chordate stock, and have no affinities whatever to the Molluscoida. HARMER, who has worked at the development both of the Ento- and Ectoproctous Bryozoa, still retains them in one group and considers that they have no affinities with *Phoronis*. See HARMER and PROUHO, Appendix to Literature of Ectoprocta, Nos. III. and V.—ED.]

a sedentary life. For the divergent position of the anal aperture and the looping of the alimentary canal in the Brachiopoda, we refer the reader to p. 81. Among the most typical features of the Molluscoida are the peculiar development of the cephalic region, the presence of a horseshoe-shaped, tentacle-bearing lophophore having a distinct part of the body-cavity belonging to itself, the so-called lophophoral cavity (circular canal of the Gymnolaemata, smaller brachial sinus of the Brachiopoda), and the possession of a fold (epistome) above the mouth, into which another part of the body-cavity is continued (epistomal cavity, larger brachial sinus of the Brachiopoda). The relations of these parts of the body-cavity *inter se* and to the lower cavity which contains the intestine are in some respects still obscure. As centre of the nervous system, we have a ganglion lying above the oesophagus, which in the Brachiopoda, however, is less massive than the ventral ganglion. The excretory organs are represented by a pair of nephridia, which at the same time function as ducts for the genital products. (In *Phoronis australis* and in *Rhynchonella* there seem to be two pairs of nephridia; *cf.* on excretory organs of the Bryozoa, p. 56.)

While we thus find far-reaching anatomical agreement between the adults of the various divisions grouped as Molluscoida, the similarity between the larval forms and their metamorphosis is less evident. We shall, however, have to lay stress upon the fact that, in the larvae of the three types to be distinguished (*Actinotrocha*, Bryozoan, and Brachiopodan larvae), the posterior section, by means of which the fixation of the adult is accomplished, first appears in an invaginated condition. This invagination in the *Actinotrocha* (Fig. 4 *C*, *iv*, p. 7) which yields the body-wall of the posterior section of the body, may be homologised with the sucker-invagination of the Ectoprocta and with the pedal section of the Brachiopodan larva, which is sunk into the mantle-fold. If we maintain this homology, we shall have to proceed to explain the metamorphosis of the Molluscoida from the *Actinotrocha* as the most primitive larval form. The *Actinotrocha* type is distantly allied to the *Trochophore* larva, being distinguished from the latter chiefly by the presence of a true coelom. We have pointed out above (pp. 57 and 78) that the derivation of the Bryozoan and Brachiopodan larva from an Actinotrochan form still presents some difficulties. We may well feel inclined to compare the posterior end of the body, which in the Molluscoidan larva appears in an invaginated condition, and by means of which fixation takes place later, with the foot of the Mollusca. Although, from the position of the organs, such a comparison is admissible, yet there do not appear to be sufficient grounds for this homology.

The *Sipunculidae* show remarkable structural agreement with the *Phoronidae*, but this similarity may possibly be explained by a similar manner of life, and does not necessitate the assumption of a nearer relationship between the two groups. The larva of the *Sipunculidae* is closely allied to the Annelidan larva and shows the true *Trochophore* type, from which the *Actinotrocha* and the other Molluscoidan larvae are to some extent removed. It ought specially to be pointed out that the *Sipunculidae* agree with the Mollusca and the Annelida in the presence of two primitive mesoderm-cells which produce paired mesoderm-bands, while, in the Molluscoida, the origin of the mesoderm from the archenteron through folding is common. The rise of the coelomic sacs from the archenteron through folding is most clearly to be recognised in the Brachiopoda, but, in the Phylactolaemata also, the coelom must be understood to develop in this way, and the statements of CALDWELL as to the formation of the mesoderm in *Phoronis* are favourable to such a view, although the observations of ROULE do not appear to support it. Although we, as stated above in describing the development of the Chaetognatha, are not inclined to lay great weight on these differences in the formation of the mesoderm, the facts must be pointed out.

The shifting forward of the anus and the consequent shortening of the dorsal area lying between the mouth and the anus is brought about differently in the *Sipunculidae* (Vol. i., p. 363) and in *Phoronis*. In the *Sipunculidae*, the shifting of the anus is a consequence of very gradual alterations brought about by growth. The invagination which gives rise to the posterior end of the body in *Phoronis* is here altogether wanting. The principal point on which stress must be laid in comparing *Phoronis* and the *Sipunculidae* is the fact that the circle of tentacles surrounding the mouth has a different mode of origin in the two groups, so that the tentacles cannot be considered as homologous. In *Phoronis*, this row of tentacles can be traced back to a formation of lobes in the region of the post-oral ciliated ring. In the Sipunculid larva, on the contrary, according to HATSCHEK (No. 5; *cf.* Vol. i., p. 363), the post-oral ciliated ring has nothing to do with the origin of the tentacles which surround the mouth. The post-oral ciliated ring of the Sipunculid larva lies still further back, and corresponds to the anterior edge of the sphincter, which, after the proboscis-like anterior part of the head (the introvert) is withdrawn, closes the aperture of the invagination thus formed (Vol. i., Fig. 159, *rm*, p. 362).

It appears from the above, that the *Sipunculidae* cannot be brought into any near relationship to the Molluscoida. Since, after careful consideration of the facts of ontogeny, we agree with HATSCHEK (No. 6) in doubting the near relationship of the Molluscoida and the Entoprocta, we are unable to adopt the view of those zoologists who use the structure and development of *Pedicellina* for explaining the conditions of the Molluscoida. This latter view has recently been adopted by BARROIS, SEELIGER, DAVENPORT, and EHLERS. Among these, EHLERS approaches our standpoint, in so far as he also denies that the crown of tentacles in the Entoprocta is homologous with that in the Ectoprocta. For the reasons which compel us to exclude the Entoprocta from the Molluscoida, we must refer the reader to the following chapter (p. 101).*

The remarkable genera *Rhabdopleura* and *Cephalodiscus* have also repeatedly been brought into near relationship to the Ectoproctous Bryozoa and *Phoronis*. Meantime, the researches of HARMER, which have recently been confirmed by SPENGEL (No. 13),† and EHLERS (No. 3) have revealed a striking similarity of organisation between *Cephalodiscus* and *Balanoglossus*. Young buds of *Cephalodiscus* show a distinct division of the body into three consecutive regions, comparable to the proboscis-, collar-, and trunk-regions of *Balanoglossus*. These regions correspond to a similar number of sections in the coelom, the proboscis-cavity being simple and unpaired, while the cavities of the collar and the trunk are each divided by a mesentery into paired halves. In the adult *Cephalodiscus*, the proboscis-cavity is restricted to the interior of the large *oral disc*, which lies like an epistome above the mouth. This cavity, according to HARMER, opens externally through two pores (proboscis-pores) which perforate the anterior part of the nervous system (Fig. 42, *ex*). These pores would correspond to the proboscis-pore or pair of pores (*B. Kupfferi*, BATESON) of *Balanoglossus*. According to EHLERS, on the contrary, these pores represent the aperture of a special excretory organ, consisting of a canal (Fig. 42) which passes over into a wide terminal section lined with epithelium. The second section of the body-cavity also opens externally through two pores (collar-pores) beneath the apron-like fold, known as the *operculum*, which hangs down behind the mouth. To this region of the body

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* [In the foregoing account of the Bryozoa, considerable stress has been laid on the supposed relationship of the Ectoprocta to *Phoronis*. Such a connection is by no means recognised by all students of the Bryozoa. HARMER (Ectoprocta Lit., No. III.) does not consider that the Ectoprocta have any connection with *Phoronis*, and he would regard any structural resemblances as the result of coincidence rather than of close relationship. Both HARMER and PROUHO (Ectoprocta Lit., No. V.) regard the Ectoprocta and the Entoprocta as nearly related.—ED.]

† *Cf.* SPENGEL'S monograph on the Enteropneusta, p. 753, etc. Prof. SPENGEL was kind enough to show us a number of drawings made from his preparation of *Cephalodiscus*. These confirmed in all essential points the statements of HARMER.

belongs the chief part of the central nervous system (n), which lies on the dorsal side continuous with the ectodermal epithelium, and at its anterior part is continued into the proboscis-region. Connected with the anterior part of the collar-region, on either side of the proboscis, are six biserial pinnate tentacles (t), each with a terminal knob, and into these the collar-cavity is continued. Further back are the pigmented apertures of the paired sac-like genital organs (g). The alimentary canal forms a dorsal loop, and the anus (a) is displaced far forward. The most anterior section of the alimentary canal shows a pair of lateral apertures, the so-called gill-slits (sp), and an antero-dorsal diverticulum (x, notochord), which lies below the nervous system and extends into the proboscis. The body of *Cephalodiscus* is provided with a stalk, but the individuals are able to move about freely within the common gelatinous coenoecium. The conditions of budding resemble those in *Loxosoma*. FOWLER'S more recent researches have revealed a considerable agreement between *Rhabdopleura* and *Cephalodiscus*. Here also the intestinal diverticulum known as the notochord is found, as well as a pair of collar-pores, while the branchial clefts and proboscis-pores are not to be recognised. From all that is known, it appears that these genera are nearly related to *Balanoglossus*, while no connection with *Phoronis* and the Bryozoa can be proved to exist,* since, as shown by LANG (No. 7), the agreement in structure between these forms can easily be shown to result from similarity in their manner of life.

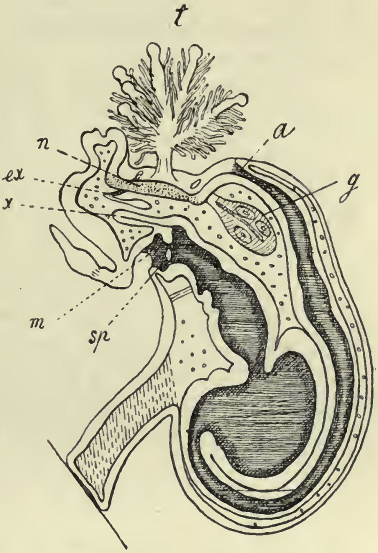

FIG. 42.—Diagrammatic median section through *Cephalodiscus* (after EHLERS, combined from McINTOSH and HARMER). a, anus; ex, excretory organ (proboscis-pore); g, genital gland; m, mouth; n, nervous system; sp, gill-slit; t, tentacle; x, intestinal diverticulum (notochord of authors).

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* [MASTERMAN'S researches on *Actinotrocha*, if confirmed, would show that *Phoronis* is undoubtedly nearly related to *Cephalodiscus* and its allies.—ED.]

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CHAPTER XVIII.

ENTOPROCTA.

The group of the Entoprocta, which, although small, is rendered of interest by the possession of many structural and developmental peculiarities, has hitherto usually been united with the Ectoproctous Bryozoa, but it is doubtful if the two should be connected. Of the forms belonging to this group, *Pedicellina*, and nearly allied genera such as *Pedicellinopsis*, *Ascopodaria* (*Barentsia*), etc., and, further, *Urnatella*, form colonies, but in *Loxosoma*, the buds do not remain connected with the parent, but become detached, so that in this genus only solitary individuals are met with in the adult condition.

Our knowledge of the embryonic development of *Pedicellina*, apart from older statements, is principally due to the researches of Hatschek (No. 6), and Harmer (No. 5). The ontogeny of *Loxosoma* has more recently been described by Harmer (No. 4), whose results agree in essential points with those of Hatschek.

The eggs of *Pedicellina* are fertilised while still in the ovary. The embryonic development takes place within the vestibule of the female,* which is transformed into a brood-cavity, the epithelium of which appears to become thickened and glandular for the nourishment of the embryos (Ehlers, No. 2). These are attached to the wall of the brood-cavity by the pointed end of the elongated, pear-shaped egg-envelope (a secretion of the epithelium lining the oviduct). The young larvae, when hatched, still remain in the brood-cavity, and are said to be attached to its wall.

In the granular and somewhat opaque spherical egg of *Pedicellina*, enclosed in its vitelline membrane, a somewhat clearer animal pole can be distinguished, near which lies the germinal vesicle. Cleavage is, as a rule, total and unequal, but approaches the equal and regular

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* *Pedicellina echinata* is hermaphrodite. In other species the sexes appear to be separate. [According to Harmer, *Pedicellina* is sometimes dioecious and sometimes monoecious, and *Loxosoma* is perhaps always dioecious.—Ed.]

type. It is, however, not altogether regular, since the two-celled stage, at which the two blastomeres are not quite equal in size, is followed first by a three-celled stage, and only later by one showing four cells, this latter stage being reached by the separation from each of the two primary blastomeres of a somewhat smaller cleavage-sphere, near the animal pole. As the blastomeres of the animal pole now rapidly increase in number, and a central cavity appears, a blastula stage arises (Fig. 43 *A*); in this, the cells of the vegetative half are remarkable for their size and granular character.

Further development leads to a formation of a true invagination gastrula (Fig. 43 *B*). The vegetative half of the embryo first flattens and then becomes invaginated towards the animal pole, the cleavage-cavity consequently being almost obliterated. The blastopore closes in the form of a longitudinal slit corresponding to the median plane, and to the middle of the future ventral surface. A flattening of the ventral side can already be noticed (Fig. 43 *C*). At that end of the slit-like blastopore which can be directly observed to give rise to the posterior or anal end of the adult, two symmetrically placed cells (*me*) now appear; these have retained the primitive character of cleavage-spheres, and are not yet externally covered by the ectoderm. These are the *primitive cells of the mesoderm.* They are soon completely grown over by the ectoderm (Fig. 43 *C*), and then lie in a space between the ectoderm and the entoderm, which is derived from the cleavage-cavity, and is considered to be the primary body-cavity. This cavity develops further during the following stages, and gradually becomes filled with mesodermal elements.

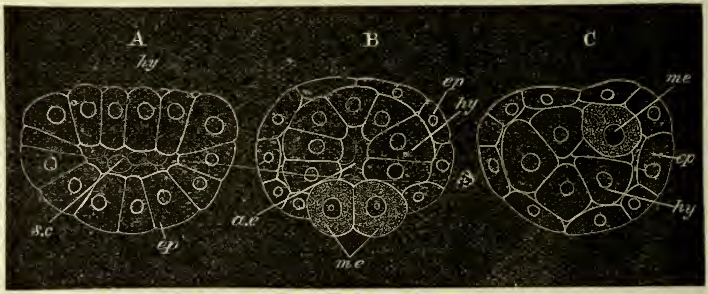

Fig. 43.—Three stages in the embryonic development of *Pedicellina echinata* (after Hatschek, from Balfour's *Text-book*). *A*, blastula stage preparatory to gastrulation. Optical section seen from the side. *B*, gastrula-stage. Optical section from above. *C*, later stage, after the closing of the blastopore, seen from the side. *a.e*, archenteric cavity; *ep*, ectoderm; *hy*, entoderm; *me*, mesoderm cells; *s.c*, cleavage-cavity.

During the next stages the development of the definitive form of the body takes place. The embryo lengthens at right angles to the flattened ventral side (Fig. 44). At the same time the ectoderm thickens over this ventral region, and thus assumes the form of a disc which, at its edge, is sharply marked off from the rest of the ectoderm, and later sinks in to form the vestibule. In the anterior half of this disc an invagination appears which soon becomes lined with ciliated cells (Fig. 44, *oe*); this is the rudiment of the oesophagus. At a somewhat later stage another similar invagination develops from the posterior part of the disc (Fig. 44 *B*, *an.i*); this is the rudiment of the hind-gut, which at first is a solid, inwardly projecting ectodermal thickening. The oesophageal invagination soon becomes connected with the rudiment of the mid-gut (Fig. 45 *A*). The establishment of communication between the mid-gut and the hind-gut, and the acquisition of an external aperture by the latter, occur only in the later stages (Fig. 45 *B*).

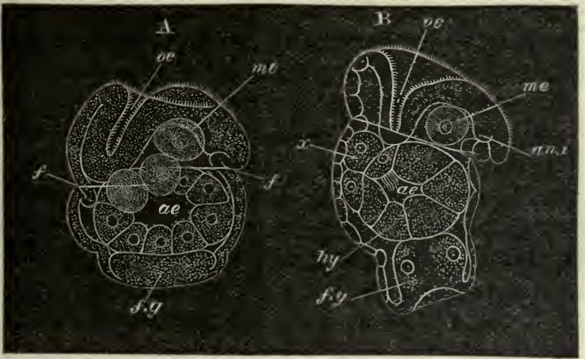

Fig. 44.—Two later stages in the development of *Pedicellina* (after Hatschek, from Balfour's *Text-book*). *ae*, archenteron; *an.i*, anal invagination; *f*, ectodermal fold; *f.g*, ciliated disc; *oe*, oesophagus; *x*, dorsal organ.

The mesoderm-cells, meantime, have increased in number, the proliferation of the two pole-cells leading first to the formation of two short mesoderm-bands. Two larval organs specially characteristic of *Pedicellina* also appear. One of these, which we shall call the *ciliated disc* (Figs. 44 and 45, *fg*), is an ectodermal thickening which lies apically and consists of large glandular cells, its margin being beset with stiff cilia. The other larval organ, which is known as the *dorsal organ* (Figs. 44 and 45, *x*), lies on the anterior side of the cup-like aboral wall of the larva, and consists of a rather deep ectodermal depression, part of the anterior section of which can be evaginated.

In the comparison which has often been made between the *Pedicellina* larva and the larvae of the Ectoprocta (especially with *Cyphonautes*), these two provisional organs have played a conspicuous part. The ciliated disc has usually been regarded as the homologue of the retractile disc of the Ectoprocta. Like the latter, it is retractile, and seems to function as a sensory organ. This, at least, seems to be proved by the observation that the larva of *Pedicellina*, when swimming, always carries this organ directed forward. The structure of the

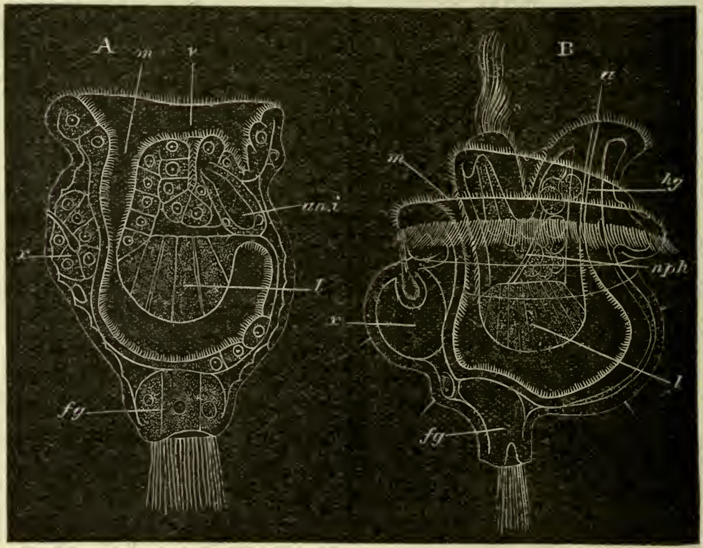

FIG. 45.—Two later stages in the development of *Pedicellina* (after HATSCHEK, from BALFOUR'S *Text-book*). *a*, anus; *an.i*, anal invagination; *fg*, ciliated disc; *hg*, hind-gut; *l*, liver; *m*, mouth; *nph*, nephridium; *v*, vestibule; *x*, dorsal organ.

dorsal organ might lead us to conclude that it was homologous with the pear-shaped organ of the Ectoprocta, but the difference in the position of the two organs relative to the ciliated ring must be taken into consideration, and such a comparison must be made with caution. The organ under consideration lies in the one case in the aboral, and in the other in the oral region. In consequence of the difficulties which, according to the most recent researches, stand in the way of comparing *Pedicellina* and the Ectoprocta (p. 101), it must be regarded as doubtful whether we are in any way justified in searching for homologies of this kind between the larvae of the two groups.

The *dorsal organ* (Figs. 44 and 45, *x*) has, up to the present, been interpreted in very various ways. HATSCHEK, who thought that he had convinced himself that an entodermal sac derived from the rudiment of the mid-gut passed into the formation of this organ, assumed it to be the first bud that attains development in the larva. According to the more recent researches of HARMER (No. 5) and SEELIGER (No. 12), however, it can no longer be doubted that the rudiments of the buds only appear later, after attachment has taken place, and in another way, and that therefore HATSCHEK's view was erroneous. HARMER, who traced the origin of the similarly formed, bilobate, dorsal organ of *Loxosoma*, which is provided with two pigmented eye-spots, explains it as a brain (supra-oesophageal ganglion) arising through an ectodermal invagination and connected with a sensory apparatus, and, further, united by fibrous commissures with the ganglion that develops between the mouth and the anus. The latter is assumed by HARMER to be the sub-oesophageal ganglion (comparable to the pedal ganglion of the Mollusca).

In the later stages, the cup-like cavity known as the atrium or vestibule (Fig. 45 *A*, *v*) forms in the *Pedicellina* larva, the oral ciliated surface becoming more and more depressed. The floor of the cavity thus formed soon shows a deep depression extending between the mouth and the anus (Fig. 45 *A*), from the wall of which the sub-oesophageal ganglion is said to originate as a simple thickening of the ectoderm (HARMER). The lateral walls of this depression separate it from an outer groove in the floor of the vestibule; this latter groove runs round the anal cone and passes over anteriorly into the funnel-shaped oral aperture. This groove corresponds to the tentacle-groove of the adult. The outer thickened edge of the cup that has thus arisen now becomes separated by a furrow from the rest of the body-surface, and develops a massive ciliated ring (Fig. 45 *B*), which functions as the locomotory organ of the larva.

As the muscle-fibres develop, the different parts of the body become markedly retractile. The floor of the vestibule, especially, can be protruded far beyond its aperture and again withdrawn. When the larva is in the condition of greatest expansion, two conical processes can be seen projecting from the aperture of the vestibule (Fig. 45 *B*). The posterior cone carries at its apex the anal aperture (*a*, anal cone), while the anterior process is distinguished by a tuft of long flagella; this latter process has the same position as the epistome, as it lies behind the oral aperture at the anterior edge of the deep depression mentioned above.

A feature of morphological importance is the presence of an excretory apparatus (*nph*) consisting of two small ciliated canals which, in position and structure, agrees with that of the adult (Fig. 48, *ex*). We may compare this with the head-kidney of the *Trochophore* larva of the Annelida. It opens externally at a point between the epistome and the ganglion.

The structure of these excretory canals has been repeatedly investigated in the adult of *Loxosoma*, *Pedicellina*, and *Ascopodaria*, a certain importance being attributed to these forms in connection with the significance of this organ as the head-kidney (protonephridium, Hatschek). The results of these investigations must not as yet be regarded as conclusive. While Harmer, Foettinger, and Hatschek regard the cells of this organ as perforate, and its lumen thus as being intracellular, Ehlers, and more recently Prouho (No. 9), do not agree with this view. According to the latter authors, the lumen of the canal lies between the cells. According to Ehlers, the canal ends blindly internally, but does not, as Harmer stated, terminate with a flame-cell. The most recent investigator of this subject (Prouho) even throws doubt on the blind termination of the internal end. According to Foettinger and Ehlers, the two canals unite to form a common unpaired duct opening by a single aperture.

Metamorphosis.

According to the statements of the older investigators (P. J. van Beneden and others), the fixation of the *Pedicellina* larva seemed to take place by means of the ciliated disc. This organ was then said to pass over into the pedal gland of the *Loxosoma* stage. It was therefore usually called, even in the larva, the "cement-gland, or sucker," or received some other similar appellation. Metamorphosis would then simply have consisted in the growing out of the apical part of the larva as the peduncle, while the organisation of the adult would be attained by the budding out of tentacles in the vestibule. On the other hand, the more recent researches of Barrois (No. 1), which were confirmed by Harmer (No. 5), have revealed the surprising fact that the fixation of the larva takes place, as in the Ectoprocta, at the oral side, by means of the edge of the vestibule. During fixation the larva is in its most retracted condition (Fig. 46 *A*), even the cell-row of the ciliated ring being withdrawn into the vestibule. The aperture of the latter is very much narrowed, and soon closes completely, and its marginal cells fuse (Fig. 46 *B*). In this way the vestibule becomes a sac closed on all sides.

In the course of further metamorphosis, the body of the larva changes in shape. The lower part narrows somewhat to form the future peduncle (Fig. 46 *B* and *C*), while the upper part swells out into the head, this swelling being at first more marked posteriorly. The body in this way becomes almost pipe-shaped (Fig. 46 *C*). At the same time the alimentary canal, together with the vestibule, changes its position, its posterior portion shifting upwards. The stomach, the principal axis of which originally lay horizontally, has now assumed a more oblique position, which finally passes into a perpendicular position. The oesophagus then lies below, while the hind-gut with the anal aperture (*a*) lies above. These two parts of the alimentary canal, the oesophagus and the hind-gut, now lie almost horizontally.

While the intestine has shifted in the way just described, the vestibule has considerably lengthened (Fig. 46 *B*). At a later stage only a part of this cavity is retained, the lower part, lying in the peduncle, disintegrating through histolysis of its walls. Further disintegration and histolysis take place also in other parts of the vestibule and of the intestinal wall. These broken down cell-masses are found in numbers in the lumen of the vestibule and in the stomach. These processes, however, do not here lead to the destruction of the whole organ, but only affect the portion nearest the peduncle. The two larval organs, the dorsal organ (*d*) and the ciliated disc (*w*), on the contrary, are completely destroyed.

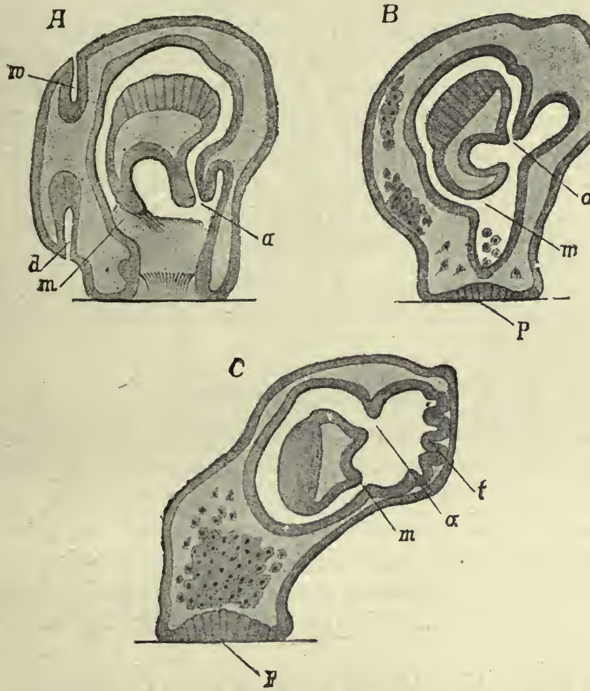

Fig. 46.—Three stages in the metamorphosis of *Pedicellina* (after Harmer). *A*, larva just attached. *B*, commencement of the rotation of the alimentary canal, and partial disintegration of the organs. *C*, the breaking through of the vestibular aperture and the development of the tentacles (*t*). *a*, anal aperture; *d*, dorsal organ; *m*, oral aperture; *p*, pedal gland; *t*, rudiments of tentacles; *w*, ciliated disc (sucker of Harmer).

After the rotation of the intestinal canal round its transverse axis, above described, has taken place, the vestibule develops a new external aperture, its outer wall fusing with the inner surface of the body-wall, and a slit-like fissure arising at the point of fusion. In close proximity to this perforation of the wall, the rudiments of the first tentacles (Fig. 46, *t*) appear as outgrowths of the vestibular wall extending into the vestibular cavity.

The stage in the development of *Pedicellina* attained by means of these transformations recalls the appearance of certain species of *Loxosoma* in the oblique position of the vestibular aperture, and the presence of a pedal gland (*p*) which has arisen as an ectodermal thickening. Only later are these characters lost, the head becoming more distinctly marked off from the peduncle and assuming an upright position, the aperture of the vestibule being apical. During the histolysis of the inner organs, many of the isolated cells pass into the body-cavity; these are gradually absorbed, and the cavity then appears filled with star-shaped mesenchyme cells.

The metamorphosis of the larva of *Loxosoma* still remains unknown. There can, however, be no doubt that it is in essential agreement with that here described for *Pedicellina.*

Asexual Reproduction.

Asexual reproduction through the *formation of buds* plays an important part in the life-history of the Entoprocta. In *Loxosoma* the buds arise in large numbers at the ventral side of the cup, on either side of the parent-animal. The buds here seem to form alternately, those of the right side alternating in age with those of the left. When the buds have attained a certain grade of development they become detached, and continue their lives as solitary individuals.

In *Pedicellina echinata*, the formation of new buds takes place from a basal stolon; since the buds retain their connection with the parent, colonies of variable size develop. These colonies are essentially bilaterally-symmetrical in their development. The stolon forms from the lower end of the peduncle of the oldest individual, on its anal side (Seeliger). The buds are arranged on the stolon in such a way that the median plane in them corresponds with that in the parent-animal. The youngest buds are found at the growing end of the stolon. Each bud develops on the oesophageal side of the bud next older than itself. In rare cases a lateral branching of the stolon has been observed in *Pedicellina echinata* (Seeliger, Ehlers). In other forms (*Ascopodaria*), such branching is common.

The stolon is formed by the simple growth of the two germ-layers present in the peduncle, *i.e.*, the ectoderm and the mesenchyme (Harmer, Seeliger). Consequently the buds formed on the stolon also owe their origin exclusively to these two germ-layers. Hatschek's view that, in addition to these constituents, an entoderm-sac also enters into the formation of each bud, this sac having arisen by abstriction from the mid-gut rudiment of the next older individual, must, according to Harmer and Seeliger, be regarded as erroneous. According to these two authors, the formation of the buds recalls that of the polypides of the Ectoprocta. The first rudiment of the bud is a bulging caused by the growth of the two germ-layers (Fig. 47 *A*, *st*), an ectodermal invagination soon forming at the apex of this swelling (Fig. 47 *B*). The sac which has thus arisen soon becomes divided by constriction into two parts (Fig. 47 *A*), the larger outer part representing the rudiment of the vestibule (*a*), and the smaller inner part that of the whole alimentary canal (*i*). In this case, as in the Ectoprocta, the mid-gut has not an independent entodermal origin. The point at which communication between the two parts of the sacs is retained becomes the future oral aperture, while the development of the hind-gut and of the anal aperture follows only later. In this respect the formation of buds in the Entoprocta deviates from that in the Ectoprocta, where the anal communication of the vestibule with the mid-gut is the first to be established (p. 40). An ectodermal invagination which forms at the base of the vestibule, between the oral and anal apertures, gives origin to the ganglion, which, as a

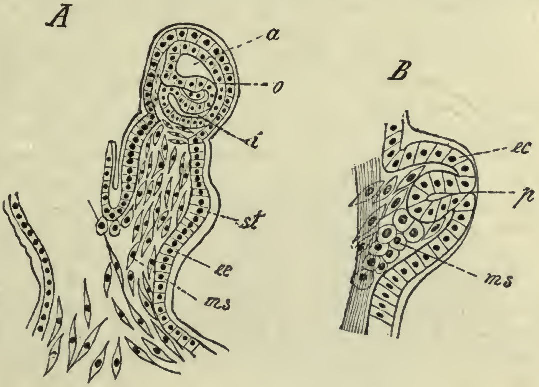

Fig. 47.—Budding in *Pedicellina* (after Seeliger). *A*, portion of a stolon with a very young rudiment of a bud (*st*) and an older rudiment in which can already be seen the separation of the vestibule (*a*) and the intestinal rudiment (*i*). *B*, bud, with simple polypide-invagination (*p*, common rudiment of the vestibule and the alimentary canal). *a*, vestibule; *ec*, ectoderm; *i*, rudiment of intestine; *ms*, mesenchyme: *o*, mouth; *p*, polypide-rudiment; *st*, young bud-rudiment.

solid cell-mass containing within it a dense network of fine nerve-fibrils (Punkt-substanz), soon becomes detached from the ectoderm. The tentacles arise as outgrowths projecting into the vestibule.

The voluntary throwing off of the head, and its subsequent regeneration from the end of the peduncle, has also recently been more carefully investigated by Seeliger. Extensive processes of degeneration occur in the "head" before it is separated. The end of the peduncle, after the detachment has taken place, shows the same composition out of two germ-layers which was found in the stolon, and the development of the new "head" actually takes place under exactly the same conditions and by just the same processes as the development of the buds on the stolon. The spontaneous throwing off of the "head" and its regeneration recall the degeneration and new formation of the polypides in the Ectoprocta.

The budding in *Loxosoma* takes place, according to Seeliger (No. 13), in just the same way as described above for *Pedicellina*. Here also an ectodermal invagination yields the common rudiment of the vestibule and the alimentary canal, while the mesoderm is derived from the immigrating mesenchyme-cells of the parent-animal. As a rule, the young bud projects early as an outgrowth om the parent, but there are certain modifications in the manner in which the buds are attached in the different species. While, in *Loxosoma singulare*, *Raja*, *cochlear*, and *phascolosomatum*, the buds appear attached to the parent by the peduncle, in *L. Kefersteinii*, according to Nitsche and Claparède, the attachment to the parent is in the region of the dorsal side of the bud at the boundary between the peduncle and the trunk. The peduncle therefore does not here grow out as a free projection from the body. According to Prouho, the budding in *Loxosoma (Cyclatella) annelidicola* is at first internal, the young bud developing in an ectodermal depression forming a kind of amniotic cavity. The buds appear to develop in the same way in *Loxosoma Raja;* this fact led O. Schmidt to trace back the formation of buds in *Loxosoma* to a parthenogenetic development.

General Considerations.

In treating of the affinities of the Entoprocta, we must start with the free-swimming *Pedicellina* larva. This larva may, without much difficulty, be traced back to the *Trochophore* type. The ciliated rings of the *Pedicellina* larva would then correspond to the pre-oral ciliated ring of the *Trochophore*, while the region lying behind the ring becomes invaginated to form the vestibule. In such a comparison, we have to regard the short line extending between the oral and the anal apertures as the ventral median line of the Entoproctous larva, the correctness of this view being confirmed by the position of the blastopore.

In comparing the Entoproctous larva with the *Trochophore*, we have left the apical plate out of consideration. Whether Harmer's view that the dorsal organ (x) is the brain of the larva and the equivalent of the apical plate is sufficiently corroborated by the facts to be observed, must be left to the decision of future investigators. Beside the points of agreement with the *Trochophore*, the Entoproctous larva shows many points of comparison with the Ectoprocta, which may also be traced back to the *Trochophore* type. We have, however, already shown (p. 94) that such a comparison meets with considerable difficulties in the details of the organisation of the two larvae.

It is of great importance for a comprehension of the adult *Pedicellina* (Fig. 48) that we should carefully consider the metamorphosis of the larva, made known by BARROIS and HARMER. Such an examination shows that the relative positions of the mouth, the anal aperture, the alimentary canal, the ganglion, and the nephridial canals undergo no alterations during metamorphosis. This latter consists solely in the rotation of the whole complex of organs now under consideration round a transverse axis. The vestibule alone undergoes any considerable change, part of it being dilated and part degenerating, a new aperture also forming. It thus results, from a careful consideration of the metamorphosis of *Pedicellina*, that the adult is here at essentially the stage of organisation of the *Trochophore*. We are thus compelled to regard the short line extending from the mouth to the anal aperture in the adult Entoproctan as the ventral median line, for this still directly corresponds to the region at which the slit-like blastopore closed. We must, then, for the sake of consistency, regard the ganglion lying at this point (n) as a sub-oesophageal ganglion belonging to the ventral side. In the same way, we would then, perhaps, be able to trace back the ring of tentacles (t) of the adult to the pre-oral ciliated ring of the larva.

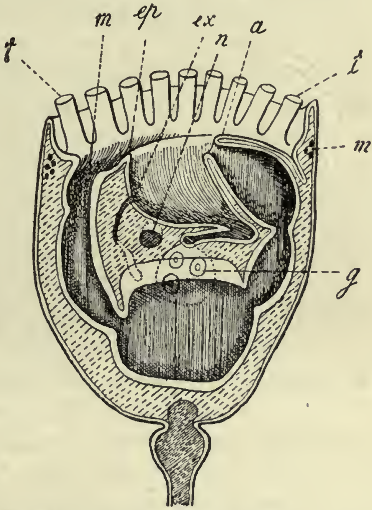

FIG. 48.—Diagrammatic median section through an adult *Pedicellina* (after EHLERS). *a*, anus; *ep*, epistome-like oral fold; *ex*, excretory organ; *g*, genital organ; *m*, mouth; *ms*, fibres of the sphincter muscle; *n*, nervous system; *t*, tentacles.

The above considerations seem to show that the Entoprocta, in spite of many remarkable points of agreement, cannot in any way be compared with or combined into the same group as the Bryozoa (Ectoprocta). We regard them as an entirely independent group, and in this respect agree with HATSCHEK

(Lehrb. d. Zool., p. 40). Just as surely as the orientation given above seems established for the Entoprocta, does that entirely different interpretation of the Ectoprocta, supported by a comparison with *Phoronis*, seem justified. In this group the oral and anal apertures are dorsal, the ganglion is supra-oesophageal, and the ring of tentacles is post-oral. The ganglia and the crown of tentacles would thus not be homologous in the two groups. If other divergences of structure be added (the want of a body-cavity in the Entoprocta, the position of the anal aperture, the characteristic nephridia formed on the type of the head-kidney), sufficient grounds are found for completely separating the Entoprocta from the Ectoprocta.

We must, however, bear in mind the fact that the foundation upon which the above view of the systematic position of the Entoprocta rests, contains a considerable number of hypothetical elements. Among the decisive reasons for separating the Entoprocta from the Ectoprocta are two observations of a very difficult nature (that of the metamorphosis and that of the structure of the nephridia), and, from these, errors may not altogether have been excluded. Until further corroborating investigations have been made, any attempts to decide the affinities of the Entoprocta must be regarded as provisional. We have, therefore, appended them to the Molluscoida, though as an independent group.*

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* [In the foregoing account of the Bryozoa, considerable stress has been laid on the supposed relationship of the Ectoprocta to *Phoronis*, and, as a consequence, the Ectoprocta are completely severed from the Entoprocta. These conclusions are by no means accepted by all students of the Bryozoa. Harmer (Ectoprocta Lit., No. III.) does not consider that the Ectoprocta have any connection with *Phoronis*, and he would regard any structural resemblances as the result of coincidence rather than of close relationship. Both Harmer and Prouho (Ectoprocta Lit., No. VI.) regard the Ectoprocta and the Entoprocta as nearly related.

An important article dealing with the Bryozoa has recently appeared in Sedgwick's *Text-book of Zoology* (1898). Here the whole question as to the morphology and relationship of the Bryozoa is discussed, and Harmer's conclusions are adopted. Important criticisms of our authors' interpretation of the surfaces of the adult and larval Ectoprocta are given.—Ed.]

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CHAPTER XIX.

CRUSTACEA.

Systematic :—

- A. ENTOMOSTRACA.
  - *a.* Phyllopoda
    - I. Branchiopoda
      - *Apus*, *Branchipus*, *Estheria*.
    - II. Cladocera.
  - *b.* Ostracoda.
  - *c.* Cirripedia.
  - *d.* Copepoda
    - I. Eucopepoda
      - 1. *Gnathostomata.*
      - 2. *Parasita.*
    - II. Branchiura (*Argulus*).
- B. MALACOSTRACA.
  - *a.* Leptostraca (*Nebalia*).
  - *b.* Thoracostraca (Podophthalmata).
    - I. Schizopoda (*Euphausia*, *Mysis*).
    - II. Decapoda
      - 1. *Macrura.*
      - 2. *Anomura.*
      - 3. *Brachyura.*
    - III. Stomatopoda.
    - IV. Cumacea.
  - *c.* Arthrostraca (Edriophthalmata).
    - I. Anisopoda (*Tanais*, *Apseudes*).
    - II. Isopoda.
    - III. Amphipoda.

The Development of the Embryo.

1. Oviposition, Care of the Brood.

The eggs of the Crustacea are, as a rule, spherical in form, although in a few cases they are somewhat ellipsoidal (*Oniscus*, *Gammarus*, *Ligia*, *Palaemon*, *Atyephyra*, *Crangon*, etc). Where the eggs are crowded together in a brood-cavity (*e.g.*, in the Arthrostraca), their shape, during the first stages of development, may be rather irregular, on account of mutual pressure.

It has been observed that, in various Crustacea, the female undergoes ecdysis before laying the eggs. This is the case with some Cladocera before the laying of the summer eggs (JURINE, GROBBEN), also with *Gammarus* (DELLA VALLE) and *Atyephyra* (ISCHIKAWA).

The adaptations for the protection of the eggs vary greatly. The eggs are laid singly (*Cypris* among the Ostracoda and *Cetochilus*, *Dias*, *Centropages* among the Copepoda), or in bands (*Argulus*), or united into masses (Stomatopoda). The winter eggs of many of the Cladocera are either, when laid, enclosed merely in their own envelopes, or are further protected by a cuticular, saddle-shaped structure, the so-called *ephippium*, which is a cuticular thickening of the dorsal integument of the brood-chamber of the mother. The summer eggs of this sub-order, on the contrary, undergo their entire development within a brood-cavity, covered by the shell of the mother, and a similar cavity shelters the eggs of the *Notodelphyidae* (Copepoda) whilst they undergo development. In the Branchiopoda there are many different adaptations for the protection of the eggs, which are carried about by the mother until they reach a certain stage of development. In *Apus*, for example, the eggs are carried in a watch-glass-shaped receptacle formed by processes of the eleventh pair of limbs; in *Branchipus*, in a pocket-like cavity of the abdomen; in *Estheria*, they are attached to filamentous appendages of the ninth and tenth pairs of legs, situated between the valves of the mother's shell. They are only deposited in the mud after the formation of the blastoderm is completed and the outer germ-layer has developed. Whereas, in the Ostracoda, the eggs are, as a rule, laid singly (*Cypridae*), in *Cypridina*, they are retained within the shell of the mother until they are hatched; this is also the case in the Leptostraca (*Nebalia*) and in the Cirripedia. In the latter, the eggs are cemented together in lamellae (*Lepadidae*) or enclosed in branched ovisacs (*Rhizocephala*). In the Copepoda, except in the cases just mentioned (*Cetochilus*, *Notodelphyidae*), the eggs are carried in ovisacs formed by a secretion of a special cement-gland, and are attached to the genital segment. In the Arthrostraca, Cumacea, and *Mysidae*, the eggs lie in a brood-chamber on the ventral side of the thorax, externally protected by lamellate appendages (*oostegites*) of the coxal joints of the thoracic limbs belonging to this region. In the Decapoda, on the contrary, the eggs are usually attached to the limbs of the abdominal segments (*pleopoda*) by means of the secretion of a special cement-gland.

2. Cleavage and Formation of the Blastoderm.

The Crustacean egg is, as a rule, distinguished by the large amount of food-yolk contained in it. The latter consists of spherical particles interspersed with fat-drops. In most cases the food-yolk is found equally distributed throughout the egg, although, as a rule, the yolk-spherules are of smaller size at the surface of the egg. In a few cases, in eggs that contain less nutritive yolk, a superficial layer of protoplasm (formative yolk) is developed (*e.g.*, many Cladocera and *Cetochilus*). As a rule, part of the formative yolk is evenly distributed between the particles of food-yolk, while the rest is massed near the first cleavage-nucleus. Rarely, as in *Moina*, the polar differentiation of the egg is made evident by the unequal distribution of the food-yolk, which accumulates in the vegetative half of the egg. In *Moina* also, the first cleavage-nucleus is found (as also in *Cetochilus*) not exactly in the centre of the egg, but in an excentric position, somewhat nearer the animal pole. The first cleavage-nucleus usually lies, together with an accumulation of protoplasm, near the centre of the egg; and even in those forms (*e.g.*, *Mysis*) in which discoidal cleavage takes place, it originally occupies a similar position.

The Crustacean egg, after the ejection of the polar bodies and subsequent fertilisation, is usually at first surrounded by a homogeneous cuticular envelope, which is probably secreted by the egg itself, and must therefore be called the *vitelline membrane.*

It is not as yet universally admitted that vitelline membrane is the correct designation for this envelope. The formation of this membrane takes place either in the lower portion of the oviduct, or only after the egg is laid (fertilisation occurring simultaneously). Claus considered that it arose as a secretion or hardening of the external layer of the yolk, and therefore assumed that it was a vitelline membrane, while Van Beneden (No. 1) thought it probable that it originated from the cells of the follicles or from the epithelium of the oviduct (in those cases where no follicles are developed), and accordingly called it the *chorion.* This latter name has been adhered to by many recent authors. H. Blanc (No. 35), in support of this view, has shown that in *Cuma* the membrane adheres more closely to the follicle-cells than to the surface of the egg. The view that it is a vitelline membrane, which Ludwig also held, receives its strongest support from the observations of Claus, who was able to prove by means of measurements that, in *Chondracanthus*, a decrease in the volume of the egg took place simultaneously with its appearance, and of Grobben, who showed that in *Cetochilus* (No. 21) this membrane is formed after the egg is laid, when a similar contraction of the egg takes place. These observations agree with those of Weismann, who watched the passage of the naked egg into the brood-cavity in various Cladocera, and the subsequent formation of the membrane. More recently, Della Valle (No. 76) has shown that in *Gammarus* also the eggs are passed on into the brood-cavity without an external envelope, and only secrete the vitelline membrane after fertilisation.

Secondary external envelopes are often present in addition to the vitelline membrane. Among these must be enumerated the external hard shell of the winter eggs of the Phyllopoda (Fig. 50, *d*, p. 108), the ovisacs of the Copepoda and the Cirripedia, and the membrane of attachment (stalked egg-shell) of the Decapoda, which does not always completely surround the egg.

There is much variation in the **cleavage of the egg** in different forms of the Crustacea, but these various types of cleavage cannot be assigned with any exactitude to the different subdivisions of the group, since distinct kinds of cleavage are to be found in nearly related forms. *Gammarus* affords an example of this, the different species of this genus showing variations of cleavage which, however, according to Della Valle (No. 76), are not so remarkable as we were led to believe by the earlier investigations of La Valette St. George (No. 77), Van Beneden (No. 1), and Bessels (No. 2). Similar examples might be cited from among the parasitic Copepoda and the Cladocera. The latter group exhibits particularly clearly how the type of cleavage is influenced by the quantity of food-yolk present, and by the possibility of the egg being otherwise provided with nutritive material. In many forms of this sub-order, the winter egg, which is rich in food-yolk, differs in the type of its segmentation from the summer egg, which is poor in yolk, and which, during the whole course of its embryonic development, receives from the mother fluid nourishment through the albuminiferous contents of the brood-cavity (Weismann, Claus).

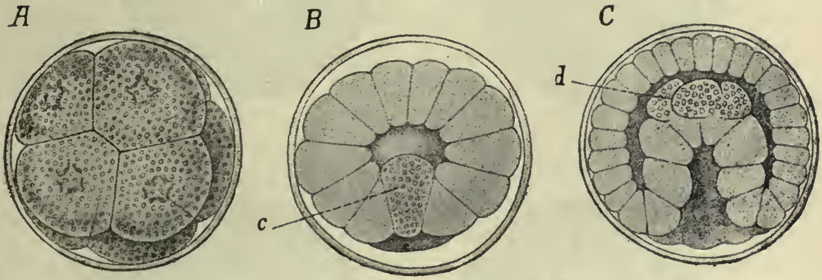

Fig. 49.—Three stages in the cleavage of the egg of *Lucifer* (after Brooks). *A*, stage showing division into eight cells. *B*, blastula stage with central cleavage-cavity. *C*, gastrula stage. *d*, yolk-containing portions arising from the cell *c*.

The following four types of cleavage* may be distinguished among the Crustacea:—

Type I. Eggs with complete and equal cleavage. This type is of very rare occurrence among the Crustacea. It is, however, to be found in the egg of *Lucifer* (Brooks, No. 43, Fig. 49), which is very poor in yolk. In this egg, after cleavage has taken place in the most regular manner, there is formed a coeloblastula consisting of few cells (Fig. 49 *B*) and having a spacious central cleavage-cavity, this stage giving rise to a very primitive invagination-gastrula (Fig. 49 *C*). All the cells at first appear to be similar in form and equally provided with spherules of yolk. At the commencement of the process of invagination, however, one cell lying at the vegetative pole (Fig. 49 *B*, *c*) is to be distinguished by the greater accumulation

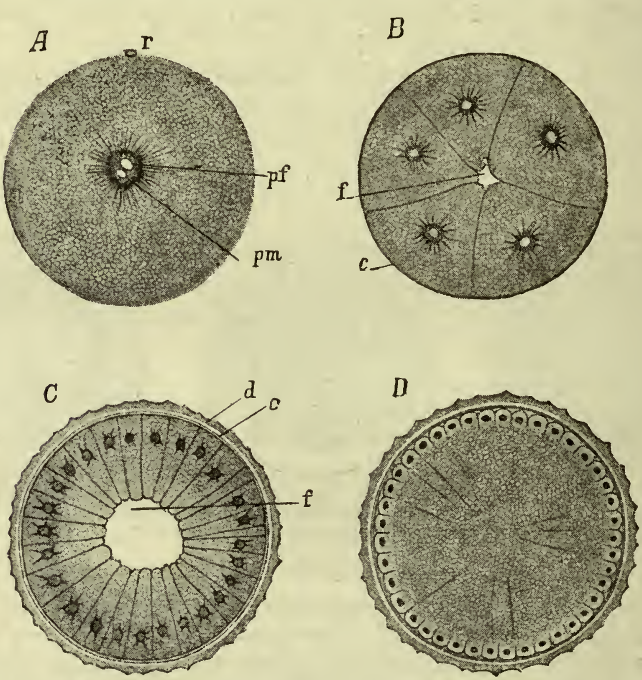

Fig. 50.—Fertilisation and cleavage of the egg of *Branchipus* (after A. Brauer). *A*, fertilisation stage. *B* and *C*, early stages showing total cleavage. *D*, older stage with superficial cleavage. *c*, vitelline membrane; *d*, secondary egg-shell; *f*, cleavage-cavity; *pf*, female pronucleus; *pm*, male pronucleus; *r*, polar body.

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* It should be mentioned that J. Nusbaum (No. 39) similarly distinguishes four types of cleavage among the Crustacea. His Types I. and II., however, do not agree with those here given.

of yolk within it. First two and then four portions become separated from this cell (Fig. 49 *C*, *d*), and these, shifting out of connection with the entoderm, come to lie within the primary body-cavity at the apex of the archenteric invagination. The significance of these portions of this cell is still doubtful (*cf.* below, p. 127).

Type II. Eggs with total cleavage in the first and superficial cleavage in the later stages. This type is very common among the Crustacea. The cleavage here begins with a total and, in most cases, an equal division (*cf.* Fig. 50 *B* and *C*), the egg dividing up first into two, then into four, eight, and sixteen cleavage-spheres of equal size, which are similarly filled with spherules of yolk. Within each of these cleavage-spheres lies a nucleus surrounded by a star-like mass of protoplasm which sends out numerous processes. The further cleavage proceeds, the more do these separate nuclei approach the surface of the egg. As a consequence of this they lose control of those portions of the now prismatic cleavage-cells which stretch inwards. The result is a stage in which cell-regions can be distinguished at the surface divided by furrows, while in the interior of the egg the originally distinct cells have become secondarily fused together (Fig. 50 *D*). The cleavage has become *superficial.* At the same time an even sharper distinction between formative and nutritive yolk takes place. The superficial cells finally contain only formative yolk, and become separated from the nutritive yolk by a distinct line. A blastula-stage (Fig. 50 *D*) is thus finally reached; this consists of a superficial layer of cells of equal size, and of an inner mass of yolk (now apparently filling the cleavage-cavity*). In the latter, no distinct demarcation between the portions belonging to the separate blastoderm-cells can, as a rule, be made out. There are, however, indications of such demarcation in the form of radial furrows, which are to be seen specially distinctly in the egg of *Astacus* (Fig. 55, p. 114) belonging to the next type of cleavage. In this egg, the central mass of yolk breaks up into the so-called *primary* or *Rathke's yolk-pyramids* (observed later by LEREBOULET, No. 58, and BOBRETZKY, No. 41) and a spherical *central body* (REICHENBACH, Nos. 64, 45). The yolk-pyramids here represent the yolk of the separate blastomeres, while the central mass represents the unseg-

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* Strictly speaking, the food-yolk does not lie *in the cleavage-cavity*, but occupies a considerably larger space than did the original cavity. We must therefore distinguish two parts in the food-yolk: a central portion which fills the original cleavage-cavity, and a peripheral portion corresponding to the fused inner ends of the blastomeres. Only the distal portions of the blastomeres have entered into the formation of the blastoderm.

mented mass of yolk which fills the actual cleavage-cavity. Similar yolk-pyramids were observed in *Palaemon* by Bobretzky; here, however, in the centre of the egg, they appear to be fused together. This is also the case in *Alpheus*, *Palaemonetes*, and *Hippa* (Herrick).

It has been observed that, in individual cases, not all the cleavage-nuclei shift to the surface to form the blastoderm, but that some of them may remain in the central mass of yolk (*Atyephyra*, Ischikawa; *Crangon*, Kingsley, No. 53). The significance of these cells is not yet clearly understood. Kingsley believes that they are belated cells, left behind in the process of blastoderm-formation. It is, however, possible that they ought to be regarded as early representatives of the vitellophags (*cf.* below, p. 134).

A very primitive form of cleavage, to be ranked with the type above described, is found in *Branchipus*, according to the unpublished researches of Brauer (Fig. 50). This form is distinguished by the fact that total cleavage is followed for a long time, giving place only in the late stages to the superficial method,* and that a gradually increasing blastocoele (*f*) appears early. Such a blastocoele is not, as a rule, to be observed in Crustacean eggs, save in the type of cleavage now under consideration, the prismatic or pyramidal blastomeres being usually in contact at the centre.

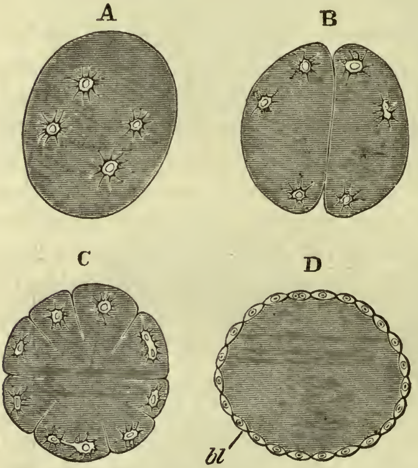

Fig. 51.—Four stages in the cleavage of *Eupagurus Prideauxii* (after P. Mayer, from Balfour's *Text-book*. *bl*, the completely formed blastoderm.

Careful examination of Crustacean eggs that abound in yolk and belong to this type reveals the fact that, even in the first stages, the blastomeres are hardly able to contain the mass of food-yolk supplied to them, or to avoid fusing with the neighbouring blastomeres. Ischikawa (No. 51) found in *Atyephyra*, that, after division into two the blastomeres once more fused to form a single ellipsoidal mass. In a similar manner division into four is inaugurated by the separation of the four blastomeres, which, however, soon lose their independence and completely fuse. Only in the later stages do the blastomeres become independent. Another instance of such disturbance seems to be afforded by the peculiar type of cleavage observed by Mayer (No. 59) in *Eupagurus Prideauxii* (Fig. 51). Here the first cleavage-nucleus divides into

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* According to Dr. Brauer's more recent researches, carried on since the above was written, the process in *Branchipus* seems to be somewhat different, inasmuch as the last stage, which was regarded as showing superficial cleavage (Fig. 50 *D*), has in reality passed into the stage of the formation of the germ-layers, and the cleavage-cavity has become filled by the immigration of entoderm cells.

two, four, and eight nuclei without separation of the individual blastomeres; the cleavage of the egg, which is at first complete, taking place only after these preliminary divisions of the nucleus. From the sixteen-cell stage onwards the egg then follows the superficial method of segmentation.

Besides the forms already mentioned (*Branchipus*, *Atyephyra*, *Eupagurus*), the following Crustacean eggs belong to this type of cleavage:—(1) The summer eggs of many Cladocera (*Polyphemus* and *Bythotrephes*, according to Weismann and Ischikawa, No. 6, the latter form having a blastocoele). (2) The eggs of the Ostracoda (*Cypris reptans*, Weismann and Ischikawa, No. 6). (3) The eggs of the free-living Copepoda (Claus, Nos. 18 and 19, Hoek, No. 22; *Cetochilus*, Grobben, No. 21; *Cetochilus* and *Harpacticus*, Van Beneden and Bessels, No. 2). (4) *Chondracanthus* among the parasitic Copepoda (Van Beneden and Bessels, No. 2), most of the Amphipoda (Uljanin, No. 75; Pereyaslawzewa and Rossijskaya, Nos. 70 to 73). From the observations of La Valette St. George (No. 77), Van Beneden and Bessels (Nos. 1 and 2), there appeared to be a considerable difference in the methods of cleavage of the different species of *Gammarus*. *G. locusta* was said to belong to the type under consideration, but the fresh-water species (*G. pulex* and *fluviatilis*) to the type here ranked as third. Della Valle (No. 76), however, in confirmation of the older observations of Leydig, has proved that in the latter cases also cleavage is total in the first stages, so that we must class all the species of *Gammarus* under the present type. (6) Some of the Decapoda are, perhaps, also to be classed here; besides *Eupagurus* and *Atyephyra*, *Palaemon* (Bobretzky, No. 41) and *Palaemonetes* (W. Faxon, No. 46) may possibly belong to this type.

This type of cleavage also, perhaps, includes the Cirripedia, whose first stages of development seem to follow a fairly simple course. In *Balanus* (Lang, No. 28; Hoek, No. 27; Nassonow, Nos. 13 and 29; Nussbaum, Nos. 30 and 31) the cleavage appears to be total, but somewhat unequal (Fig. 52), in which case we should have an example of unequal cleavage in the Crustacea. The somewhat elongated egg has one pole rounded and the other pointed. By the first cleavage, which takes place horizontally or somewhat obliquely, the egg breaks up into two dissimilar spheres; the one near the rounded, *i.e.*, the future anterior pole, consisting entirely of formative yolk (*a*), yields the ectoderm, while that near the pointed or posterior pole (*b*), which is rich in food-yolk, yields the elements of the mesoderm and entoderm. The next division takes place in the ectoderm-sphere and leads to the formation of a cap-like mass of cells (Fig. 52 *B*, *C*), which gradually grow round the sphere containing food-yolk (Fig. 59 *A*, *b*).

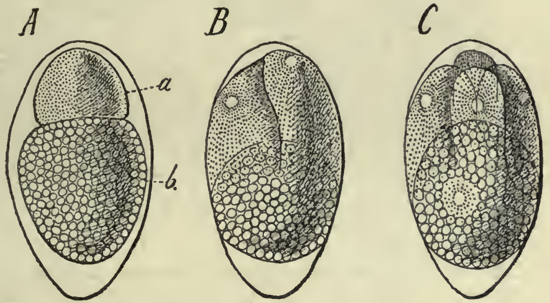

Fig. 52.—Three consecutive stages in the cleavage of *Balanus* (after Lang). *A*, stage of division into two cells. *B*, the upper cell *a* has divided into two. *C*, the same after division into four.

This circumcrescence has been described as epibolic gastrulation (LANG), but it must still be considered doubtful whether this is the correct interpretation. According to NASSONOW's drawings (No. 13), it appears that when the formation of the blastoderm is completed, cell-elements are ejected by the central food-yolk sphere also, and become massed more superficially near the point last affected by the circumcrescence of the blastoderm (blastopore, LANG, NASSONOW). Even this may, perhaps, be only a modification of a primarily complete and later superficial cleavage. The gastrula-stage would have to be sought later, when a small depression of the surface appears (Fig. 59 *B*, *blp*, p. 126) at the above-mentioned point, and a simultaneous immigration of the entoderm-cells (*en*) into the mass of food-yolk takes place. This method of formation of blastoderm would belong to that order of superficial cleavage in which the blastoderm originally appears as a disc, but would be distinguished from the typical examples of that method by the fact that the point at which the disc appears here lies opposite to the blastopore, while in other cases the two points agree in position (*cf.* p. 115).*

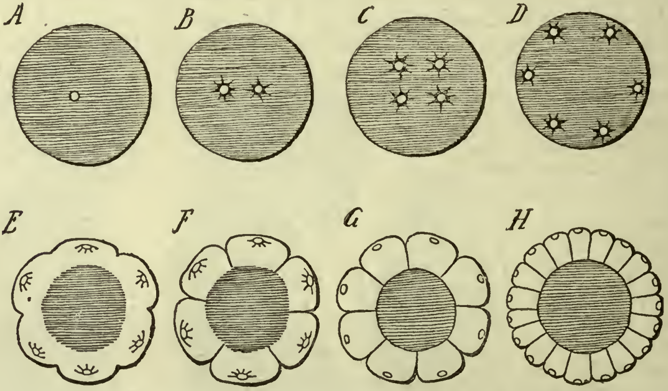

FIG. 53.—Diagram of the cleavage of *Callianassa subterranea* (after MERESCHKOWSKI). In the stages *F–H*, the food-yolk is limited to the central portion of the egg.

Cleavage takes place somewhat differently in *Sacculina* (VAN BENEDEN, No. 25; KOSSMANN). In this egg, the formative and the nutritive yolk become separated only in the four-celled stage which is reached by total and regular cleavage. We then have four micromeres consisting of formative yolk and four macromeres consisting of food-yolk. Whilst the micromeres increase by fission and cover the surface of the egg with a blastoderm-layer, the macromeres fuse to form a simple central mass of food-yolk. The cleavage of the yolk, which

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* [According to GROOM (No. I., *App. to Lit. Cirripedia*), the smaller of the two cells resulting from the first cleavage, which he terms the first blastomere, forms only a portion of the ectoderm. The second blastomere is formed from the yolk, and the blastoderm is formed partially from the blastomeres already present, but largely also from fresh blastomeres (*merocytes*) yielded by the yolk. The first division consequently does not divide the egg into ectoderm and entoderm, but simply into a macromere (yolk-cell) and a micromere, the latter being but one of the future blastomeres, of which the macromere gives off a number. He further concludes that the gastrula is formed by epiboly, and that there is no superficial cleavage during the later period of division.—ED.]

has been observed by KOSSMANN, seems here also to be a secondary process occurring in the later stages. As the cleavage of *Sacculina* appears to belong to the Type II. *b*, described below, p. 115, it tends to confirm the view of the cleavage of *Balanus* to which preference was given above.

Type III. Eggs with purely superficial cleavage. In this type, the formative yolk, from the very beginning, has no control over the mass of food-yolk. The first cleavage-nucleus, lying in the centre of the egg (Fig. 53 *A*), divides regularly into two, four, eight, etc., nuclei (Figs. 53 *B–D* and 54 *A*), which are surrounded by radiate masses of protoplasm. The areas of the separate cells, however, do not become marked off by furrows cutting right through the egg, although, in a few cases, such furrows are indicated even in early stages as grooves on the surface (Fig. 53 *E*). The larger the number of cleavage-nuclei becomes, the more do they shift towards the surface (Figs. 53 *D* and 54 *B*), and a regular blastoderm is formed in the same way as that described under Type I. (Fig. 53 *F–H*).

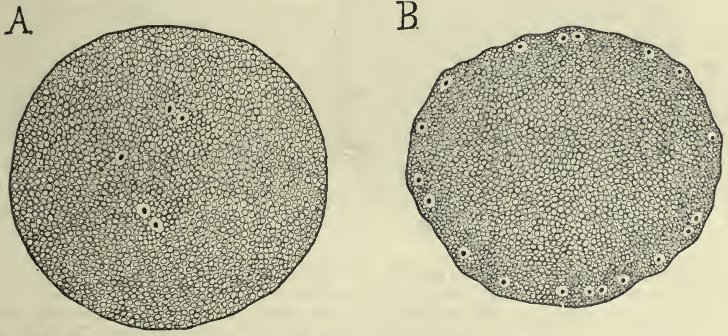

FIG. 54.—Two stages in the cleavage of the egg of *Astacus* (after MORIN). *A*, younger stage with a few cleavage-nuclei within the egg. *B*, older stage with superficial distribution of the cleavage-nuclei and a correspondingly wavy surface.

The processes here described as taking place within the egg, *i.e.*, the division of the cleavage-nuclei and the shifting apart of the radiate islands of protoplasm which surround them have often been called *cleavage*. Indeed, these islands of protoplasm have even been named *cleavage-cells*, which then appear in a certain contradistinction to the masses of food-yolk. In so far, however, as we regard the *whole egg* as the equivalent of a cell, and the two, four, eight, etc., separate spheres produced by its total cleavage as cells, it is evident that we ought not to consider these protoplasmic islands, which are designated "cleavage-cells," as fully equivalent to blastomeres. They represent merely the centres of blastomeres, whose areas, owing to the absence of furrows, have not been demarcated. In the first stages of superficial cleavage, the egg is on the level of a multinucleate cell. This view is supported by the frequently observed fact that the so-called "cleavage-cells" are connected together by a reticulum of fine protoplasmic processes. If, therefore, we understand by cleavage here, as elsewhere, the act of marking off separate cell areas, it follows that the term *superficial cleavage* is applicable to the present type, since cleavage actually occurs here only in the superficial parts of the egg.

This type of segmentation is also very common among the Crustacea. It is found in the following eggs:—(1) In the *summer eggs* of many Cladocera (*Moina*, *Daphnia*, *Sida*, *Leptodora*, *Daphnella*, Weismann and Ischikawa, No. 6), and in all *winter eggs* (*Moina*, *Daphnia*, *Sida*, *Bythotrephes*, *Polyphemus*, *Leptodora*, Weismann and Ischikawa, No. 16). There is thus among the Cladocera a group of forms (*Bythotrephes*, *Polyphemus*), the summer eggs of which belong in their cleavage to Type II., while the winter eggs belong to Type III. (2) In the eggs of several Isopoda (*Asellus*,* Van Beneden, No. 79; *Porcellio*, Reinhard (No. 91) and Roule (No. 92). This type of cleavage may, perhaps, be more common among the Isopoda than has hitherto been thought. (3) In the eggs of *Penaeus* (Haeckel, No. 47), *Callianassa subterranea* (Mereschkowski, No. 60), *Astacus* (Morin, No. 61), *Homarus* (Herrick, No. 50a).

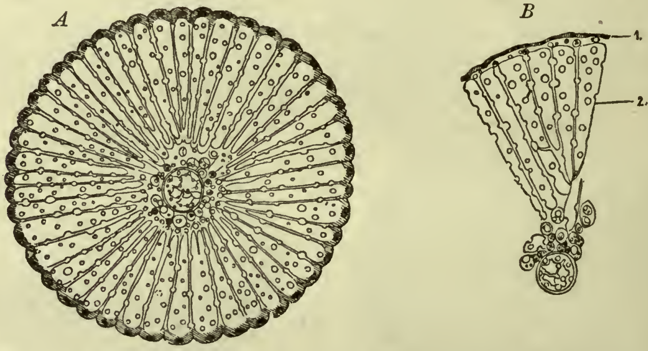

Fig. 55.—Later stages in the cleavage of the egg of *Astacus* (after Reichenbach, from Hatschek's *Text-book*). *A*, section of one of the stages. The formative yolk has collected at the surface. The food-yolk has divided into separate yolk-pyramids. The central body is found within it. *B*, later stage in which the layer of blastoderm-cells (*1*) has become distinct from the yolk-pyramids (*2*).

It is very important, in the formation of the blastoderm which follows the superficial cleavage, to distinguish clearly two subsidiary methods:

(*a*) *The formation of the blastoderm takes place all over the surface simultaneously*, *e.g.*, in *Astacus*, *Branchipus*, and the free-living Copepoda.

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* According to more recent statements by Roule (No. 92), which are not very clear, it appears as if the cleavage of *Asellus* were at first total and only later superficial. Van Beneden, on the contrary (No. 79), emphasises the fact that at first a mere increase in the number of nuclei within the yolk takes place, that these nuclei become distributed later at the surface of the egg, and that it is at the surface that the limitation of their areas occurs, while nearer the centre the mass of yolk remains unfurrowed. In this case, the egg of *Asellus* undoubtedly belongs to Type III.

(*b*) *The blastoderm develops first on the ventral side of the egg.* Its formation begins at one point on the surface and proceeds gradually from this point, which always represents the future ventral side of the egg; in the Decapoda the point denotes the most posterior end of the ventral side, or the spot at which, later, the gastrula invagination appears. This has been observed in *Palaemon* and *Eriphia*, in which the formation of the blastoderm is completed over the whole surface of the egg and closed on the dorsal side, only when the rudiments of the embryo are already to be seen on the ventral side.

These modifications in the formation of the blastoderm are found both in Type II. and Type III., and thus result in four subsidiary methods of cleavage, which deserve detailed description :

Type II. a. The cleavage is at first total, and later superficial, being followed by the simultaneous formation of the blastoderm all over the surface; *Branchipus*, free-living Copepoda, summer eggs of *Polyphemus* and *Bythotrephes*, *Eupagurus*.

Type II. b. The cleavage is at first total, later superficial, the blastoderm developing first on the ventral side. This method is exceedingly common among the Amphipoda. As, in this method, the cells on the future ventral side divide more rapidly, and there is in this region an early separation of the blastoderm-cells from the food-yolk, a considerable difference is found between the cells of the ventral side and the large cells of the future dorsal side which abound in yolk. It is evident that this type of cleavage, which is seen in various Amphipoda (especially in *Gammarus locusta*, according to Van Beneden and Bessels, No. 2), greatly resembles in its first stages total, unequal cleavage. An important distinction, however, arises from the fact that in this case the pole at which the small cells are found belongs to the vegetative half, that portion of the surface at which, later, the formation of entoderm takes place, while the larger cells belong more to the animal region (the later dorsal side). In any case the two axes here compared (that passing through the animal and vegetative poles, and that from the small-celled to the large-celled pole) do not appear to coincide, but to cross each other obliquely (*cf.* below, p. 142).

Type III. a. The cleavage is purely superficial, the subsequent formation of blastoderm taking place all over the surface simultaneously; many Decapoda (*Penaeus*, *Astacus*, *Callianassa*), all the winter eggs and many summer eggs of the Cladocera.

Type III. b. The cleavage is purely superficial, the blastoderm developing first on the ventral side of the egg. In this case a few of the numerous elements to be found within the yolk first shift to a definite point at the surface, there to be transformed into blastoderm-cells. There thus arises a small blastoderm-disc, corresponding in position to the future ventral side of the egg; this disc gradually increases in size, new elements from within the yolk constantly rising to its periphery and becoming changed into blastoderm-cells. This method of cleavage consequently strongly resembles the discoidal cleavage to be described presently. The distinction between the two types consists in the fact that in Type III. *b*, the increase of the blastoderm is due to the accession of new elements from the inner portion of the egg, while in true discoidal cleavage (IV.), the increase takes place exclusively by the division of the elements already present in the blastoderm-disc. It is probable that these two types have been confused one with the other, since in many cases in which the occurrence of discoidal cleavage in Crustacea has been maintained, the observations were not confirmed by the systematic examination of sections. It therefore appears probable to us that most parasitic Copepoda, to which VAN BENEDEN and BESSELS (No. 2) ascribed discoidal cleavage, in reality develop according to Type III. *b*. The same is possibly the case with the Isopoda (*Oniscus*, *Ligia**), for which discoidal segmentation was asserted by BOBRETZKY (No. 80) and VAN BENEDEN (No. 1). We are, indeed, justified in raising the question whether true discoidal cleavage ever occurs in the Crustacea, and whether more careful examination might not lead to the complete absorption of Type IV. in Type III. *b*. Among the Decapoda also there are some representatives of this last type, such as *Homarus*, *Eriphia*, and perhaps also *Palaemon*. It is possible, however, that the last-named genus, on account of the total (?) cleavage that takes place in the first stages, should, like *Atyephyra*, be assigned to Type II. *b*.

Type IV. Eggs with discoidal cleavage. In the types of cleavage which we have so far considered, two processes go on side by side simultaneously, viz., (1) the increase of the elements, and (2) the separation of the blastomeres from the food-yolk (*i.e.*, the separation of the plastic portion of the egg from the nutritive). In the blastula stage, which finally results in Types II. and III., we then find a superficial layer of epithelium and an inner mass of food-yolk, in which, as a rule, no cell-nuclei or other plastic elements are still to be found. If we now imagine this process of separation between the blastomeres and the food-yolk to be shifted back to the earliest stages, we obtain an explanation of discoidal cleavage, as it has been observed in *Mysis* (VAN BENEDEN, No. 37; NUSBAUM, Nos. 38 and 39) and *Cuma* (No. 35), as well as in some other forms.† Here the very first cleavage-cell becomes entirely separated from the food-yolk, on the surface of which it comes to lie. The food-yolk from this time onward contains no more cleavage-nuclei. The formation of the blastoderm begins with the superficially placed cleavage-nucleus, which divides (Fig. 56 *A*), and thus yields a cap of blastomeres (Fig. 56 *B*); these increase in number by continual division, and gradually grow over the whole surface of the sphere of food-yolk. The starting-point in the formation of the blastoderm here corresponds to the spot where, later, gastrulation takes place (posterior end of the ventral side of the embryo), while the blastoderm is finally completed on the dorsal side. At this ventral starting-point of the blastoderm there is from the first a thicker

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* Quite recently NUSBAUM has again maintained the presence of discoidal cleavage in *Ligia* (No. 85*a*).

† [BOUTCHINSKY (*Zool. Anz.*, xx., 1897, p. 219) describes a discoidal segmentation in *Nebalia*.—ED.]

deposit of cells, which are here deeper and form a rounded thickening (germinal disc).

Not only the eggs of *Mysis* and *Cuma*, but those of several Isopoda are said to show this type of segmentation (*Oniscus*, according to BOBRETZKY, No. 80, *Ligia*, according to VAN BENEDEN, No. 1). It is also said by VAN BENEDEN and BESSELS (No. 2) to occur in many *parasitic Copepoda* (*Anchorella*, *Caligus*, *Clavella*, *Lernaea*, *Lernaeopoda*, *Brachiella*, etc.). It must, however, be considered probable that the greater number of these cases really belong to Type III. *b*. This view is supported by the observations of BOUTCHINSKY (No. 37a), who, according to the plates given in his Russian treatise, observed a simple superficial cleavage in *Paradopsis cornuta*. Our retention for the present of the discoidal type of cleavage for the Crustacea is due entirely to NUSBAUM'S recent description of *Ligia oceanica*, according to which a type of segmentation agreeing with that given above for *Mysis* actually occurs (No. 85a).

The type of discoidal cleavage here described shows some superficial resemblance to that kind of discoidal cleavage which, in many groups of animals (*e.g.*, Cephalopoda), is developed from a total, unequal cleavage. Closer examination reveals, however, that what we are now considering is a *peculiar process of discoidal development of the germ*, which has evidently developed independently among the Crustacea out of a superficial type of segmentation. For where discoidal cleavage has developed out of total, unequal cleavage, we find that the pole of formation of the germ-disc corresponds to the animal pole, its gradually out-spreading edge to the blastopore, and the plug of yolk to the vegetative pole of the egg. Here, however, in the discoidal cleavage of the Crustacea, it is quite otherwise. The formative pole of the germinal disc corresponds to the ventral side of the embryo, and all observations point to the fact that here also the formation of the germ-layers commences, and the important but somewhat obscured process of gastrulation. The circumcrescence of the food-yolk here proceeds from the ventral to the dorsal side, and has evidently in this case nothing to do with gastrulation, since we should otherwise be compelled to assume, in Crustacea with discoidal cleavage, a blastopore closing dorsally, which would be in contradiction to the conditions found in other Crustacea.

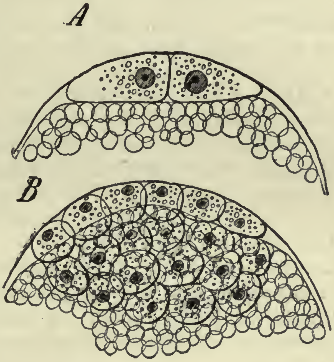

FIG. 56.—Two stages in the segmentation of *Mysis* (after VAN BENEDEN) as an example of discoidal cleavage. *A*, two cells are to be seen at the surface of the yolk. *B*, the two cells have increased by division and form a cap.

By the above considerations we are led to regard the discoidal cleavage of the Crustacea as an extreme case of that type of cleavage described above as Type III. *b*. In the discoidal method, the formation of blastoderm at the pole where it originates is carried out so early, that its rudiment originally consists of a single blastoderm-cell, which, by subsequent successive division, yields the whole blastoderm.

If we consider the variations found in the different planes of organisation among the Vertebrata, we find a certain element of similarity between the discoidal cleavage of these latter and of the Crustacea in the fact that in both cases a deposit of food-yolk on one side of the principal axis takes place, and determines the peculiar type of development. In those Vertebrates in which discoidal cleavage occurs, the dorsal side of the body takes the lead in development, while the ventral side is hindered in its development by the accumulation of food-yolk. The blastopore is here shifted to the dorsal side. In those Crustacea in which discoidal segmentation is found, on the contrary, the rudiments of the ventral side appear first, and the blastopore takes up a ventral position corresponding with the plan of organisation of the group. In this case, the dorsal side of the body is influenced in its development by the accumulation of food-yolk.

In many Crustacea, when the formation of the blastoderm is complete, a cuticle is secreted at the surface of the blastoderm cells. We follow VAN BENEDEN (No. 79) in calling this membrane the *blastodermic cuticle* (cuticula blastodermica). Its appearance can only be explained by a process of ecdysis shifted back to an early embryonic period. Similar membranes are given off by the eggs of the Arachnids and of *Limulus*.

The formation of a blastodermic cuticle is to be observed specially among the Malacostraca. It has, however, also been seen in the parasitic Copepoda (VAN BENEDEN, No. 17). In the Malacostraca it is very common, being found in *Nebalia* (VAN BENEDEN, No. 79), the Cumacea (H. BLANC, No. 35), in many Decapoda (LEREBOULLET, No. 58, and REICHENBACH, Nos. 64 and 65, found it in *Astacus;* P. MAYER, No. 59, in *Eupagurus;* BOBRETZKY, No. 41, in *Palaemon;* KINGSLEY, No. 53, and VAN BENEDEN, No. 79, in *Crangon;* DOHRN, in *Portunus*), in the Amphipoda (VAN BENEDEN and BESSELS, No. 2, in *Gammarus locusta;* VAN BENEDEN, No. 79, in *Caprella;* ULJANIN, No. 75, *Orchestia*); finally, in the Isopoda (VAN BENEDEN, No. 79, in *Asellus;* BOBRETZKY, No. 80, in *Oniscus*). Further, it has been observed by DOHRN in *Tanais.*

The formation of this blastodermic cuticle is, in many Crustaceans, followed by other ecdyses in later embryonic stages. This is especially the case where the development is abbreviated, *i.e.*, where many of the stages of development are shifted back into embryonic life. The cuticles formed during these ecdyses are usually distinguished by swellings corresponding to the rudiments of the limbs. These membranes are called *larval integuments.*

As there is considerable variation in the time of appearance of all these cuticular membranes, it is often difficult, in single cases, to distinguish between the actual egg-integument, the blastodermic cuticle, and the larval integuments which appear later, and to establish with exactitude the homology of the special cuticular structure in each individual case. There can, however, be no doubt that the cuticle very common among the Arthrostraca, and observed in *Ligia* by F. MÜLLER (No. 4), and further, the integument developed in *Mysis* and the Decapoda after the completion of the *Nauplius* stage are equivalent to larval integuments (VAN BENEDEN, No. 79). In the Decapoda, a second larval integument is often developed in later stages; this surrounds the hatching *Zoaea*, and was assumed by CONN to be the cuticle of the *Protozoaea* stage. In *Anchorella* and *Lernaeopoda* (VAN BENEDEN, No. 17), the embryo moults three times during the course of its development: (1) When the blastodermic cuticle is formed, (2) when the Nauplius cuticle develops, and (3) during the transition to the *Cyclops* stage. DOHRN has bestowed special attention on the subject of larval integuments in his various works (*cf.* his treatise on the larval integument of the Cumacea, of *Tanais*, and on the *Nauplius* stage in the egg of *Daphnia longispina*). On account of the great variety prevailing among the Crustacea, and the uncertainty in the identification of the cuticles in the different cases, we should be overstepping the limits of this work were we to enter upon all the cases illustrating this point.

The peculiar processes which were observed in the winter eggs of many Cladocera by WEISMANN and ISCHIKAWA (No. 16), and described as *paracopulation*, synchronise with the phenomena of cleavage. Here, after the ejection of the polar bodies and subsequent fertilisation, there is found a body resembling a nucleus surrounded with an accumulation of protoplasm; this is called the *copulation-cell.* During the first division of the cleavage-nucleus, by which the purely superficial segmentation of the type (III.) is introduced, the copulation-cell remains apparently passive near the vegetative pole of the egg; it, however, soon approaches one of the nuclei which result from the division and becomes completely fused with it. The further fate of the cleavage-nucleus thus entering into paracopulation has not been traced. The view that it is destined to yield the genital rudiments is a mere assumption. The copulation-cell appears first at the time of the formation of the egg. When the latter is maturing in the ovary, chromatin particles are ejected from the germinal vesicle; these unite to form the nucleus of the copulation-cell, which, at a later stage, becomes surrounded by a mass of protoplasm, probably arising from the cell-body. So far no hypothesis has been formed as to the significance of the processes of paracopulation. The origin of the copulation-cell recalls the ejection of chromatin particles by the germinal vesicle observed by STUHLMANN and BLOCHMANN in the eggs of insects. Similar processes have also been noted in the maturing eggs of Myriopoda (BALBIANI) and *Araneae* (LEYDIG) and in other groups of animals.

3. The Formation of the Germ-layers.

A. Copepoda.

Among all the Crustacea, so far as our present knowledge of their ontogeny enables us to judge, the Copepoda most closely resemble the Annelida in their development. In them we have an invagination-gastrula and the formation of the mesoderm through the separation of two primitive mesoderm-cells. The formation of the germinal layers in the Copepoda was made known by the researches of GROBBEN (No. 21), HOEK (No. 22), and URBANOWICZ (Nos. 23 and 24). We have utilised the minute observations of the first of these writers in the account of *Cetochilus* here given.

Cetochilus, like most free-living Copepoda, belongs to our second type of cleavage. At first the cleavage is total, in later stages superficial (*cf.* p. 109). As early as the thirty-two-cell stage, the transition to the actual blastula-stage commences, the first histological differentiation in the different germinal layers becoming perceptible. At this stage there is found a small segmentation-cavity in which the food-yolk is deposited, and into which the polar bodies also find their way. A similar immigration of the polar bodies was noticed by **Weismann** and **Ischikawa** (No. 6) in the summer eggs of *Bythotrephes*. It is probable that the small cell observed by **Urbanowicz** in the cleavage-cavity of *Cyclops* is also to be referred to the polar bodies.

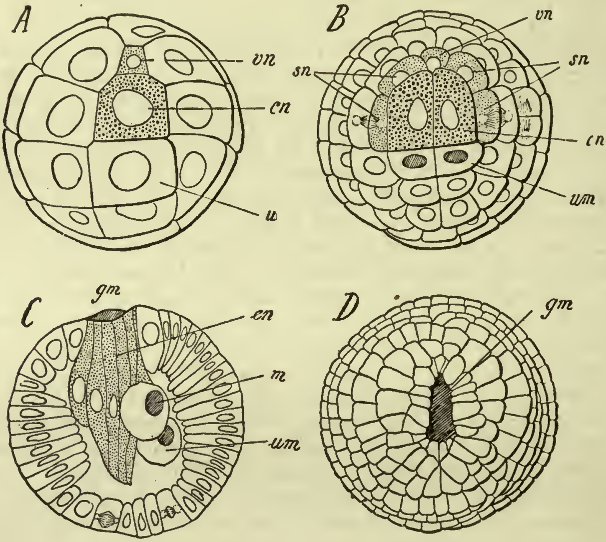

Fig. 57.—Four stages in the development of *Cetochilus* (after **Grobben**). *A*, thirty-two-cell stage seen from the ventral side. *B*, later stage, same aspect; all the germinal layers are already distinct. *C*, longitudinal section of the gastrula-stage. *D*, ventral aspect of the gastrula-stage, in which the blastopore is closing. *cn*, central entoderm-cell; *gm*, mouth of the gastrula (blastopore); *m*, mesoderm-cell; *sn*, lateral entoderm cells; *um*, primitive mesoderm-cells; *vn*, anterior entoderm-cells.

If we examine the vegetative pole at the thirty-two-cell stage of *Cetochilus*, a decidedly bilateral arrangement of the blastomeres can be recognised (Fig. 57 *A*). We find two cells, a larger one (*cn*), distinguished by the coarse granulation of its protoplasm, and a smaller anterior cell (*vn*). These two cells lie in the median plane;

and at a later stage yield exclusively entoderm-elements. They are distinguished as the *central* (*cn*) and the *anterior* (*vn*) *entoderm-cells*. The four blastomeres (*lateral cells*) situated symmetrically on each side of these two, yield, by future division, both entodermal and ectodermal elements. The cleavage-sphere (*u*), which lies behind the central entoderm-cells, also appears to be of importance. This divides later into four elements, two larger anterior cells representing the *primitive mesoderm-cells* (Fig. 57 *B*, *um*), while two posterior cells become ectodermal elements.

Fig. 57 *B* shows us the central entoderm-cell (*cn*) divided to form two blastomeres; the lateral entoderm-elements (*sn*) have also become distinct by the division of the lateral cells. We thus have the rudiment of the entoderm consisting of seven cells, behind which lie the two primitive mesoderm-cells (*um*). The immigration of the mesoderm elements towards the centre of the embryo next takes place. The primitive mesoderm-cells yield by division two laterally placed elements (Fig. 57 *C*, *m* and *um*), and these four mesoderm-cells (of which the two median cells are to be considered as the pole-cells of the lateral mesodermal band) shift into the segmentation-cavity (Fig. 57 *C*). Soon after this there occurs the invagination of the entodermal elements (*en*), by which the *gastrula-stage* is reached (Fig. 57 *C*). The blastopore, a longitudinal fissure (Fig. 57 *D*), now closes from before backward, and the entoderm which has sunk inwards thus becomes a closed vesicle. It appears that the blastopore corresponds in position to the future ventral side of the embryo. If so, the part that closes latest would lie in the neighbourhood of the future anal aperture.

The stomodaeum and the proctodaeum, according to the researches of Urbanowicz in connection with *Cyclops*, arise as ectodermal invaginations, the former appearing during embryonic development, while the latter develops only in the earliest larval stage. They both become connected with the archenteric vesicle.

The gastrula-stage in the Copepoda was first investigated and described by Hoek.

The statements made by Urbanowicz as to the formation of the germ-layers in *Cyclops* do not agree with Grobben's views. In *Cyclops* there is, at first, only one entoderm-cell which sinks inwards, the blastopore closing above it; this cell then yields by division the whole entodermal rudiment. A mesenchyme next arises by the abstriction of ectodermal elements, this mesenchyme giving rise to most of the mesodermal structures of the *Nauplius*, while the actual mesoderm is a later, secondary structure, probably originating from the entoderm and yielding exclusively the mesoderm-band. When, however, we take into consideration the fact that round the central entoderm-cell in *Cetochilus* there lie elements which divide into ectodermal and entodermal elements, it appears possible that URBANOWICZ has taken this process for the formation of the mesenchyme.

The later fate of the mesoderm in the Copepoda has not yet been clearly made out. It appears, however, that its elements, in the segments of the *Nauplius* stage, become divided more irregularly, after the manner of a mesenchyme, and very soon become grouped as the organs of the *Nauplius*. Certain cells come to lie along the intestine, and give rise to its musculature, others form the muscles of the limbs, or unite to form the antennal gland. The body-cavity here exhibits the character of a pseudocoele. In the posterior part of the body of the larva, which yields the remaining and greater number of body-segments, on the contrary, a true paired mesoderm-band is developed; in this, according to URBANOWICZ (No. 23) and FRITSCH (No. 20), the rudiments of true coelomic vesicles appear. The most anterior pair of these vesicles represents the maxillary segment. The dissepiments between the consecutive coelomic vesicles, which GROBBEN also (No 21) appears to have observed in the abdomen of *Cetochilus*, disappear in the later stages, whereas a dorsal and a ventral mesentery are said to persist throughout life (FRITSCH). The dorsal mesentery is attached to the back by the separation of its two halves, thus leaving a median dorsal sinus which must be regarded as a remnant of the blastocoele and as the homologue of the cardiac cavity. This dorsal sinus is connected with the anterior portion of the body-cavity, which develops as a pseudocoele. Even in early stages, when the mesoderm-band is still short, one large cell can be distinguished from the rest; this is the genital cell, which develops on each side into the rudiment of the genital glands. [*Cf.* HACKER (App. to Lit., Copepoda, No. I.)]

The food-yolk, in *Cetochilus*, is present in small quantities, and is of little importance. In the eggs of the parasitic Copepoda, in which it is plentiful, it appears, according to VAN BENEDEN, that the cells of the entoderm at first migrate into the yolk and take it up into themselves, thus bringing about the appearance of a secondary segmentation of the yolk. At a later stage, however, the cells again rise to the surface of the mass of food-yolk, there forming an epithelium which becomes the wall of the mid-gut (Fig. 73 *C*, *en*, p. 148). The latter thus finally surrounds the remains of the food-yolk decreased by gradual absorption (*cf.* below the formation of the mesenteron in the Cirripedia, pp. 126, 174).

B. Phyllopoda.

The formation of the germ-layers in the Phyllopoda is best known in the case of the summer eggs of *Moina*, one of the Cladocera, which have been closely investigated by Grobben (No. 11). There is considerable resemblance between the processes here and those already described in connection with *Cetochilus*. We must not, however, lose sight of the fact that two factors in the development of the eggs of *Moina* have brought about a difference: (1) The nourishment by means of the blood-plasma transuding into the brood-cavity, which probably leads to secondary diminution of the food-yolk (in *Cetochilus* also the yolk seems to be secondarily diminished, although from other causes), and (2) the *paedoparthenogenesis*, which is connected with the precocious development of a distinct genital cell.

Cleavage here, as in most Cladocera, is purely superficial (Type III., *cf.* p. 113). As early as the thirty-two-celled stage we find the blastomeres at the surface fairly sharply marked off from the central mass of food-yolk. As in *Cetochilus*, at the vegetative pole of the egg, certain differentiations appear which accompany the formation of the germ-layers. In this region are found those rudiments which, at a later stage (after a certain amount of displacement), lie at the ventral surface of the embryo. There is here a central richly-granular cell, which may be called the *genital cell* (Fig. 58, *g*), and from which, later, the paired genital rudiment arises. Behind this lies a cell represented in the act of division, which as the *entoderm-cell* (*en*) represents the rudiment of the whole entoderm. At a somewhat later stage, these two rudiments have, by division, become multicellular. An area composed of numerous entoderm-cells (Fig. 58 *B*, *en*) can then be distinguished, and, anteriorly to this, four genital cells (*g*). Around the latter are a number of cells representing the *rudiment of the mesoderm* (*ms*). All the remaining cells now form the *ectoderm*.

Even at this stage the rudiment of the mesoderm has a tendency to migrate inwards below the genital cells (Fig. 58 *B*). In later stages, this process is completed (Fig. 58 *C*, *ms*). The mesoderm now lies entirely within the embryo, and at the same time the entodermal area becomes invaginated, the *gastrula stage* being thus reached (Fig. 58 *C*).

Soon after the mouth of the gastrula has completely closed, the eight genital cells, produced by division from the four above-mentioned, shift inwards and lie upon the entoderm (*cf.* below, Fig. 72 *A*, *g*, p. 147). **Grobben** holds that the point at which the blastopore closes corresponds to the future oesophageal invagination. It would, however, be more in agreement with the conditions met with in other Crustacea, especially in the Decapoda, if we might assume that it lay in the neighbourhood of the future anal aperture.

While the embryo lengthens, the Nauplius limbs grow out and the rudiment of the brain becomes distinct at the anterior end of the dorsal surface as an ectodermal thickening (*neural plate*, Fig. 72 *A*, p. 147); the rudiments of the internal organs also undergo corresponding development. The entoderm (*en*) develops into a cylindrical body, the cells of which, in cross section, appear radially arranged; no lumen is, however, at first to be seen. The stomodaeum and proctodaeum (Fig. 72 *B*, *m*, *af*) arise as ectodermal invaginations; the former is distinct even in the *Nauplius*, the latter only at a later stage. They become connected with the rudiment of the mid-gut. The mesoderm (*ms*) has spread over the whole ventral surface and has extended anteriorly until it comes to underlie the neural plate. It is situated on either side of the rudimentary intestine and is bilaterally symmetrical; there is, however, no complete separation of the two parts of the mesoderm-band. The genital rudiment divides to form a paired mass of cells lying on either side of the intestinal canal.

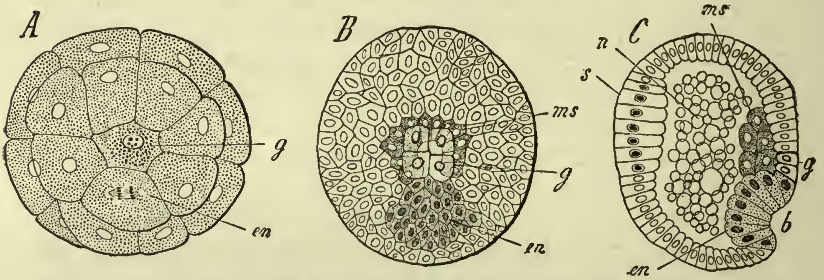

Fig. 58.—Three stages in the development of the summer egg of *Moina* (after **Grobben**). *A*, egg in the thirty-two-cell stage seen from the vegetative pole. *B*, blastula stage, same aspect. *C*, median section of gastrula stage. *b*, blastopore; *en*, endoderm-cells; *g*, genital cells; *ms*, mesoderm-cells; *n*, food-yolk; *s*, neural plate.

The food-yolk originally lies in the primary body-cavity. It is absorbed in proportion as the inner organs fill that cavity. In later stages, a few cells separate from the mesoderm and penetrate the food-yolk. They then come to lie on the dorsal side of the embryo and become the fat-body in the adult.

It would be interesting to learn something of the formation of the mid-gut, and of the part here played by the food-yolk in the eggs of those Cladocera or Branchiopoda in which it abounds. *Moina* is a striking exception to the rule in being poor in yolk. In young *Branchipus* larvae all the tissues, even the ectoderm, appear to be permeated with granules of food-yolk (*cf.* CLAUS, No. 9).

In *Daphnia similis*, according to the recent researches of LEBEDINSKY (No. 11a), a blastoderm, of equal thickness throughout and completely covering the egg, is first formed by superficial cleavage. This only thickens later at points where the cells become elongated in the region of the cephalic lobe and on the ventral side of the egg. The formation of the germinal layers is commenced by the appearance of a very shallow depression (blastopore), from which point immigration of amoeboid cells into the yolk takes place. The latter represent the meso-entoderm. While the mesoderm-cells become arranged into two symmetrical bands running forwards from the blastopore (mesoderm-bands), the entoderm forms a solid strand, in which a cavity develops at a later stage. Not all the entoderm-cells, however, take part in the formation of this mid-gut strand. "A few of them form a covering to the food-yolk, and give rise to two large symmetrically-placed provisional hepatic vesicles." (?)

In *Moina*, the breaking-up of the mesoderm into somites and the development of a true coelom has not been observed. In the Branchiopoda, where the formation of the germ-layers is not yet known, we must fall back on observations recorded in connection with the larval stages of *Artemia* and *Branchipus*. In the earliest *Nauplii* of *Artemia*, there is, according to the figures of NASSONOW (No. 13), a temporary development of paired coelomic vesicles. In *Branchipus*, on the contrary, whose youngest or *Metanauplius* stage has been carefully investigated by CLAUS (No. 9), the process is different. Here the mesoderm in the region of the actual Nauplius segments and of the terminal segment has already become modified for the formation of organs, and has attained definite histological differentiation. The same is the case with the splanchnic layer along the whole of the alimentary canal (Fig. 88 *A*, *sp*, p. 179). In those segments which are interposed between the mandibular and the terminal segment, and are found in the act of appearing, the somatic layer bears a more embryonic stamp. It is here arranged in paired mesoderm-bands, whose cells appear to be segmentally arranged in a definite manner. This arrangement is due merely to a regular grouping of the mesoderm-cells, which to some extent recalls the arrangement described below (p. 137) in connection with the Isopoda. In the most posterior regions of the body, the mesoderm-bands are united to form a plate lying below the intestine, and here is found the budding zone, from which proceeds the formation of new segments. GROBBEN thought himself justified in assuming that two cells lying behind this budding zone, at the edge nearest the terminal segment, were primitive mesoderm-cells; but Claus proved that these cells, of which there are two on each side, in the stages hitherto examined, do not take part in the production of mesodermal elements. The most striking peculiarity in *Branchipus* appears to be the early development of the splanchnic mesoblast forming the intestinal muscles.

C. Cirripedia.

After the blastoderm is fully formed (*cf.* p. 111), the embryo of *Balanus* consists of a layer of cells (ectoderm) completely covering the surface of a central mass of food-yolk (Fig. 59 *B*). Near the posterior pole of the egg, where an insignificant depression (*bl*, the blastopore) is perceptible, the blastoderm consists of several layers. The deeper layers represent the rudiment of the entoderm (*en*) and the mesoderm (*ms*). From this point the mesodermal elements are distributed along the ventral side of the egg (Fig. 59 *C*) in the form of a symmetrical mesodermal plate, the ectoderm being correspondingly thickened, so that in this way a ventral thickening of the superficial layers of the embryo resembling a germ-band arises. The elements of the entoderm, on the contrary, are now evenly distributed through the food-yolk (Fig. 59 *C*, *en*); then, by a secondary cleavage of the yolk, the formation of definite cell-areas is brought about.* Finally the nuclei of the yolk-laden entoderm-spheres shift to the surface to form the epithelium of the mid-gut, whose cavity arises by the absorption of the food-yolk (*cf.* below, p. 174). The details of all these processes are still far from clear. Nassonow's text being in Russian, it was only possible to gather the most important points from the figures. It appears that the blastopore corresponds in position to the future anal aperture. These stages of

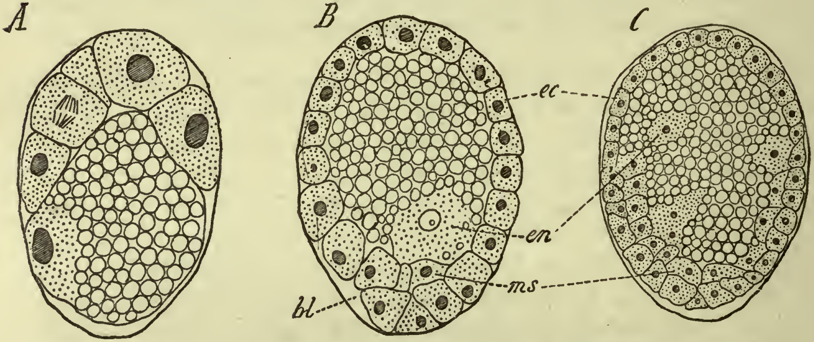

Fig. 59.—Longitudinal sections through three embryonic stages of *Balanus improvisus* (after Nassonow). *A*, later stage of segmentation (*cf.* above, Fig. 52, p. 111). *B* and *C*, stages in which the germinal layers are being formed. *bl*, blastopore; *ec*, ectoderm; *en*, entoderm; *ms*, mesoderm.

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* [See Groom (App. to Lit., Cirripedia I.). The cleavage of the yolk is not a sudden secondary process, but is complete from an early stage.—Ed.]

development should be further studied in NUSSBAUM's recent treatises (Nos. 30 and 31), which, in the important points, agree with the description here given. According to NUSSBAUM, the anterior cleavage-sphere produced by the first division yields a cap of cells which entirely grows round the second cleavage-sphere. When this circumcrescence is nearly completed, division of cells begins actively in the superficial layer near the pointed pole of the egg, where a gastrula-invagination now forms. The layer formed by this invagination, and which is now turned inward, starting from the pointed pole on one side, grows round the inner (food-yolk) sphere towards the blunt pole. "In the meantime this inner sphere (or the second lower cleavage-sphere) has also divided, and continues to divide ; but it is certain that the inner layer of cells of the gastrula are not formed from the cells derived from the inner or lower cleavage-sphere." According to NUSSBAUM, the anterior cleavage-sphere would thus yield not only the ectoderm, but the entoderm as well. The opposition between his view and that of NASSONOW is, however, lessened, if we may assume that the superficial layer of cells does not arise exclusively from the division of the anterior cleavage-sphere, but that other elements derived by micromere-formation from the posterior sphere also take part in it.* The latter would then play the same part as the central mass of food-yolk in other Crustacean eggs that have superficial cleavage.

The distribution of the mesodermal elements in the later embryonic stages, as well as in the young *Nauplius* stages of the Cirripedia appears to be irregular. GROBBEN (No. 21), however, found in the posterior part of the body of *Sacculina* and *Balanus* a few large cells, evidently caught in the act of proliferating, arranged on each side as a short mesoderm-band.

D. Decapoda.

The very primitive invagination-gastrula of *Lucifer*, which develops from a coeloblastula, has already been described (p. 108) and figured (Fig. 49 *C*—*cf.* BROOKS, Nos. 42 and 43). Unfortunately the stages which connect this gastrula with the *Nauplius* have not been investigated.

The development of the egg of *Lucifer* is characterised : (1) By the small quantity of food-yolk which at first appears equally distributed in the blastomeres, (2) by the very regular course of the cleavage and the development of a comparatively large blastocoele, (3) by the development of an invagination-gastrula. The archenteron thus arising has at its apex four spheres rich in food-yolk ; these spheres have been constricted off from the neighbouring entoderm-cells, and their significance is as yet undetermined. BROOKS considers them to be vestigial yolk-pyramids, which would correspond to the primary pyramids of *Astacus* and *Palaemon*. The form which resembles *Lucifer* most closely is perhaps *Penaeus*, inasmuch as the mid-gut here also develops direct from the primary invagination—archenteron (HAECKEL, No. 47).

Among the other Decapoda, a comparatively primitive position is occupied by *Astacus*, whose development has been made known chiefly by the researches of BOBRETZKY (No. 41) and REICHENBACH

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* [See GROOM, App. to Lit., Cirripedia I., and footnote, p. 112].

(Nos. 64 and 65). Its primitive character is shown by the fact that the cells of the gastrula-invagination retain their original connection, so that the archenteric vesicle persists as such until its transformation into the mid-gut, even although the abundant food-yolk here already somewhat modifies the development.

In *Astacus*, the blastoderm arises through purely superficial cleavage (Morin, No. 61). After the cleavage-nuclei have become arranged at the surface of the egg, the food-yolk which represents the separate cleavage-cells breaks up into the so-called *primary or Rathke's yolk-pyramids* (Fig. 55, p. 114), a spherical central mass remaining unaffected by this process of cleavage (*cf.* above, p. 109). After the separation of the blastoderm-cells from the food-yolk and the complete development of the blastoderm, the primary yolk-pyramids again fuse. At this stage, the rudiment of the embryo is perceptible on the ventral side of the egg as a thickening of the blastoderm, in which the rudiment of the future germ-band is visible. There are originally five distinct thickenings (Fig. 60) in connection with this rudiment, viz.—the two *optic lobes* (*K*), the two *thoraco-abdominal rudiments* (*TA*), and an unpaired thickening behind these, the entoderm-disc (*ES*), which in the next stage, by invagination, yields the archenteric vesicle (Fig. 61). The invagination of this disc is inaugurated by the appearance of a crescentic furrow enclosing its anterior edge; this soon becomes a circular furrow by the development of a posterior portion. In consequence of this, the central portion of the entoderm-disc, which has sunk below

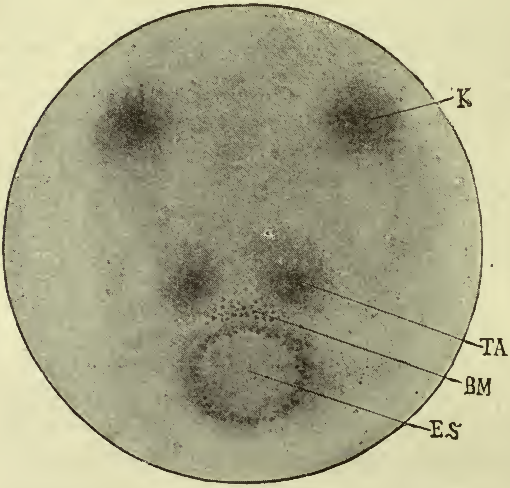

Fig. 60.—*Astacus fluviatilis*, part of the surface of an egg, with embryo beginning to form (after Reichenbach, from Lang's *Text-book*). *BM*, formative zone of the mesoderm; *ES*, entoderm-disc; *K*, cephalic lobes with the rudiment of the eyes; *TA*, thoraco-abdominal rudiments.

the surface, projects for a time in the form of a small mound into the lumen of the archenteric vesicle (entodermal mound, Fig. 62, *eh*). Even before the process of invagination begins, active proliferation of cells takes place at the anterior edge of the entoderm-disc (Fig. 60, *BM*); in this way a number of cells are produced which shift below the blastoderm (Figs. 61 and 62, *mes*). These form the first rudiment of the *mesoderm*, which thus, in *Astacus*, has its origin at a definite point on the anterior margin of the blastopore, where the ectoderm passes into the entoderm.

After the invagination of the gastrula is completed, the blastopore closes at a point corresponding to the most posterior portion of the embryonic rudiment. According to Reichenbach, this lies somewhat behind the spot at which the ectodermal proctodaeal invagination will arise later.

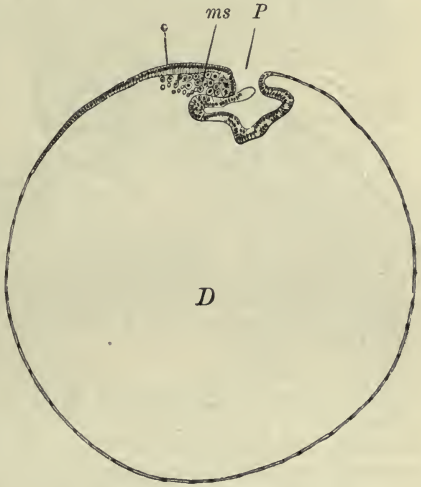

Fig. 61.—Longitudinal section through the gastrula stage of *Astacus fluviatilis* (after Reichenbach, from Hatschek's *Text-book*). *D*, food-yolk; *ms*, mesoderm; *P*, blastopore; * indicates the spot at which the anterior end of the body develops.

The archenteric vesicle which results from the invagination is at first small in relation to the size of the egg. Its cells increase in size later by absorbing food-yolk (Fig. 63 *A*, *en*), which is deposited in each individual entoderm-cell in such a manner that the nucleus and the principal mass of protoplasm come to lie on the outer surface of the archenteric vesicle. This absorption of food-yolk takes place most actively at the dorsal and lateral parts of the archenteric vesicle, the ventral wall, which is in closer contact with the other embryonic rudiments, taking a smaller share in this process (Fig. 63). Finally, the entire mass of food-yolk is absorbed by the entoderm-cells. These latter consequently swell into exceedingly large and columnar elements, arranged radially, and form the so-called *secondary yolk-pyramids.* This archenteric vesicle, the surface of which, in later stages, becomes divided into lobes, gives rise to the definitive mid-gut and liver (mid-gut gland)

of *Astacus.* The outer portions of the entoderm-cells, *i.e.*, t
and protoplasmic portions of the cells, increase in numbe
from their inner yolk-bearing portions, the yolk-pyramids
into contact with each other, thus forming the mid-gut
while the secondary yolk-pyramids break up and forr
yolk now situated within the archenteron, which is late
(*cf.*, for the development of the mid-gut, p. 174).

A remarkable arrangement of the rudiment of the mid-gut
Astacus, which was not noticed by Bobretzky and Reichenb
fore must be regarded as of only occasional occurrence, has
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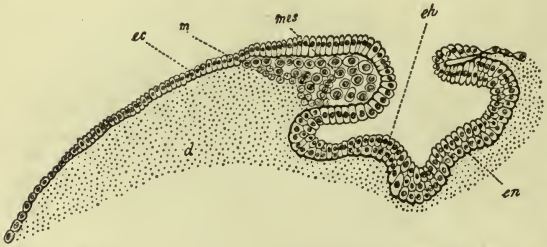

Fig. 62.—Median longitudinal section through the gastrula stage of *Astacus fluviatilis* (after Reichenbach). *d*, food-yolk; *ec*, ectoderm; *eh*, entoderm-mound; *en*, entoderm; *m*, secondary mesoderm; *mes*, mesoderm.

entoderm-cells; in later stages it seems to be absorbed.
compares it with those inner cells of the germ of the mi
Palaemon, which do not rise to the surface to form the e
eventually break up in the interior of the gut (*cf.* below, p.

The most characteristic feature in the development
of *Astacus* is that the food-yolk, which originally
gastrula-vesicle and fills the cleavage-cavity, is la
the wall of the entoderm-vesicle, and finally, in th
the mid-gut, reaches its lumen. All other Decapod
investigated differ from *Astacus* in the fact that
entoderm-vesicle lose their epithelial character, and
through the yolk as wandering cells, and only at a
unite at the surface of the yolk to form the ep
mid-gut. In these forms, the lumen of the original
disappears; the hepatic rudiment is solid as long a
cells are distributed in the yolk, and the lumen
arises only when, later, its contained yolk becomes
absorbed.

In *Palaemon*, for instance, according to Bobretzky (No. 41), a small gastrula-invagination (Fig. 64 *A*) develops at a time when the blastoderm is not completely formed, *i.e.*, when the blastoderm-cells have not separated from their yolk-pyramids over the whole circumference of the egg. The cells of this gastrula-invagination, after the closing of the blastopore, lose their epithelial character (Fig. 64 *B*). From the lateral walls of the entoderm-vesicle (*ms*), elements arise which, at a later stage, lying on the germ-band, represent the mesoderm, while the entoderm-cells arising from the floor of the vesicle (*en*) pass into the yolk, traversing it like wandering cells, and increasing in number within it. Each of these entoderm-cells swallows in an amoeba-like manner the surrounding food-yolk, so that the whole of the yolk

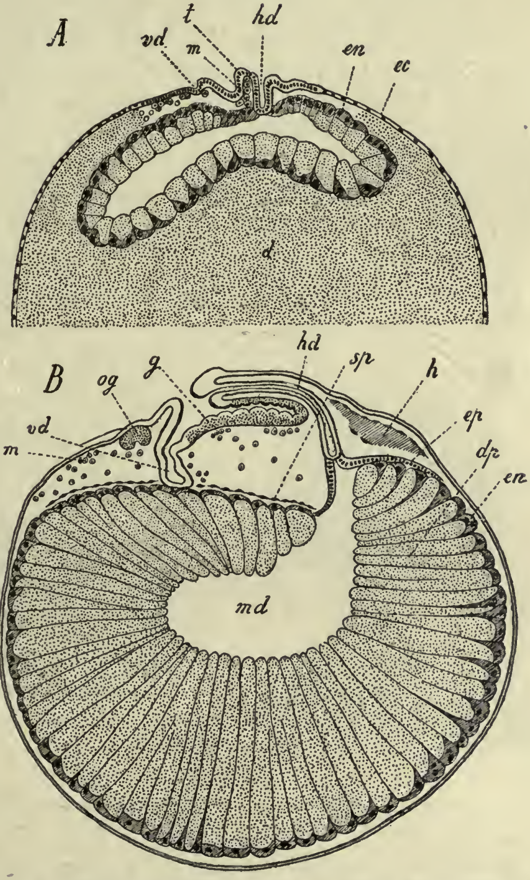

Fig. 63.—Median longitudinal section through two embryos of *Astacus fluviatilis* (after Reichenbach). *A*, section through the *Nauplius* stage. *B*, through the stage in which the rudiments of the ambulatory limbs have formed. *d*, food-yolk; *dp*, secondary yolk-pyramids; *ec*, ectoderm; *en*, entoderm; *ep*, entoderm plate; *g*, rudiment of the ventral chain of ganglia; *h*, rudiment of the heart; *hd*, hind-gut; *m*, mesoderm; *md*, mid-gut; *og*, supra-oesophageal ganglion; *sp*, splanchnic layer of the mesoderm; *vd*, fore-gut; *t*, thoraco-abdominal rudiment.

breaks up by an apparent secondary cleavage (the so-called cleavage of the yolk) into spheres, each of which represents an entoderm-cell; these spheres are a homologue of the secondary yolk-pyramids of *Astacus.* In later stages, the nuclei, each with a certain amount of protoplasm, rise to the surface of these yolk-pyramids, and there form an epithelium, which represents the wall of the mid-gut (Fig. 64 *C*), and which here, as in *Astacus,* contains within it the food-yolk. Another group of the entoderm-cells, however, seems to take no part in the formation of the mid-gut, but, remaining within the yolk, shares its fate in becoming broken up and finally re-absorbed. These cells must be considered as the homologue of the vitellophags to be described later (p. 134) in connection with *Mysis* (*cf.* also Bobretzky, No. 80).

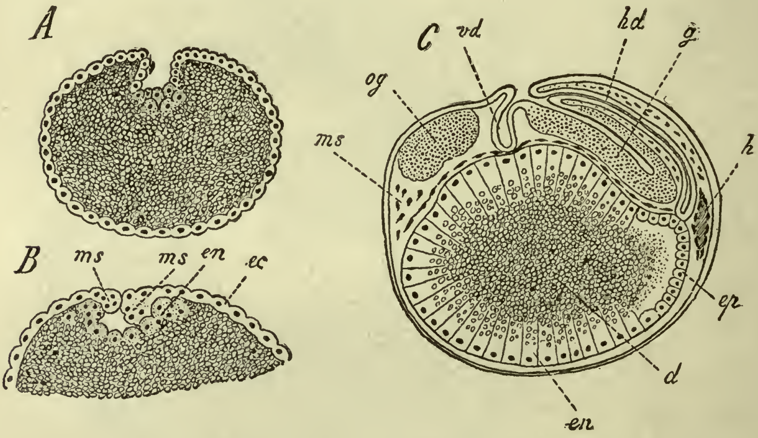

Fig. 64.—Three sections through the embryo of *Palaemon,* to illustrate the formation of the germinal layers (after Bobretzky, copied from W. Faxon's Selections from Embryological Monographs). *A*, gastrula stage. *B*, closing of the mouth of the gastrula. *C*, longitudinal section through a later stage. *d*, food-yolk; *ec*, ectoderm; *en*, entoderm; *ep*, mid-gut epithelium; *g*, ganglia of the ventral cord; *h*, rudiment of the heart; *hd*, proctodaeal invagination; *ms*, mesoderm; *og*, supra-oesophageal ganglion; *vd*, stomodaeal invagination.

In *Homarus*, according to Herrick (Nos. 50 and 50a), in place of the invaginate gastrula, there is a quite shallow depression, starting from which a solid wedge-like growth of cells (the keel) passes into the yolk. The cells derived from this ingrowth soon absorb the yolk-elements.

The immigration of amoeboid entoderm-cells into the food-yolk, and the formation of the epithelium of the mid-gut at the surface of the latter appears, in many cases, to be carried out in the manner already described. The relation of the wandering entoderm-cells to the food-yolk varies, however, in individual cases. Thus, according to P. Mayer (No. 59), in *Eupagurus*, after the immigration of the entodermal elements, the food-yolk undoubtedly breaks up into a number of irregular portions and undergoes a kind of re-arrangement, although the entoderm-cells do not here contain these masses of food-yolk, but occupy the intervening spaces. The same is perhaps the case in *Atyephyra* (Ischikawa, No. 51). In *Crangon* and *Alpheus*, on the contrary, nothing in any way resembling the secondary cleavage of the yolk is apparently to be found (Kingsley, No. 53, and Herrick, No. 49).

In all these cases, the formation of the germ-layers begins with the development of a gastrula. Some recent researches by Lebedinsky (No. 57) as to the formation of the germ-layers of a Brachyuran, *Eriphia spinifrons*, seem to us to require further explanation. Here also there is a gastrula-invagination, from the inner portion of which the entoderm-cells that immigrate into the yolk proceed, while, from the lateral walls of the vesicle, the mesoderm proliferates. Nevertheless, even before the development of this invagination, a separation into three layers lying one above the other, and corresponding to the three germ-layers, could already be made out in the multilaminar germ-disc. Further, the ectoderm of the germ-band is said to give off mesodermal elements along its whole inner surface by the division of its cells. The entoderm-cells scattered in the food-yolk finally rise to its surface and there become arranged to form the wall of the mid-gut. At the same time, however, the food-yolk breaks up into columnar masses corresponding to the separate cell-areas, so that here also, at a late stage, secondary yolk-pyramids are developed.

The mesoderm arises in *Astacus* (Bobretzky, No. 41, and Reichenbach, Nos. 64 and 65) and in *Eupagurus* (Mayer, No. 59) from a definite point at the anterior margin of the blastopore (Figs. 60, *BM*, and 62, *mes*). Other authors have less definitely assigned its origin to the neighbourhood of the blastopore (Kingsley, No. 53, for *Crangon*, Haeckel, No. 47, for *Penaeus*), or to the lateral walls of the archenteron (Bobretzky for *Palaemon*, No. 41, and Lebedinsky for *Eriphia*, No. 57). The first rudiment of the mesoderm is always multicellular. Its cells, which rapidly increase by division, spread out apparently in an irregular manner between the ectoderm of the germ-band and the food-yolk (Fig. 63, *m*). Only in a few stages is the distribution of the mesodermal elements into paired mesoderm-bands perceptible. The indications of its division into segments is equally slight. In *Astacus*, a grouping of the mesodermal elements into paired segmentally-arranged coelomic vesicles was found by Reichenbach only in the abdomen at quite a late stage, when the abdominal limbs had already begun to form. In the anterior region of the body, coelomic vesicles evidently do not develop, the body-cavity at this part having the character of a pseudocoele.

Besides the usual mesodermal cells, Reichenbach found, in the mesodermal rudiment, smaller cells whose protoplasm exhibited a peculiar foam-like structure (Fig. 62, *m*, and Fig. 82 *A*, *sm*, p. 161), and which contained several very small deeply staining nuclei. These, which were defined by him as elements of the *secondary mesoderm*, are said to originate by a process of endogenous cell-formation* in the entoderm-cells of the ventral wall of the gastrula-vesicle. These secondary mesoderm-cells disappear later, and REICHENBACH holds that they are transformed into blood-corpuscles. A similar secondary mesoderm has been observed by ISCHIKAWA in *Atyephyra*, and by LEBEDINSKY in *Eriphia*, and further by HERRICK in *Alpheus* and *Homarus*.

E. Schizopoda.

The formation of the germ-layers in the Schizopoda is best illustrated by the observations of J. NUSBAUM on *Mysis chamaeleo* (Nos. 38 and 39). Cleavage is here discoidal (*cf.* p. 116). The first cleavage-nucleus attains an entirely superficial position, and yields, by division, a rounded germ-disc, corresponding in position to the ventral side of the egg and the later posterior end of the body. Even from the earliest stages, the germ-disc can be seen to be composed of two layers. The more superficial of these two layers spreads out more and more, finally covering the whole egg as a delicate blastoderm, while the cells of the inner layer pass into the food-yolk, become distributed within it, and are an essential factor in its disintegration, engulfing the yolk and digesting it like amoebae. These so-called *vitellophags* are commonly said to take no part in the later formation of the embryo; it is, however, possible that, at a later stage, they form blood-corpuscles.

After the complete development of the blastoderm, the position of the former germ-disc is still indicated by a thickening which soon differentiates into three lobes. Two lateral lobes grow out anteriorly to form the lateral paired halves of the germ-band, while the unpaired, median and somewhat posterior lobe must be considered as the caudal or *abdominal rudiment* (Fig. 77 *A*, p. 153). In this latter region, below a transverse furrow which must doubtless be referred to an ingrowing caudal fold, the entoderm arises by delamination from the cells of the inner layer. The mesoderm, on the contrary, is said to arise from the ectoderm along the whole length of the paired lateral halves of the germ-band, either by the division of individual blastomeres, the inner portions of which shift into the mesoderm-layer, or else by the immigration of complete blastomeres. In the *Nauplius* stage, the mesoderm-layer thus formed shows not only a distinct arrangement into paired mesoderm-bands, but a division of the same into separate segments; the formation of coelomic sacs, on the other hand, has never been observed.

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* [Recent research on cell-division has shown that most of the cases in which cells are said to arise by endogenous cell-formation can be differently interpreted. The whole theory of endogenous cell-formation is indeed very improbable.—ED.]

Assuming that the foregoing observations are correct, the most striking feature in the development of *Mysis*, apart from the absence of the gastrula-invagination,* is the relation of the entoderm to the food-yolk. The rudiment of the entoderm here remains in close connection with the germ-band (Figs. 65, *en*, *l*, and 66, *l*), and does not enter into any closer relations to the food-yolk, except at the close of development, when it grows round the yolk to form the mesenteron. The disintegration of the food-yolk is here not achieved by the actual entoderm-cells, but by the vitellophags above mentioned. We are none the less led by a comparison with *Astacus* and *Palaemon* to see, in both these elements, constituent parts of the entoderm. Even in *Astacus*, it was evident that the cells of the ventral wall of the entoderm-vesicle took little part in the assimilation of the food-yolk. From this region, especially from the point lying immediately upon the

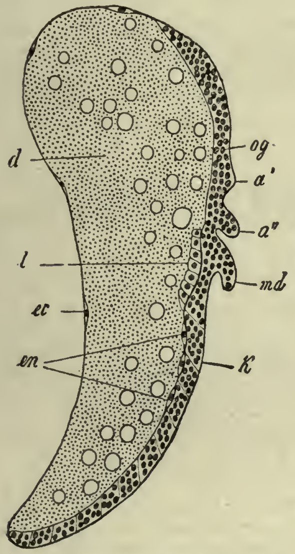

FIG. 65.—Longitudinal section (somewhat lateral) through the *Nauplius* stage (*cf.* Fig. 77 *C*) of *Mysis* (after NUSBAUM) *a'*, first antenna; *a''*, second antenna; *d*, food-yolk; *ec*, ectoderm; *en*, entoderm; *k*, germ-band; *l*, rudiment of the liver; *md*, mandible; *og*, rudiment of the optic ganglion.

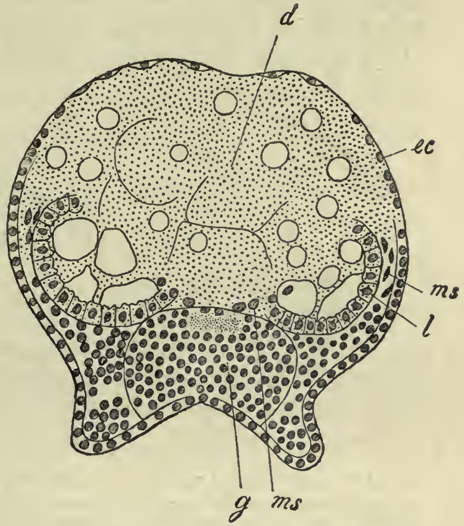

FIG. 66.—Transverse section through a somewhat older stage of *Mysis* (after NUSBAUM). *d*, food-yolk; *ec*, ectoderm; *g*, rudiment of the ventral ganglia; *l*, hepatic rudiments; *ms*, mesoderm.

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* According to WAGNER, of whose treatises only the second has come into our hands, the gastrula-invagination appears, in *Mysis*, to be represented by an ingrowth of cells in which, later, a fissure-like cavity appears (No. 40).

blind end of the hind-gut (Fig. 63 *B*, *ep*), the development of the definitive wall of the mid-gut proceeds in the Decapoda (*cf.* below, p. 174). In *Palaemon*, on the other hand, it was observed that not all the entoderm-cells to be found in the food-yolk rise to its surface, to take part in the formation of the epithelium of the mid-gut, but that individual cells remain within the yolk and are later absorbed. We thus see here the beginning of a differentiation of the entoderm into two parts, a plastic portion taking part later in the development of the mesenteron and a transitory portion, the cells of which function solely as vitellophags. A similar condition of the entoderm will be found repeatedly in other animals, especially among the Insecta.

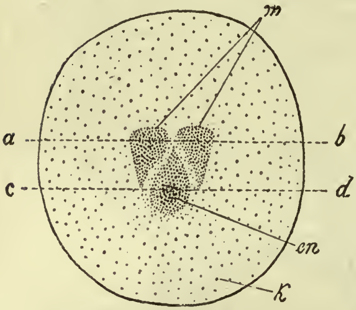

Fig. 67.—Surface view of the egg of *Ligia oceanica*, at the stage in which the germ-layers appear (after Nusbaum). *en*, point of ingrowth of the entoderm; *k*, blastoderm-nuclei; *m*, paired points of ingrowth of the mesoderm.

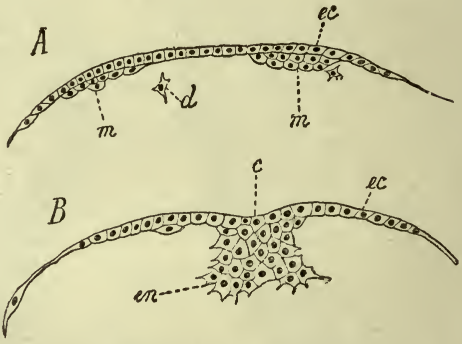

Fig. 68.—Two transverse sections through the germ-disc of *Ligia oceanica* (after Nusbaum). *A*, transverse section through the anterior region, on the level *ab* in Fig. 67. *B*, transverse section through the posterior region on the level *cd*, Fig. 67. *d*, yolk-cells; *ec*, ectoderm; *en*, entoderm; *m*, mesoderm; *c*, central depression of the germ-disc (blastopore).

F. Arthrostraca and Cumacea.

Nusbaum's observations on the development of the *Mysidae* are closely connected with his studies of *Ligia oceanica* (No. 85a), and afford to a certain extent a key to the comprehension of the formation of the germ-layers in the former group. Here also, after the development of the blastoderm is completed, a thickening is found corresponding to the future ventral side; this is the *germ-disc*, which soon shows signs of breaking up into three parts (Fig. 67). The two anterior paired portions represent the areas of formation of the mesoderm (Fig. 67, *m*), while the posterior unpaired thickening (*en*), in which, especially at the centre, very active ingrowth of cells takes place, yields the elements of the entoderm (*cf.* the cross sections, Fig. 68 *A* and *B*). The processes here revealed are easily connected with the type of germ-layer formation found in *Astacus.* The posterior unpaired formative zone of *Ligia* is comparable with the entodermal area (Fig. 60, *ES*) in *Astacus*, which becomes invaginated later, and anteriorly to which is found the zone of formation of the mesoderm (*BM*). The latter, in *Astacus* also, according to Reichenbach, shows, even in early stages, a distinct bilateral symmetry in the distribution of its elements. In *Ligia*, these are found distributed in two paired areas of formation corresponding with the two halves of the later germ-band. In what way the formation of the actual germ-band out of these zones proceeds is not known in detail. We may, however, assume that the elements of the mesoderm shift anteriorly below the ectoderm, and that the part of the ectoderm lying above them thickens. In any case, later stages of *Ligia* and *Cymothoa* afford a distinct proof that the zone of formation of the mesoderm just described must be considered as answering to the posterior end of the future germ-band. For, in the *Nauplius* stage of *Ligia* (Fig. 69), behind the third pair of limbs (*3*), and situated anteriorly to the rudiment of the anal aperture (*a*), there is found a formative zone (*k*) for the posterior end of the body which develops in this region. This formative zone already consists of two layers (ectoderm and mesoderm), the cells of which, by division, have yielded a transverse row of large formative cells lying posteriorly in front of the anal aperture (*a*); the arrangement of these cells into transverse and longitudinal rows, both in the ectoderm and the mesoderm, is exceedingly regular. According to Patten (*Quart. Journ. Micro. Sci.*, Vol. xxxi., 1890, p. 371), in each of the transverse rows on either side, in *Cymothoa*, lie four mesoderm-cells (Fig. 70, *ms*), by whose increase in number in the anterior and more advanced segment-rudiments, the mesoderm of the whole segment is developed, in such a way that the descendants of the three lateral cells become connected, while the fourth more medianly placed cell unites with the corresponding cell of the other half of the body to form a common complex. This unusually regular arrangement of the cell-material in the developing segments of the posterior part of the body, recalls the very similar conditions observed by Claus in the same region of the embryo of *Branchipus.* On the other hand, the arrangement of the mesoderm-cells in a longitudinal row running forwards through all the segments, calls for comparison with conditions observed in the Oligochaeta by Wilson, and more recently by Bergh (Vol. i., p. 294, note). The symmetrical growth of the mesoderm-bands appears, however, to prove that in *Ligia* and *Cymothoa*, the two original formative zones of the mesoderm correspond in position to the posterior end of the future germ-band. We may therefore suggest that this is the case in *Mysis* also, and that the two lateral lobes of the germ-disc above-mentioned answer to the paired zone of formation of the mesoderm. In this case we might assume that the entire mesoderm of the germ-band arises by proliferation which starts from this formative zone, and not, as Nusbaum assumes for *Mysis*, by a kind of delamination from the inner surface of the ectoderm of the germ-band.

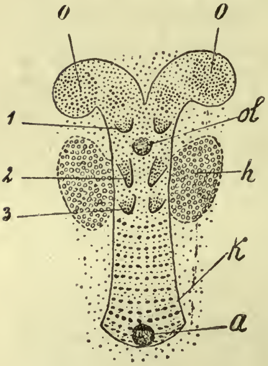

Fig. 69.—Germ-band in the *Nauplius* stage of *Ligia oceanica* (after Nusbaum) *a*, anus; *h*, entoderm-lobes (hepatic rudiments); *o*, optic-lobes; *1*, *2*, *3*, first, second, and third pair of Nauplius limbs; *ol*, upper lip; *k*, formative zone of the segments.

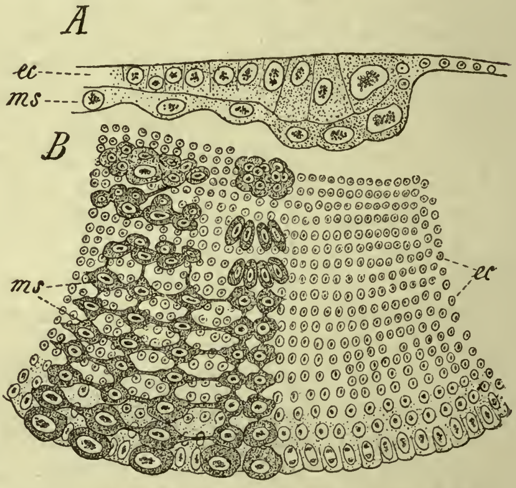

Fig. 70.—A portion of the segment-forming zone of the germ-band in *Cymothoa* (after Patten). *A*, median longitudinal section. *B*, inner aspect of the posterior end of the germ-band (Fig 69). On the right the three lateral cells of the mesoderm-layer are omitted. *ec*, ectoderm; *ms*, mesoderm.

In *Ligia* and in the Isopoda generally, there is only a small number of yolk-cells, which play the same part as those of *Mysis*. These separate in early stages from the lower layer of the embryonic rudiment, wander into the yolk, as vitellophags take part in its disintegration, and finally disappear. The actual entoderm does not here pass into the yolk, but forms a paired mass of cells, which remains in close connection with the germ-band and soon becomes arranged in two halves (Fig. 69, *h*). As to the way in which the future mid-gut is formed out of these rudiments, Nusbaum's account is not very clear. The two rudiments unite in the anterior part of the embryo, and there form the wall of the mid-gut; two channel-like processes also grow out posteriorly; these are open and concave towards the yolk, and convex externally, and are closely applied to the germ-band; they are the rudiments of the primary hepatic tubes, which only at a later stage divide into four by longitudinal constriction. The rudiment of the mid-gut is covered posteriorly and dorsally by the mass of yolk. This latter, as the entoderm-cells increase in number by division, becomes completely surrounded by the epithelium of the mid-gut, and in this way this rudiment which, in the younger stages, was open dorsally, becomes gradually closed. The mid-gut rudiment in *Ligia*, as in *Porcellio*, is fairly large, whereas in *Oniscus* it seems to be limited to the hepatic outgrowths and the parts of the intestine lying immediately adjacent to their openings.

The method of formation of the germ-layers which has been described by Nusbaum for *Ligia* may, perhaps, be fairly common among the Isopoda, although our knowledge of these processes is still too incomplete to enable us to form a decided opinion on the subject. One of the forms in which the origin of the germ-layers is best known is *Oniscus*. Here also the blastoderm is said (Bobretzky, No. 80) to arise by discoidal cleavage, although, perhaps, it may belong to our Type III. *b* (p. 115).* That region of the surface at which the blastoderm first appears is here also, as in *Mysis* and *Ligia*, indicated, at a later stage, by a rounded thickening, the *germ-disc*. This corresponds with the future ventral surface of the embryo, and yields the germ-band. The formation of the germ-layers (as in *Ligia*, but without previous demarcation of the mesodermal and entodermal areas) is commenced by an immigration of cells at the centre of the germ-disc. The gastrula-invagination is here replaced by a simple ingrowth of cells, by means of which the germ-disc becomes multilaminar. While its outer layer is transformed into the ectoderm of the germ-band, the inner layer yields the mesoderm and the entoderm. Bobretzky (No. 80), to whom we owe the first comprehensive description of the development of *Oniscus*, observed that from the inner layer single cells wander into the food-yolk, traverse it, and by increasing in number within it, bring about by a kind of secondary cleavage the disintegration of the yolk (Fig. 71, *hy*). These cells are said to represent the entoderm, and later, like the cells in the yolk of *Palaemon*, to give rise to the mid-gut (especially to the liver). The cells of the intermediate layer which remain close to the germ-disc are, on the contrary, said to represent the mesoderm (Fig. 71, *m*). Nusbaum has recently

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* This view is also in agreement with the observations of Roule (No. 92), although these latter are far from clear. According to this author, a superficial layer of cells forms in *Porcellio*; this increases by the addition of new protoplasmic elements from the yolk. The nuclei in this layer of cells are, however, said to arise spontaneously. This blastoderm, which Roule calls an ectoderm, first appears in the anterior part of the embryo, spreads back from here over the ventral surface, and finally also spreads over the dorsal surface. The inner mass of food-yolk, enclosed by this cell-layer, is assumed by Roule to be the meso-entoderm.

opposed this view (No. 85), maintaining that the yolk-cells, which, further, immigrate not merely from the germ-disc, but from the whole circle of the blastoderm, take no part in the further structure of the embryo, but merely function, as in *Mysis* and *Ligia*, as *vitellophags.* According to NUSBAUM, the actual entoderm in *Oniscus* originally lies, united with the elements of the mesoderm, in the inner layer of the germ-disc, soon, however, becoming arranged into two lateral masses of cells, which fuse and form the mid-gut rudiment, as well as the hepatic diverticula (Fig. 71 *B*, *li*). In *Oniscus*, the two primary hepatic diverticula seem to develop before the mid-gut; a band-like entoderm-rudiment starts from the cell-masses above mentioned, and bends round on each side to form a hepatic diverticulum; these two unite at a later stage, when a short mid-gut develops. In *Porcellio*, on the contrary, according to REINHARD (No. 91), the mid-gut forms before the hepatic diverticula become marked off. The two primary hepatic diverticula divide later into four by longitudinal constriction. It should be noted that the mid-gut in *Oniscus*, as generally in the higher Crustacea, is restricted to a very short tract near the openings of the hepatic diverticula, the larger portion of the alimentary canal arising from the stomodaeum and the proctodaeum. During these processes of development, the layer of mesoderm-cells spreads regularly below the lengthening germ-band, and enters into the rudiments of the limbs. It must be mentioned, however, that according to WASILJEFF (see GROSGLIK, No. 84), the mesoderm, in *Oniscus*, breaks up into somites.

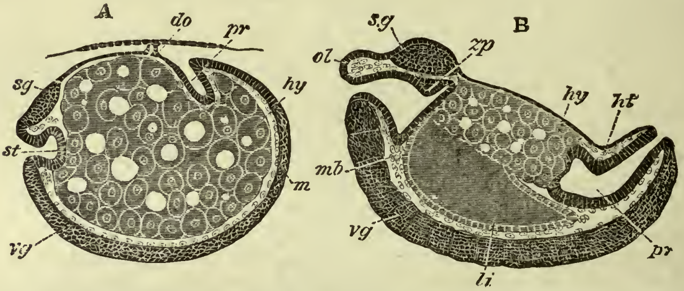

FIG. 71.—Two longitudinal sections through the embryo of *Oniscus murarius* (after BOBRETZKY, from BALFOUR'S *Text-book*). *A*, younger, *B*, older stage. *do*, dorsal organ; *hy*, food-yolk with yolk-cells; *ht*, rudiment of the heart; *li*, liver; *m*, *mb*, mesoderm; *ol*, upper lip; *pr*, proctodaeum; *sg*, brain; *st*, stomodaeum; *vg*, ventral nerve-cord; *zp*, rudiment of the gastric teeth.

Considerable agreement will be found in this description of the formation of the germ-layers in *Ligia* and *Oniscus*, which rests chiefly on NUSBAUM'S observations, and is supported by BULLAR'S work on *Cymothoa* (No. 81), and the results obtained by PEREYASLAWZEWA (Nos. 70 and 71) and ROSSIJSKAYA (Nos. 72 and 73) with the eggs of various Amphipoda (*Gammarus poecilurus*, *Orchestia*, *Caprella*, *Sunamphithoë*, *Amphithoë*). The elements of the entoderm here arise from an immigration of separate blastomeres into the deeper layers; these, after dispersing temporarily in the food-yolk, soon become arranged into two lateral entoderm-bands, which first appear in the anterior part of the embryo and join to form the tube of the mid-gut. The primary hepatic diverticula form as outgrowths of the mid-gut, the two soon dividing into four. The process in *Caprella* and *Sunamphithoë* differs in so far that, in these genera, the rudiments of the hepatic tubes become differentiated before the rest of the mid-gut. In this respect the above forms resemble *Oniscus.* The mesoderm, on the contrary, is said to arise at a comparatively late stage in the rudiments of the individual limbs, by a kind of delamination from the ectoderm (?).

The Cumacea agree most nearly with the Isopoda in the formation of the germ-layers, the position and form of the germ-band, and of the dorsal organ. In them, discoidal cleavage gives rise first to a rounded disc, which gradually grows over the surface of the egg. Before, however, the blastoderm is completely formed, a proliferation of cells at the centre of the disc takes place, leading to a massing of the cells beneath the blastoderm. In these inner cells, two layers, mesoderm and entoderm, are soon discernible. These processes are very similar to those described by BOBRETZKY for *Oniscus.* The two lower layers then spread along a band-like area on the ventral side of the egg, the area in this way developing into the embryonic rudiment or "germ-band." The latter is not confined to the ventral side, for its anterior and posterior ends soon spread over the dorsal parts of the egg. At the same time a mass of cells, known as the "dorsal organ" (p. 150), develops on the dorsal side. In all these ontogenetic processes the food-yolk apparently takes no active part. At first, also, no cell-elements are perceptible in the yolk, but after the germ-band has developed, isolated crescent-shaped cells, each enclosing a granule of yolk, appear within it. There are also quite isolated, large, finely granulated cells in the food-yolk. These cells do not appear to assist in any way in the development of the mid-gut, and their function is still uncertain. In later stages (when the limbs develop) the food-yolk has been observed to break up into large spheres (H. BLANC, No. 35).

G. General Considerations.

We have first to consider the position of the blastopore. If, in this respect, we institute a comparison with allied groups of animals, especially with the Annelida (see Vol. i., p. 265, the closing of the blastopore in *Eupomatus*), we should similarly be inclined to regard as the blastoporal region in the Crustacea the whole area lying between the mouth and the anal aperture. Such an extension of its position is indicated, however, in the ontogeny of only a very few forms; for example, in the fissure-like primitive mouth of *Cetochilus*, which closes from before backwards (GROBBEN, p. 121), and in the forward extension of the point of ingrowth of the entoderm in *Ligia* (Fig. 67, p. 136), between the two mesoderm-germs. In by far the greater number of cases, the observations made suggest that the blastopore corresponds in position to the posterior end of the germ-band, and perhaps to the anal aperture which forms later. We must here, however, bear in mind the extreme shortness of the first embryonic area (germ-disc) in many Crustacea, and imagine that as this short rudiment developed to form the longer germ-band, elements which originally lay in the region of the closing blastopore came, through the changes in position that take place during growth, to lie more anteriorly, so that, perhaps, the blastopore in the Crustacea ought to be regarded as having a greater extension forward than is usually claimed for it.

If we consider that the position of the future posterior end of the body and the vegetative pole of the egg is indicated by the closing of the blastopore, we should then (taking into account the conditions in the Annelida) assume for the position of the anterior end, the rudiment of which is distinctly indicated by the development of the cephalic lobes (optic lobes), the diametrically opposite point of the periphery of the egg. Such a position is only, however, approximately gained by the cephalic lobes in a few cases (e.g., *Moina*, Fig. 58 *C*, *b*, *s*, p. 124, and *Cetochilus*). In eggs rich in yolk, the cephalic lobes and the blastopore belong to the same hemisphere of the egg, and lie more or less close to one another (see Fig. 61, p. 129, where the anterior end of the body is indicated by a star). It is thus evident that, within the egg, the rudiment of the future ventral surface is much shorter than that of the dorsal side, or, in other words, the dorsal side of the embryo seems considerably swollen by the deposit of masses of food-yolk, and is correspondingly retarded in its development. The food-yolk sphere thus lies excentrically with relation to the longitudinal axis of the developing embryo, being shifted dorsally. Comparison with the Vertebrata, where the blastopore lies dorsally and the food-yolk shifts to the ventral side, is in many respects instructive (p. 118).

When we come to consider the manner in which the germ-layers develop, taking first the origin of the **entoderm**, we find that only a few forms, with eggs comparatively poor in yolk, show a primitive condition which can be compared directly to the method of development among the Annelida. Here again *Cetochilus* must be mentioned first, as showing an archenteric vesicle arising by invagination which, after the blastopore has closed, probably becomes transformed direct into the rudiment of the mid-gut. *Moina*, and perhaps also *Lucifer* and *Penaeus*, seem to approach *Cetochilus* in this respect. On the whole, the formation of the entoderm by invagination is fairly common among the Crustacea. In other cases—Arthrostraca, *Mysidae*, Cumacea, Cirripedia (?)—an invagination does not occur, the entoderm appearing as a solid ingrowth of cells (Fig. 68 *B*, p. 136).

Important and characteristic variations in the fate of the mass of entoderm-cells are to be found in the development of Crustacean eggs rich in yolk. In those processes by which the rudiment of the mid-gut with its hepatic diverticula becomes differentiated, the relation of the masses of food-yolk to this rudiment produces a marked influence. At the beginning of development, after the blastoderm has formed, the blastocoele appears filled with food-yolk. As a consequence, when gastrulation commences, the nutritive yolk lies outside the archenteric vesicle in the so-called primary coelom. Later, however, the rudiment of the mid-gut is, as a rule, developed in such a way that it contains within it the whole of the food-yolk. A change has thus taken place in the relative position of the rudiment of the entoderm and the yolk. This change may take place in three different ways in the Crustacea, giving rise to three different types of development of the mid-gut, which may be characterised as follows:—

I. Development of the mid-gut through the filtration of the food-yolk, *e.g.*, in *Astacus* (Fig. 63, p. 131). The food-yolk which lies in the primary coelom is gradually taken up into the entoderm-cells. When this process is completed, the secondary yolk-pyramids having developed, the nuclei of the entoderm-cells shift to the surface of the yolk, where, with the protoplasm surrounding them, they form the epithelium of the mid-gut, within which the whole mass of yolk is ultimately situated. The typical feature of this process is that the archenteric cavity formed by invagination persists throughout development, the lumen of this vesicle passing into the lumen of the future mid-gut. The entoderm-cells, further, never lose their epithelial continuity. The food-yolk, originally lying outside the entoderm-vesicle, first enters the wall of this vesicle and finally passes into its lumen. This method of formation of the mid-gut, of which *Astacus* is the only case known, appears to stand quite alone; it is of all the greater interest as affording a key for the comprehension of the two other types of development.

II. Development of the mid-gut by the interpenetration of the food-yolk, *e.g.*, *Palaemon* (Fig. 64, p. 132). The cells of the gastrula that arise by invagination here very soon lose their epithelial continuity, the archenteric vesicle itself apparently disappearing in this process. The entodermal elements, in the form of amoeboid wandering cells, pass separately into the yolk and traverse it, finally becoming arranged at its surface to form the epithelium of the mid-gut. It is evident that in this case also the direction in which the entoderm-cells move is the same as in Type I. The difference between the two types consists in the fact that in the type we are considering, the wall of the archenteron temporarily loses its continuity. So as to deduce this type from the last, we should have to imagine that, in consequence of the small number of the entoderm-cells and the greater volume of the yolk, the intervals between the entoderm-cells, as they shifted apart during the increase in size of the archenteron, became so great that the epithelium could not retain its continuity. The temporary independence of the entodermal wandering cells appears, however, to have afforded a simplification of the process of development, by means of which the commencement of immigration into the yolk was made possible at an earlier stage. This second type of development seems to be very common among the Crustacea. It is found in most Decapoda, and apparently also in the eggs of many Entomostraca which abound in yolk (those of the Cirripedia, Copepoda, Cladocera). We shall also find it in many other groups of Arthropoda, *e.g.*, *Limulus*, the Araneae, etc. During the process of wandering through the food-yolk, the scattered entoderm-cells frequently give rise to a secondary demarcation of the yolk into the cell-areas; this has been called *yolk-cleavage*, but has, of course, no connection with actual cleavage, which must be regarded as concluded when the blastoderm has developed.

III. Development of the mid-gut by circumcrescence of the food-yolk, *e.g.*, *Mysis* and *Ligia* (Fig. 66, p. 135). Here, as in the preceding type, individual cells become separated from the mass of entoderm-cells (which, in forms belonging to this type, always arises by solid ingrowth); these separated cells enter the yolk and become scattered within it. They do not take any part in the later structure of the mid-gut; as *vitellophags* they assimilate food-yolk and either become disintegrated later, or else, perhaps, persist as blood-corpuscles. The chief mass of entoderm-cells, however, does not join in this immigration, but remains near its place of origin at the surface of the yolk, and changes later into two paired, disc-shaped layers of entoderm-cells, which lie below the germ-band, and, as the cells increase in number by division, spread out gradually over the surface of the yolk until they completely surround it. The entoderm has here, as explained on p. 136, divided into two parts, one plastic and the other transitory. We may further recall that in Type II. also, not all the wandering cells scattered through the yolk came to the surface (p. 132) to take part in the formation of the mid-gut epithelium, but that some of them remained in the yolk and finally disintegrated. Such cells evidently correspond to the vitellophags in this type. The actual key to the processes here described is to be found by a close examination of the method of development already described for *Astacus*. We have shown (p. 129) that the cells of the entoderm-vesicle in *Astacus* do not participate alike in the absorption of the food-yolk. Those of the dorsal half are most concerned in this process, while those of the ventral half are less affected by the filtration of the yolk. It is from the latter cells, however, that the formation of the definite mid-gut at first proceeds. We find first, near the blind end of the proctodaeum, a plate of entoderm-cells (Fig. 63 *B*, *ep*), which already shows the distinctive characters of the mid-gut epithelium, and has a certain tendency to overgrow the other unmodified parts of the entoderm. A precisely similar entoderm-plate is also developed in Type II. (Fig. 64 *C*, *ep*), so that there also some of the entoderm-cells scattered in the yolk show greater plastic capacity than the rest. We thus find here a beginning of a division of labour which is completely developed in Type III. (*cf.* p. 136). To Type III. belong the *Mysidae*, the Arthrostraca, and the Cumacea (?). This type is found also in other divisions of the Arthropoda, modified in various ways; it is met with, for instance, in the Scorpiones and in the Insecta.

Mesoderm. Only in the small egg of *Cetochilus* does the mesoderm arise from paired primitive mesoderm-cells. In most Crustacea the rudiment is from the first multicellular. Among the many accounts of the origin and position of the mesoderm in the various groups of the Crustacea, its first appearance (in the Decapoda) at the anterior part of the lip of the blastopore may be regarded as a comparatively primitive process, from which it is possible to deduce the process described for *Ligia* (p. 136), and, through this form, perhaps, that in many other Crustacea.

It is a striking fact that there is very little tendency in the cells of the mesoderm from the very first to form regular layers. Mere indications of an arrangement into a paired band and a segmentation of such a band can be found. Here again we are reminded of *Ligia* and *Cymothoa.* Only a few slight observations are recorded as to the appearance of metameric coelom-sacs; these have already been alluded to (pp. 122, 133, and 140). As a rule, the body-cavity of the Crustacea develops like a pseudocoele as a system of irregular lacunar spaces within the mesoderm. The more these spaces extend, the greater must be the interval between the surface of the body and the mass of food-yolk enclosed by it. The cavity of the coelom is, as a rule, filled with fluid; though it should be mentioned that Nusbaum found masses of food-yolk filling the spaces in the anterior part of the embryo of *Mysis.*

4. Development of the External Form of the Body.

A. Entomostraca.

In Entomostraca whose eggs are poor in yolk, the embryos often hatch at an early ontogenetic stage (as *Nauplii*); here the form of the larval (Nauplius) body evolves very gradually from the spherical shape of the egg. As the egg lengthens, the boundaries of the separate segments of the Nauplius body appear as transverse constrictions, while the limbs arise as outgrowths of the surface of the body (Fig. 72 *A*), in which both the ectoderm and the subjacent cell-mass of the mesoderm take part. These processes are to be observed in the embryos of *Branchipus*, free-living Copepoda and Cirripedia, and also in certain Cladoceran embryos distinguished by the paucity of food-yolk (*Moina*, Grobben, Fig. 72). In the embryos of those forms which pass the *Nauplius* stage within the egg, when the posterior body-segments develop and the embryo thus lengthens, a dorsal curvature of these segments takes place (*Apus productus*, Brauer; *Moina*, Fig. 72 *B* and *C*, Grobben). In these cases, the rudiment of the cephalic carapace or shell (*s*) can be made out early as a folding of the dorsal integument at a point corresponding to the maxillary region.

The development of the embryo in the yolk-laden eggs of many Cladocera (*e.g.*, *Daphnia longispina*, Dohrn, No. 10, and *Leptodora*, P. E. Müller, No. 12) pursues a different course. In these embryos, a certain contrast between the embryonic rudiment which lies primitively on the ventral side of the egg and the dorsally-placed mass of food-yolk is recognisable. This distinction is still more evident in the embryos of parasitic Copepoda (Fig. 73 *A* and *B*, Rathke, No. 89, and Van Beneden, No. 17), in which a short ventral *germ-band* is already clearly distinguishable from a dorsal mass of yolk.

With regard to the order in which the body-segments develop, the general rule is that the rudiments of the most anterior segments appear first, while from a budding zone at the posterior end of the body, but in front of the terminal or anal segment, which develops early, new segments are successively formed. The pairs of limbs develop correspondingly from before backwards, although some variations in the time when the limbs appear are to be found in the different regions of the body. The Nauplius limbs, for instance, often appear simultaneously or in quick succession, and the *Nauplius* stage is generally distinguished by a period of rest (and frequently by the development of a larval cuticle), while the posterior limbs, characteristic of the later stages, usually develop in regular succession. In the Phyllopoda, where the maxillae are but feebly developed, these limbs appear very late, when the embryo is fully developed (Fig. 72 *B* and *C*, Zaddach).

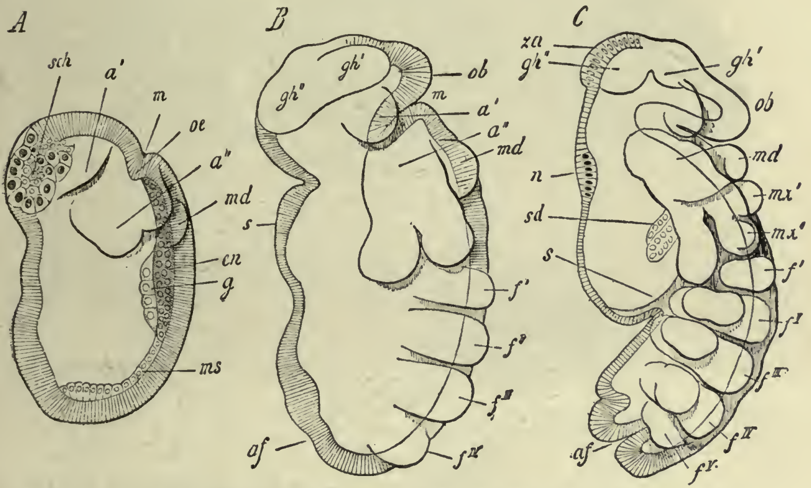

Fig. 72.—Three embryonic stages of *Moina recticostris*, side view (after Grobben), consecutive to the stages in Fig. 58, p. 124). *A*, *Nauplius* stage. *B*, stage with four thoracic limbs and the first rudiments of the shell (cephalic carapace). *C*, stage with five thoracic limbs and the two pairs of maxillae. a', first antenna; a'', second antenna; *af*, anus; *en*, entoderm; f^{I}, f^{II}, f^{III}, etc., first, second, third, etc., thoracic limbs (in *C*, with the rudiments of the branchiae); *g*, genital rudiment; gh', primary brain; gh'', secondary brain; *m*, mouth; *md*, mandible; *ms*, mesoderm; mx', first maxilla; mx'', second maxilla; *n*, nuchal gland; *ob*, upper lip; *oe*, oesophagus; *s*, shell; *sch*, neural plate; *sd*, shell-gland; *za*, compound eye.

B. Arthrostraca and Cumacea.

In the Arthrostraca, that region of the egg where later the embryonic rudiment develops is often indicated, even during cleavage, by the small size of the blastomeres, or by the earlier formation of the blastoderm. A germ-disc forms which is at first round, but soon spreads out into a germ-band covering the whole ventral surface of the egg, and occasionally also extending dorsally over the anterior and posterior extremities (Fig. 74 *A*) The anterior end of the germ-band is indicated by paired enlargements, the *cephalic lobes* (Fig. 69, *o*, p. 138), from which the rudiments of the eyes and of the brain arise, while the germ-band itself soon appears divided up by furrows into the separate body-segments (Fig. 74 *B*). This segmentation and the first appearance of the pairs of limbs takes place from before backwards; the segmentation, however, frequently occurs almost simultaneously in all regions of the body. As the lengthening germ-band has no room for free development, a characteristic curvature soon comes about. In the Isopoda, the curvature, which is originally dorsal (Fig. 74 *B*), only gives place to the reverse curvature at the end of embryonic life, whereas, in the Amphipoda, such a ventral curvature appears at an earlier

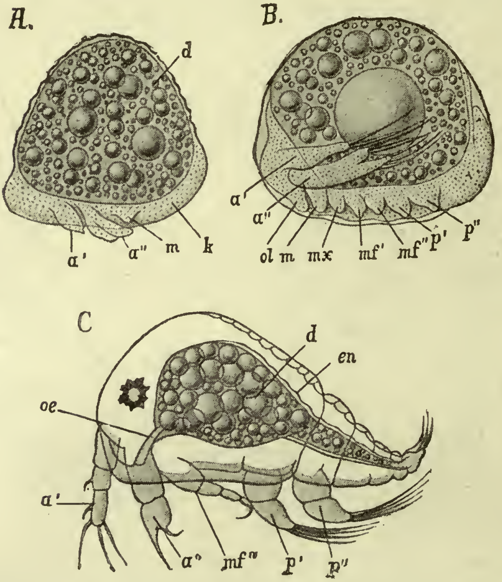

FIG. 73.—Three stages in the development of parasitic Copepoda (after VAN BENEDEN). *A*, Nauplius stage of *Brachiella Thynni*. *B*, older embryo of *Anchorella*, with the limbs of the first *Cyclops* stage. *C*, *Cyclops* stage of *Hessia colorata*. a', first antenna; a'', second antenna; *d*, food-yolk; *en*, entoderm (wall of the mid-gut); *k*, germ-band; *m*, mandible; *mx*, first maxilla; mf', first maxillipede; mf'', second maxillipede; *oe*, oesophagus; *ol*, upper lip; p', p'', first and second pairs of thoracic (rowing) limbs.

stage of development, the embryos consequently showing throughout embryonic life a ventral curvature of the abdomen (Fig. 75).

Although, as a rule, the limbs appear to take their rise almost simultaneously, yet in *Asellus*, whose ontogeny exhibits several primitive features, we find a *Nauplius* stage* characterised by the presence of two pairs of antennae and the secretion of a larval cuticle (Fig. 74 *A*). The mouth-parts and six pair of thoracic limbs, and, finally, the abdominal appendages appear later (Fig. 74 *B*). After the rudiments of the limbs have appeared, paired prominences form behind the mouth; these become the rudiments of a bilobate lower lip (*paragnatha*).

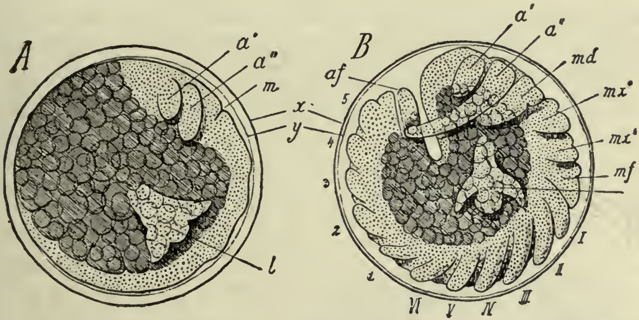

Fig. 74.—Two stages of development of *Asellus*, seen from the side (diagrammatic). *A*, *Nauplius* stage (Van Beneden). *B*, older stage (Dohrn). a', first antenna; a'', second antenna; *af*, anus; *l*, lobe-like appendages; *md*, mandible; mx', first maxilla; mx'', second maxilla; *mf*, maxillipede; *I–VI*, first six pairs of ambulatory limbs; *1–5*, first five pairs of pleopoda; *m*, mouth; *x*, vitelline membrane; *y*, blastodermic cuticle.

The course of development of the germ-band observed in *Asellus* is connected with that in *Ligia* by the presence of a distinctly recognisable *Nauplius* stage (Fig. 69, p. 138). The chief point worthy of notice in the later development of this form is that the rudiments of the thoracic limbs are originally biramose (Nusbaum, No. 85a), and that the adult limbs arise from these by the suppression of the exopodite. This is in harmony with the presence of vestigial exopodites on the two anterior pairs of thoracic limbs of the Anisopoda, and supports the deduction that the Isopoda, and with them of all Arthrostraca, arose from ancestors resembling the Schizopoda.

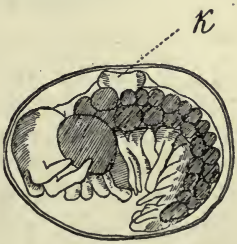

Fig. 75.—Embryo of an Amphipod (*Corophium*, F. Müller). *K*, dorsal organ.

A feature apparently universal in the Isopoda is the temporary suppression in the embryo of the posterior of the seven pairs of ambulatory limbs (thoracic limbs), and its re-appearance in the young only after leaving

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* Former observers failed to find a rudiment of the mandible in the *Nauplius* stage of *Asellus*, but Boas (No. 4, Crustacean Metamorphosis) was able to prove the presence of such a rudiment in a few individuals.

the egg. Larval integuments like that in the *Nauplius* of *Asellus* are of very common occurrence among the Arthrostraca.

An apparent exception to the rule that the germ-band in the Isopoda exhibits a dorsal curvature in its early stages is afforded by *Cymothoa* (Bullar, No. 81). The germ-band, which here lies on the ventral side of the egg, which is very large and richly supplied with food-yolk, shows for the greater part of its course the same dorsal curvature as that of other Isopoda. Its most posterior end (the rudiment of the telson) is, however, bent round ventrally.

As the germ-band broadens in later stages, its lateral portions grow up over the dorsally superimposed food-yolk, and thus give rise to the lateral parts of the embryo. The further extension of this growth finally leads to the coalescence of the lateral edges of the germ-band in the dorsal middle line, whereby the enclosure of the mass of yolk within the embryo is completed. It should be noted that during this process that part of the ectoderm which formerly covered the dorsal accumulation of yolk is crowded into a smaller space, and finally degenerates. This process has apparently some connection with the development in the dorsal region of many Arthrostracan embryos of an organ discovered by Meissner in *Gammarus* and described as a *micropyle apparatus*; this was found later in many Amphipoda and a few Isopoda, and, as the *spherical or dorsal organ*, it has received many different explanations. In the Amphipoda, the dorsal organ appears during the differentiation of the germ-band as a dorsal disc-shaped thickening of the blastoderm (Fig. 75, *K*) projecting inwards towards the yolk; when the larval integument develops, this organ adheres closely to it. A perforation is formed here (the micropyle), while the central parts of the disc form a small cavity by invagination (Fig. 76). In later ontogenetic stages, when the heart develops below the dorsal organ, the latter degenerates, mesoderm-cells wandering in between its cells and apparently taking an active part in its disintegration (Rossijskaya, No. 72).

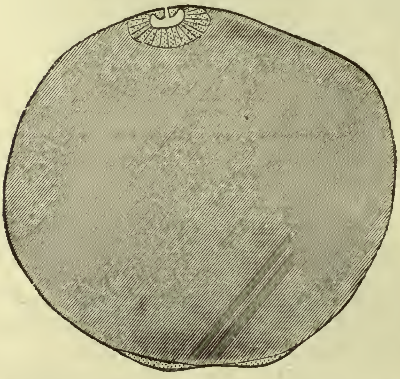

Fig. 76.—Diagrammatic transverse section through the embryo of *Cymothoa* (after Bullar, from Balfour's *Text-book*). Below is seen the germ-band in cross section, above, the dorsal organ

A dorsal organ developed in this way has been proved by F. MÜLLER to exist in many Amphipoda; also in some Isopoda (Fig. 76)—*Cymothoa*, CLAUS and BULLAR, No. 81; *Praniza*, DOHRN. An interesting variation is found among the Amphipoda in the genus *Orchestia*, where the dorsal organ originally develops on the lateral edge of the germ-band, and only later shifts towards the median dorsal line (ULJANIN, No. 75; ROSSIJSKAYA, No. 72).

Another method of development of the dorsal organ is seen in *Oniscus* (DOHRN, No. 83; BOBRETZKY, No. 80), where the cells of a large area thicken to form a saddle-shaped plate adhering closely to the larval integument (Fig. 71 *A*, *do*, p. 140). This plate, in the further course of development, becomes more and more separated, by an infolding of its margin, from the embryo, with which finally it is connected only by a thin, hollow column. The plate, when this connection is lost, undergoes disintegration. A similar dorsal organ is found in *Ligia* (FR. MÜLLER, No. 4; ROSALIE NUSBAUM, see J. NUSBAUM, No. 39, p. 168).

A dorsal organ similar to that in the Amphipoda has been observed in the Cumacea (DOHRN, No. 36). In *Mysis* it is originally paired (Fig. 77, *d*). The paired disc-like thickening found in *Tanais* (FR. MÜLLER, No. 4) connected with the larval integument, might also be thus interpreted. Among the Decapoda, the dorsal organ is found in a reduced condition in *Crangon* (KINGSLEY, No. 53), and perhaps (?) also in *Pandalus* and *Palinurus* (DOHRN, No. 45), as well as in *Homarus* (HERRICK, No. 50).

Among the various explanations given of this organ, the one originated by FR. MÜLLER (No. 4), and put forward later in more detail by GROBBEN (No. 11), has met with the widest acceptance. According to these authors, the dorsal organ is the vestige of a once functional adhesive structure, equivalent to the nuchal gland (*neck-gland*, Fig. 72 *C*, *n*), which is still functional in the young stages of the Phyllopoda and is there sometimes retained throughout life. Such a nuchal gland was also found by GROBBEN and URBANOWICZ in Copepoda (*Cyclops*, *Ergasilus*), and by GROBBEN in *Euphausia*. Although this homology appears very probable, we do not think it entirely established. It is possible, as already mentioned, that the dorsal organ is merely the expression of the complication of the blastodermic covering of the food-yolk caused by the lateral growth of the germ-band. This complication would then be expressed by an invagination in the Amphipodan type, and by a nipping off in the *Oniscus* type. These processes are perhaps analogous to the formation of the dorsal organ in the Insecta.

Among those structures which have often been homologised with the dorsal organ, are the paired *lobe-shaped appendages* (Fig. 74, *l*) of the *Asellus* embryo. The true significance of these latter was first explained by CLAUS (No. 82) by a comparison with his observations on the young stages of *Apseudes*. In *Apseudes*, in the maxillary region, there are two wing-like integumental folds; these are the rudiments of a shell which spreads over the small respiratory cavity, and under which the palp of the anterior maxilla and the vibratile epipodial lamella (*scaphognathite*) of the maxillipede come to lie. In *Asellus* the shell-fold is reduced to a triangular rudiment which (RATHKE, No. 88) may function as an embryonic gill.

The Anisopoda just mentioned (*Tanais*, *Apseudes*), in the conformation of their embryos, most resemble the Isopoda, having in common with them the dorsal curvature and the absence of the seventh pair of thoracic limbs. In other respects, they more nearly approach the Cumacea, all the abdominal limbs except the last (sixth) pair being still wanting when the young animal is hatched (Fr. Müller, No. 4; Claus, No. 78). It has already been shown (p. 151) that the paired disc-like thickenings observed by Fr. Müller in the *Tanais* embryo are probably to be referred to the dorsal organ.

The embryos of the Cumacea also, through the absence of the seventh pair of thoracic limbs, and the presence of a dorsal organ (resembling that of *Cymothoa*) are allied to the Isopoda. As in the Anisopoda, the embryo when hatched possesses only one (the sixth) pair of abdominal limbs.

C. Leptostraca, Schizopoda, Decapoda.

There are two factors which, as a rule, influence the ontogenetic development of these groups. (1) The food-yolk which, in most cases, is present in very considerable quantities, and which determines the size of the egg and the entirely superficial extension of the embryo in the first stages; (2) the gradual development of the long germ-band out of an originally short rudiment consisting of a few segments (distinctly marking the *Nauplius stage*).

Nothing further is known of the presumably very primitive condition shown in the development of the larval body of those genera which leave the egg in the *Nauplius* form (*Euphausia*, *Penaeus*, *Lucifer*).

We may take the ontogeny of *Mysis* as the starting-point of our description, following chiefly E. Van Beneden (No. 37) and Nusbaum (No. 39). The eggs of *Mysis* develop (as in the Cumacea and Arthrostraca) in a brood-sac covered by horizontally-placed lamellae (oostegites) of the thoracic limbs. The first development of the embryo appears at the point from which the formation of the blastoderm originated, and which corresponds to the future ventral surface. The formation of the blastoderm is commenced by the development of a rounded disc, the germ-integument, which ultimately spreads over the surface of the egg; a later stage shows a similar rounded blastodermic thickening (the germ-disc) which represents the first embryonic rudiment. This soon breaks up into three lobes, the middle one representing the rudiment of the caudal region, and the paired lateral lobes the rudiments of the germ-band. The latter soon grow forward as two diverging bands, from which the rudiments of the Nauplius limbs bud out as rounded prominences (Fig. 77 *A*). The broadened anterior ends (*o*) of these halves of the germ-band correspond to the *cephalic lobes* of the Entomostracan and Arthrostracan germ-bands. As they give rise exclusively to the rudiments of the compound eyes and the optic ganglia, we shall give them the more precise name of *optic lobes*. On either side of the short germ-band, between but somewhat above the first and second pairs of antennae, lies the disc-shaped paired rudiment of the

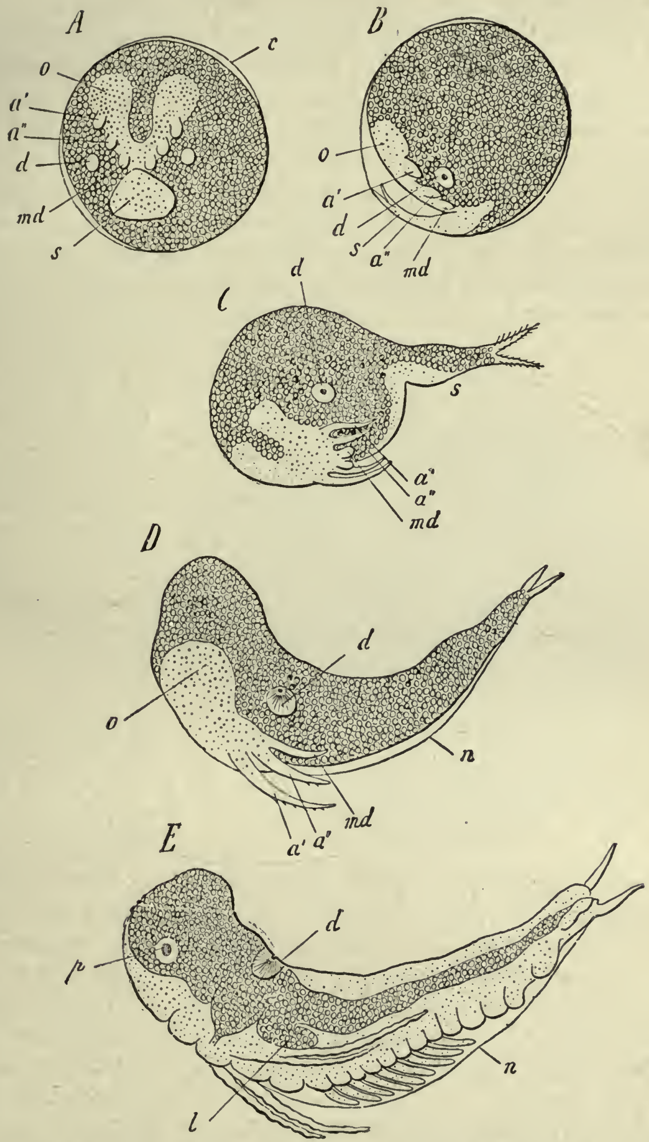

FIG. 77.—Five embryos of *Mysis* (after NUSBAUM). *A*, youngest *Nauplius* stage. *B*, older *Nauplius* stage in profile. *C*, *Nauplius* after the disappearance of the vitelline membrane, in three-quarters profile. *D*, later *Nauplius* stage with the Nauplius integument (*n*). *E*, larva with thoracic limbs. *a'*, first antenna; *a''*, second antenna; *c*, vitelline membran *d*, dorsal organ; *md*, mandible; *n*, Nauplius integument; *o*, optic lobe; *p*, rudiment of the compound eye; *s*, caudal region.

dorsal organ (*d*). The plate-shaped rudiment of the caudal region (*s*) is bounded anteriorly by the transverse depression (abdominal fold). The latter soon becomes covered over by the posterior end of the body (Fig. 77 *B*, *s*), which grows forwards to form the caudal fork. In this way the *Nauplius* stage, with the tail region bent over ventrally, is reached (Fig. 77 *B*).

After this stage has been reached, the vitelline membrane is thrown off, a new cuticle (the Nauplius integument) being secreted simultaneously. The embryo now lies free in the brood-cavity, surrounded somewhat loosely by the Nauplius cuticle. The abdomen has meanwhile lengthened and straightened out (Fig. 77 *C*), and becomes more and more filled with food-yolk evenly distributed within it, while the whole body finally assumes a distinct dorsal curvature. We can now (as in the Arthrostraca) distinguish a ventral germ-band from the dorsally-placed mass of food-yolk. The latter, especially in the cephalic region, swells considerably. The posterior parts of the embryo become distinctly segmented. The mouth-parts and the thoracic limbs appear simultaneously (Fig. 77 *E*), the rudiments of the abdominal limbs following in a later stage. During these changes the disc-shaped dorsal organs have coalesced in the dorsal middle line, and, as an invagination takes place there, they are here, both in position and form, comparable with the dorsal organ of the Amphipoda.

The embryo of *Nebalia*, according to METSCHNIKOFF's account (No. 33), strongly resembles in form that of *Mysis*. Here also we have the ventrally flexed *Nauplius* stage, as well as a lengthening and dorsal curvature taking place after the shedding of the vitelline membrane. The presence of a dorsal organ has, however, apparently not yet been observed in this form (p. 252).

The embryos of the Decapoda differ from those of *Mysis* chiefly in the position of the parts of the body; the ventral curvature which at first characterises the *Nauplius* of *Mysis* (*i.e.*, the ventral flexure of the abdomen) is here retained to a much later stage until the larva is hatched, this being connected with the much later rupture of the egg-envelopes. In other respects the ontogenetic processes are very similar. In *Astacus*, of whose development a very detailed account can be compiled from the researches of RATHKE (No. 63), LEREBOULLET (No. 58), BOBRETZKY (No. 41), and REICHENBACH (Nos. 64 and 65), after the blastoderm has developed, the first embryonic rudiments are perceptible as five thickenings consisting of a simple layer of cells (Fig. 78). The anterior pair of the thickenings (*K*) corresponds to the optic rudiments of *Mysis*, and may here also be described as *optic lobes.* The posterior pair of formative centres (*TA*), which lie nearer one another, answer to the unpaired caudal rudiment of *Mysis.* But, since here not only the segments of the abdomen, but thoracic segments as well have begun to form, these discs may be called the *thoraco-abdominal rudiments.* The most posterior unpaired disc is the *entoderm disc* (*ES*). Anteriorly to this there is a point where active proliferation yields cells which spread out below the blastoderm-layer, this is the *formative zone of the mesoderm* (*BM*). While, by processes already described in detail (pp. 128, etc.), the invagination of the entoderm-disc and the gradual closing of the blastopore take place, the thoraco-abdominal rudiments come together to form an unpaired plate (Fig. 79, *TA*), in the middle of which the proctodaeal invagination (*A*) is soon perceptible. The anterior margin of this plate then becomes more sharply marked by a transverse depression (the *caudal fold*), which, in the further course of development, sinks deeper, sloping obliquely backward. The thoraco-abdominal plate grows forward round and below this depression, forming the long posterior portion of the body; this is curved ventrally and closely applied to the other embryonic rudiments (Figs. 80 and 63 *B*, p. 131).

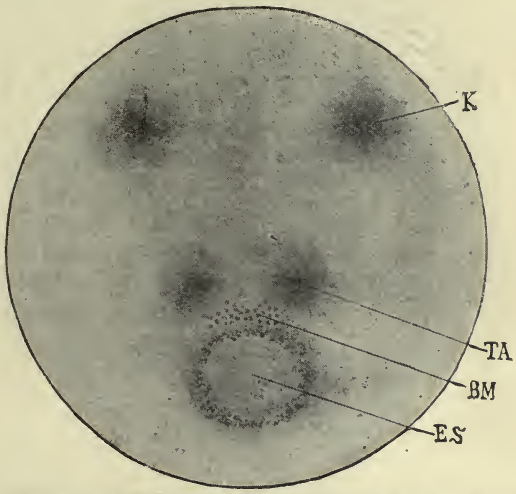

FIG. 78.—Part of the surface of an egg of *Astacus fluviatilis*, with embryo beginning to form (after REICHENBACH, from LANG'S *Text-book*). *BM*, formative zone of the mesoderm; *ES*, entoderm-disc; *K*, cephalic lobes (optic lobes); *TA*, thoraco-abdominal rudiments.

While these processes are going on in the posterior half of the body, active growth takes place on each side in a band connecting the optic lobes with the thoraco-abdominal rudiment (paired rudiment of the germ-band), which finally lead to the development of three pairs of limbs (Nauplius limbs, Fig. 79). These are the mandibles and the two pairs of antennae, the former, according to **Bobretzky** and **Reichenbach**, appearing somewhat earlier than the latter. The middle region between these rudiments long retains the character of an undifferentiated blastoderm; in the anterior region, however, an unpaired swelling arises as the rudiment of the *labrum* (*l*), and behind it the *stomodaeal invagination*, while, mesial to the rudiments of the limbs, the pairs of ganglia belonging to them (ga_2, *gm*) are recognisable as ectodermal thickenings. The *Nauplius* stage thus attained marks a natural period in the ontogenetic development of *Astacus*, this being also indicated by the appearance of a larval integument (Nauplius cuticle).

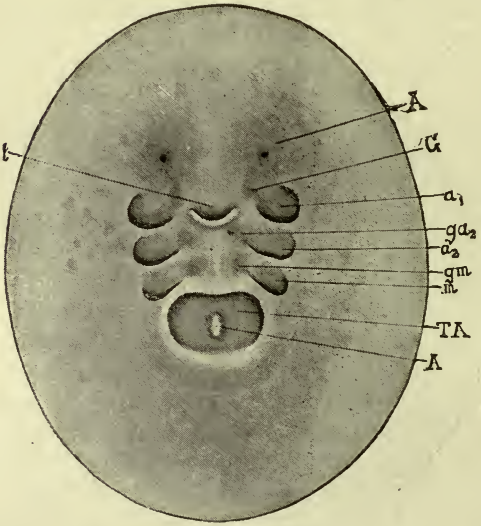

Fig. 79.—Embryo of *Astacus fluviatilis* in the *Nauplius* stage (after Reichenbach, from Lang's *Text-book*). *A* (above), rudiment of eye; a_1, first, and a_2, second antenna; *G*, cerebral ganglion; ga_2, ganglion of the antenna; *gm*, ganglion of the mandible; *m*, mandible; *l*, upper lip; *TA*, thoraco-abdominal rudiment; *A* (lying in *TA*), anus.

It should be noted that, in the *Nauplius* stage, the different parts of the embryo lie nearer one another than when they first arise (*cf.* Figs. 78 and 79 drawn to the same scale). Such an approximation of the rudiments in the embryo at these stages appears universal in the Decapoda.

The *Nauplius* stage in other Decapoda develops in the same way as in *Astacus*. The embryonic rudiments, however, in most cases, only appear after the closing of the mouth of the gastrula; there is then found, in the immediate neighbourhood of the closed blastopore, an unpaired rounded prominence, in which the rudiment of the posterior end of the body can be discerned; this is not, as in *Astacus*, paired. In the *Loricata*, according to **Dohrn** (No. 45), as in *Astacus*, this may be described as the thoraco-abdominal rudiment, whereas, in other cases, it seems to give origin exclusively to the abdominal segments. This rudiment soon shows wing-like outgrowths running forward, and establishing connection with the optic lobes which in the meantime have made their appearance. The rudiments of the Nauplius limbs then appear in the neighbourhood of these connecting strands.

A transverse projection connecting the posterior parts of the optic lobes becomes the rudiment of the labrum, behind which the stomodaeal invagination soon appears. The latter, as a rule, lies in the space between the first and second pairs of antennae, but KINGSLEY has specially emphasised the post-oral position of the first pair of antennae in *Crangon.* Paired swellings arise near the posterior margin of the oral aperture; these are the rudiments of the *paragnatha* or bilobed lower lip.

The later stages (Figs. 80, 81, and 83) are characterised by the further growth of the thoraco-abdominal rudiment, which soon breaks up into segments, and also by the development of the posterior pairs of limbs which appear from before backward. At the same time the typical biramose character is found in the anterior limbs which were the first to develop, as well as a segmentation corresponding with the developing joints (for the number and shape of the limbs of the hatching embryo, which vary greatly in the different groups of the Decapoda, see below, p. 257: Metamorphosis of the Decapoda). The optic lobes gain in independence, bulging forwards and gradually rising from the surface below them, so that the club-like shape of the stalked eye can be recognised in the rudiment (Fig. 81).

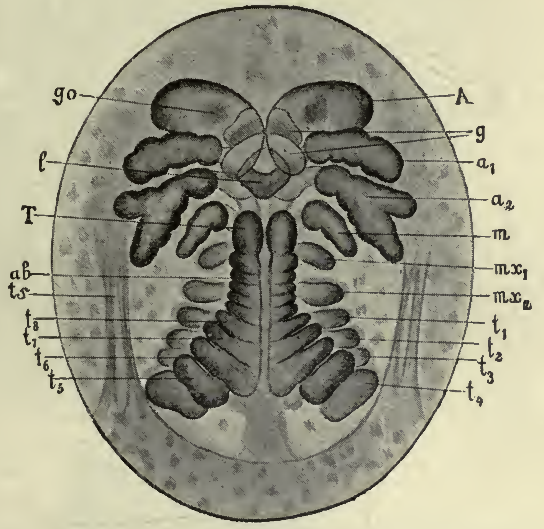

FIG. 80.—Embryo of *Astacus fluviatilis*, with the thoracic feet beginning to form (after REICHENBACH, from LANG'S *Text-book*). *A*, eyes; a_1, a_2, first and second antennae; *ab*, abdomen; *g*, rudiment of the brain (procerebrum+antennal ganglion); *go*, optic ganglion; *l*, upper lip; *m*, mandible; mx_1, mx_2, first and second maxillae; *T*, telson; t_7, t_8, thoracic limbs; t_1, t_3, maxillipedes; t_4, t_8, ambulatory limbs; *ts*, rudiment of the thoracic shield.

The posterior part of the body undergoes important alterations. There is here an early separation of the *terminal or anal segment* (Figs. 80, 81, *T*) from a budding zone composed of large cells which lies in front of this segment (in the embryo, however, owing to the forward curvature of the tail, further back). The anal aperture is originally formed on that surface of the terminal segment which afterwards becomes the dorsal surface, later it shifts into the space between the two lobes into which the terminal segment soon divides, and through this space gradually reaches the later ventral side, and, in this way, its final position.

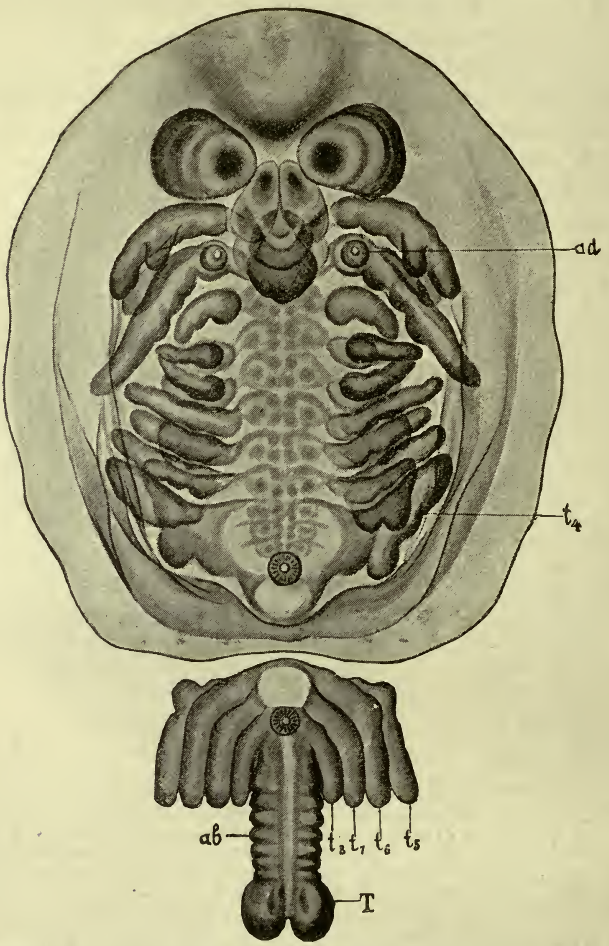

FIG. 81.—Embryo of *Astacus fluviatilis* with the rudiments of all the limbs (Fig. 83, p. 163) (after REICHENBACH, from LANG's *Text-book*). The thoraco-abdomen, which in reality curves forward ventrally, is cut off and laid back. *ad*, antennal gland; *ab*, abdomen; t_4, first pair of ambulatory limbs (chelate feet); t_5–t_8, second to fifth pair of ambulatory limbs; *T*, telson.

Immediately behind the thoraco-abdominal rudiment, at the point where this is connected with the rest of the body, in later stages, an accumulation of mesoderm-cells is discerned, forming the first rudiment of the *heart* (Figs. 63, 64, *h*, pp. 131, 132).

In early stages the thoraco-abdominal rudiment is surrounded by a clear area bounded externally by closely contiguous blastoderm-cells. The latter soon become raised so as to form a fold which is specially distinct in its lateral parts; this is the first rudiment of the *thoracic shield* (Fig. 80, *ts*). The clear area thus referred to is the rudiment of the *branchial cavity*.

A remarkable structure lying like a dorsal disc on the embryo and called the "carapax" has been described in the early stages of *Atyephyra* by ISCHIKAWA.

The development of the Decapoda is principally characterised by the fact that the whole mass of food-yolk is confined to the anterior part of the dorsal side of the body, while the thoraco-abdominal rudiment is free from yolk. Even in late stages, in which the form of the hatching animal is already quite distinct, the cephalo-thoracic portion appears swollen up by food-yolk until almost spherical.

Formation of the Organs.

Our knowledge of the development of the different organs in the Crustacean embryo is still somewhat limited. The Decapoda are in this respect best known to us from the researches of BOBRETZKY (No. 41), REICHENBACH (Nos. 64, 65), and KINGSLEY (No. 52–55). Besides these we have the observations of NUSBAUM (No. 39) on *Mysis*, of BOBRETZKY (No. 80) and NUSBAUM (No. 85) on *Oniscus*, of GROBBEN (Nos. 11 and 21) on *Moina* and *Cetochilus*, of CLAUS (Nos. 8 and 9) on *Branchipus*, *Apus*, and others.

A. External Integument.

As the superficial ectoderm of the embryo yields on its external surface the chitinous skeleton of the larva, it gradually acquires the character of the *hypodermis* or the matrical layer of this skeleton. It has been recently proved by T. TULLBERG that, in the Lobster, the origin of this chitinous skeleton may be traced back to a direct transformation (chitinisation) of the body of the cell. It is an interesting fact that the hypodermal cells not only are able to change into chitin at their external ends, which are directed to the body surface, but that occasionally even their basal portions are similarly modified. Thus REICHENBACH observed that, in *Astacus*, single hypodermal cells lengthen inwards and grow out into chitinised strands and pillars which function partly as supports for the carapace, and partly as points of attachment for the groups of muscles. In individual cases it is often impossible to distinguish between these ectodermal ingrowths and true connective tissue. This inner chitinous supporting tissue belonging to the ectoderm was found by Claus (No. 9) very richly developed in *Branchipus*.

B. Endoskeleton.

A further development of internal chitinous structures is brought about by infolding and invagination of the external integument. In this way are developed those tubular chitinised ingrowths which, as affording attachment for the more important muscles, have been called chitinous tendons, and some of which even, as was proved for the mandibular muscle of *Astacus* (Baur), are renewed at ecdysis. A striking development of chitinous tendons of this kind, formed from ectodermal invaginations (Reichenbach), is found, as is well known, in the penultimate joint of the pincer in *Astacus fluviatilis.* The inner sternal skeleton (endophragmal system) which bridges over the thoracic ganglia in *Astacus* develops in a similar manner, as a series of invaginations of the external integument (Bobretzky, No. 41), by a process of infolding of the inner wall of the branchial cavity and of the sternal surface of the thorax. Nusbaum (No. 85) was able to observe in *Oniscus* the origin from paired lateral invaginations of a similar chitinous diaphragm covering over the chain of ganglia in the thorax. A hemispherical, chitinous articular fold also arises as an ectodermal invagination in connection with the movable eye of the Cladocera and of most Branchiopoda (Grobben).

C. Nervous System.

Although probably belonging to a common rudiment,* the supraoesophageal ganglion (brain) and the ventral chain of ganglia must be separately dealt with. The whole of the central nervous system arises as an ectodermal thickening. Even in early stages, paired ectodermal thickenings can be recognised on the inner side of the

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* Most authors agree that, in the Crustacea, the rudiment of the brain, from its first appearance, is connected with the primitive swellings of the ventral chain of ganglia by means of paired ectodermal thickenings (rudiments of the oesophageal commissures). This view, however, has been opposed. Urbanowicz, for example, found that in *Cyclops* (No. 23) the brain and a suboesophageal ganglion originate independently, and only become connected later by the development of the oesophageal commissures. This observation cannot, however, be considered as affording direct proof of Kleinenberg's views as to the original independence of the rudiments of these two parts of the central nervous system (Vol. i., p. 288), for it is easy to understand that the rudiments of the more massive parts of the central nervous system should become earlier perceptible as ectodermal thickenings, while those of the more delicate parts (*e.g.*, of the oesophageal commissures) are only visible at a later stage.

rudiments of the limbs; these represent the rudiments of the paired ventral ganglia belonging to the individual segments. The consecutive pairs of ganglia are, however, connected by thickened ectoderm-bands, the rudiments of the longitudinal commissures, so that we may regard two longitudinal ectodermal swellings (the "*Primitivwülste*," Hatschek, Fig. 82, *pw*) as the first rudiment of the ventral chain of ganglia; these show segmental swellings (rudiments of ganglia), and are separated by the *primitive groove* (*pr*). In the later stages of development (Fig. 82 *B*), in the region of the primitive swellings, the ectoderm is seen to be composed of several layers, an outer one, which now is changed into the hypodermis (*h*) of this region, being separated from the inner layers. The latter now, as *lateral strands* (*s*) represent the rudiment of the ventral cord. Reichenbach, on whose description of the development of the nervous system in *Astacus* our account chiefly rests, was able to prove that, in the formation of each pair of ganglia of the ventral cord, there enters, besides the corresponding portion of the lateral strands, a median invagination (*m*); this is to be traced back to the primitive groove, and is known as the *median strand.* This agrees with the discoveries of Hatschek in connection with the origin of the ventral chain of ganglia in the Insecta.

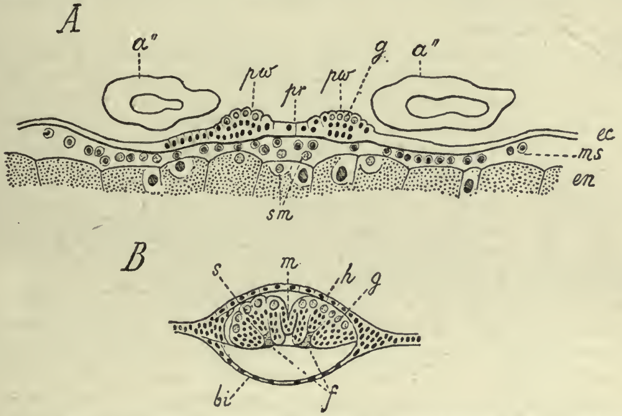

Fig. 82.—Development of the ventral chain of ganglia in *Astacus fluviatilis* (after Reichenbach). *A*, cross section through the mandibular segment of an embryo in which the maxillipedes have already appeared. *B*, cross section through the ganglionic rudiment in a maxillary segment of an embryo in which the maxillipedes have already developed. a'', cross section of the second antennae; *bi*, connective tissue covering over the inner side of the ganglionic rudiment; *ec*, ectoderm; *en*, entoderm; *f*, bundle of fibres in cross section; *g*, large ganglion-cells; *h*, hypodermis; *m*, invaginated median strand of the ganglionic rudiment; *ms*, mesoderm; *pr*, primitive groove; *pw*, primitive swelling of the ganglionic rudiments; *s*, lateral strand; *sm*, secondary mesoderm.

The lateral strands are originally composed of simple embryonic cells. In later stages, however (Fig. 82 *B*) their structure is found to be more complicated, a cross section revealing three constituent parts. The first commencements of the formation of nerve-fibres (*f*) can soon be made out in the innermost (or basal) portion ; these run as two longitudinal bundles below the lateral strands, and are connected with very fine processes of those cells of the strands which become changed into ganglion cells. Besides these paired bundles of fibres, there is, in the rudiment of every pair of ganglia, an unpaired mass of nerve-fibres which perhaps arises from the median strand and gives rise to the transverse commissures. The lateral strands at an early stage become invested with a layer of mesodermal tissue ; this covering, according to Reichenbach, represents the neurilemma, and penetrates not only into the ganglia, but even into the central mass of fibres. The appearance of masses of fibres at the inner or basal side of the lateral strands has probably the significance of an ontogenetic recapitulation of a primitive condition, in which the whole nervous system was an epithelial structure, with the masses of fibres developed on its inner or basal side.

Even in quite early stages, Reichenbach could distinguish, in the rudiments of the ganglia, larger and smaller cells of varying histological character. This distinction is also evident in the fully developed condition. The larger elements (Fig. 82 *B*, *g*) give rise to the so-called large ganglion-cells in the central nervous system of *Astacus*. Similar large cells were observed by Nusbaum even in early stages in *Mysis*. In the later stages, massive accumulations of pigment have occasionally been found in the ventral ganglia ; these are probably deposited in mesoderm-cells. Instances of this are to be found in the ganglion which is connected with the sixth pair of appendages of *Crangon* (Kingsley), and in the thoracic ganglia of *Mysis* (Nusbaum).

Reichenbach's view as to the participation of a median invagination in the formation of the chain of ganglia has since received only partial confirmation. Nusbaum, indeed, observed it in *Mysis*, and Grobben thought that it could be assumed for *Moina*. Claus, however, denied that a median invagination took part in the formation of the ventral cord in *Branchipus*. On the other hand, Nusbaum recently recognised the presence of the median strand in Isopoda (*Oniscus*, No. 39), in which group Bobretzky (No. 80) and Bullar (No. 81) described the origin of the ventral cord from an unpaired thickening which only at a later stage divided into symmetrical halves.

With regard to the development of the *peripheral nerves*, Reichenbach (No. 65) and Claus (No. 9) have shown that it is probable that these do not originate as outgrowths from the rudiments of the central nervous system, but that they appear as distinct ectodermal thickenings at a time when the whole nervous system is still connected with that layer. The transverse commissures which are double in each segment in *Branchipus* arise in a similar way, according to Claus (No. 9).

In tracing the development of the *brain* or *supraoesophageal ganglion*, we must first study Reichenbach's minute descriptions of its origin in *Astacus* (No. 65). According to this author, the whole central nervous system of the pre-oral part of the body arises in the form of three pairs of ganglia, equivalent to one another and belonging to three separate body-segments (Fig. 83). The most anterior of these ganglia, which develops in the proximal portion of the eye-stalk, yields the optic ganglion (*o′*, *o″*), while the remaining two belong to the first and second pairs of antennae and enter into the formation of the brain proper or supraoesophageal ganglion. Of these last, that lying in the segment of the first antenna (*antennule*) very soon becomes divided by a transverse constriction into a pair of ganglia (*a*, *b*), the anterior of which (*a*) we will distinguish by PACKARD's name of *procerebrum*, while the posterior, since it gives off the nerve to the first antenna, has been called the *antennular ganglion* (*b*). It should be mentioned that REICHENBACH believed that he observed, in late stages, a similar transverse division of the posterior pair of ganglia which give off the nerves to the second antennae, and are therefore called the *antennal ganglia* (*c*); this latter division, however, is not so striking, and also not of the same significance as the division which takes place in early stages between the procerebrum and the antennular ganglion.

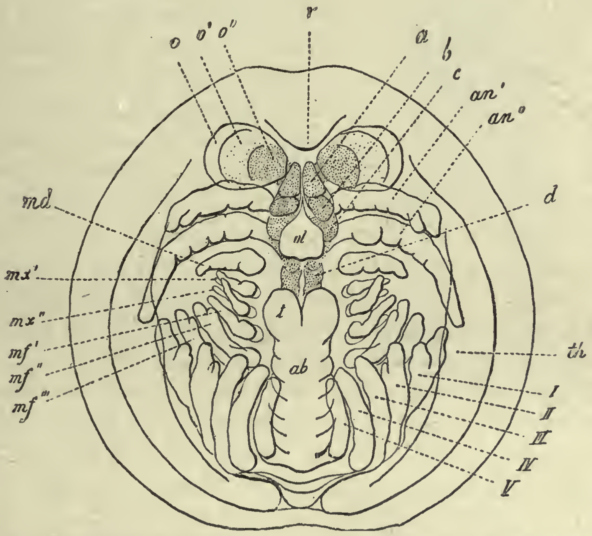

FIG. 83.—Embryo of *Astacus fluviatilis* with the rudiments of all the limbs (after REICHENBACH). *a*, anterior, *b*, middle, *c*, posterior portion of the rudiment of the brain; *ab*, abdomen; *an′*, first antenna; *an″*, second antenna; *d*, mandibular ganglion; *md*, mandible; *mx′*, first maxilla; *mx″*, second maxilla; *mf′*, *mf″*, *mf‴*, first, second, and third maxillipedes; *o*, rudiment of the compound eye; *o′*, the part of the optic ganglion which has arisen from the optic invagination; *o″*, inner part of the optic ganglion; *ol*, upper lip; *r*, rudiment of the rostrum; *t*, telson; *th*, fold of the thoracic shield; *I–V*, first five pairs of ambulatory limbs.

It is an important fact that the pairs of ganglia just described show, according to Reichenbach, in their development, great agreement both *inter se* and with the ganglia of the ventral cord. In each of these pairs of ganglia we can distinguish lateral strands and a median strand; the lateral strands, in cross section, are seen to be broken up into three parts, as are the ganglia of the ventral cord. The median strand, however, varies in different regions. In the region of the optic ganglion, the two halves of the median strand shift far apart, and enter separately into connection with the corresponding ganglia. In the region of the procerebrum and the antennular ganglion, on the other hand, is found that median invagination of this strand which doubtless leads to the development of the commissural portions of the brain. In the region of the antennal ganglion, again, there is no median invagination. Reichenbach believes that this invagination has shifted forwards and is represented by that established between the antennular ganglia. If, however, we believe that the transverse commissure between the antennal ganglia was originally post-oral, and is perhaps still to be looked for in such a position (Claus, No. 78), we shall not be surprised at the absence of the median invagination between these ganglia. In later stages, the invaginations of the median strand are no longer distinct from one another in the region of the procerebrum and the antennular ganglion, a closer union between the different parts of the brain being then generally apparent. The procerebrum, according to Reichenbach, gives origin principally to the "anterior cerebral swelling," while the antennular ganglion is connected with the development of the "lateral swellings" (Krieger, Dietl).

These observations of Reichenbach are to a certain extent in agreement with those of Kingsley, who found in *Crangon*, apart from the optic ganglia, three consecutive pairs of ganglia taking part in the formation of the brain. The most anterior of these (the procerebrum) Kingsley, however, regarded from the first as an independent structure, it alone being originally pre-oral and homologous with the supraoesophageal ganglion of the Annelida. The two pairs of ganglia which follow (the antennular and antennal ganglia) are, when first developed, post-oral in position, and must thus be considered as ganglia of the ventral cord drawn into the cephalic region.

The above observations lead us up to the question of the primary segmentation of the pre-oral portion of the head in the Crustacea. Reichenbach, with whom also Nusbaum (No. 39) is in essential agreement, has been led by his ontogenetic researches to assume for this region of the body three component parts, homonomous with the other body-segments; these are the optic, the antennular, and the antennal segments. In the *optic segment*, the optic ganglia would represent the segmental pair of ganglia, while the general position of the parts in the *Astacus* embryo incline Reichenbach to return to the old view of Milne-Edwards, according to which the eye-stalks represent the limbs of this segment. This last view, which subsequently found supporters in Huxley and Spence Bate,* has, however—and, as it appears to us, rightly—been disproved by Claus and Fr. Müller, by reference to the ontogeny of the stalked eye of the Phyllopodan larva (*Branchipus*) and of the *Zoaea* of *Lucifer*, which indicates that the eye-stalks are to be regarded as secondarily abstricted lateral portions of the head which have become independently movable, while the optic-ganglion, as a part of the brain shifted anteriorly, also attains only a secondary independence. These conclusions remove all ground for assuming the presence of an independent optic segment.

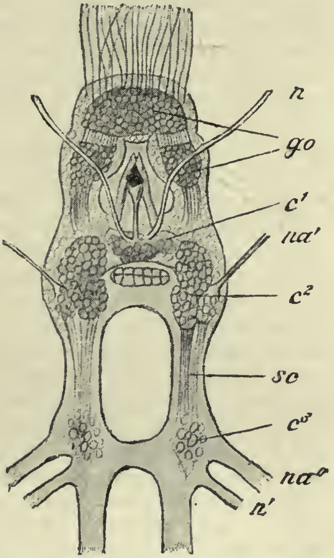

Fig. 84.—Ventral aspect of the brain of *Daphnia similis* (after Claus). c^1, anterior, c^2, middle, c^3, posterior section of the brain; *go*, optic ganglion; *n*, nerve of the sensory organ of the neck; *na'*, nerve of the first antenna; *na''*, nerve of the second antenna; *n'*, second nerve of the second antenna; *sc*, oesophageal commissure.

With regard to the segment of the body corresponding to the *second pair of antennae*, there can hardly be any doubt that we here have to do with an originally post-oral body-segment, *i.e.*, with a true trunk-segment, which only secondarily underwent displacement forwards, and thus attained a closer union with the pre-oral parts of the head. This view is supported by the changes brought about during embryonic development in the relative positions of the mouth and the second antennae (p. 157), and above all by the condition of the nervous system, in which are to be found all transitions between the independent development of the pair of ganglia on this segment and their close fusion with the cephalic mass. It has been known, since the observations of Zaddach, that, in *Apus*, the origin of the pairs of antennal nerves is to be sought post-orally in the oesophageal commissures, and later researches (Pelseneer, No. 14) showed the ganglia at this point to be connected by means of a post-oral transverse commissure, although this has to some extent been otherwise explained. Similar conditions are found in other Phyllopoda. Thus, in Claus' drawing of the brain of a Cladoceran (Fig. 84), three sections can be distinguished, only the two anterior being pre-oral in position. The most anterior section (c^1, corresponding to Packard's

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* [See also C. Herbst, Uber d. Regeneration v. antennenähnlichen Organen an Stelle v. Augen, *Archiv. f. Entwickl. Mechanik*, Bd. ii., 1895–96, p. 543; and B. Hofer, Ein Krebs mit einer Extremität statt eines Stielauges, *Verh. Deut. Zool. Gesell.*, 1894, p. 82.—Ed.]

procerebrum) gives off the nerves to the eyes and to the frontal and other sensory organs, the second section the nerves to the first pair of antennae (*na'*), while the posterior section (c^3), which lies on the course of the oesophageal commissure (*sc*) behind the oesophagus, supplies nerves to the second antenna (*na''*). Among other Crustacea, the antennal ganglion undergoes more or less displacement forwards along the commissure and a subsequent fusion with the brain. The acceptance of this view of the alterations in position is attended with a certain amount of difficulty owing to the course of the transverse commissures (originally running behind the oesophagus) connecting this pair of ganglia. The following alternative is offered us: either to suppose that a secondary pre-oral transverse connection is developed, or to assume that the transverse fibres, after the ganglia have completed their wanderings, retain their original course behind the oesophagus. CLAUS (No. 78) believes that this primary connective retains its original position in the adult, and he would identify as that structure the transverse post-oral connection between the oesophageal commissures, which is found in many Crustacea (*Apseudes*, Stomatopoda, Decapoda), lying in front of the mandibular ganglion. In other cases, this fibrous connective is perhaps fused with the transverse commissure of the mandibular ganglion.

The question now arises whether we are justified in considering the part of the brain lying in front of the antennal ganglion as an originally single complex, or whether, in this also, a separation into (two) consecutive segments can be recognised. We must here mention RAY LANKESTER'S theory (No. 15), which distinguished in the Crustacean brain an anterior section connected with the optic ganglion under the name of *archicerebrum*, this only being enlarged into a *syncerebrum* when the ganglia of two following segments (the antennular and antennal segments) are drawn into it. This view has been accepted by PACKARD (No. 86), who distinguishes in the brain of *Asellus* as separate sections: (1) the optic ganglia, (2) the procerebrum, (3) the antennular ganglia, (4) the antennal ganglia. In this case, we should have to find the homologue of the Annelidan brain, which develops out of the neural plate, in the procerebrum alone, while the optic ganglia would be a secondary portion of the brain* arising during the later development of the paired lateral eyes, and the antennular and antennal ganglia would be ganglia of the ventral cord. This view stands opposed to that of CLAUS (No. 78), according to which the antennular ganglia, together with the procerebrum, formed an originally single complex, the primitive brain. This portion, which is to be deduced from the neural plate of the Annelidan larva, contains the ganglia of the former median sensory organs (Nauplius eye, frontal organ) and the anterior antennae, which are morphologically to be homologised with the Annelidan palps already connected with the neural plate. This latter view would be supported by the observations of REICHENBACH, according to which the rudiment of the corresponding part of the brain is originally to be found as a single complex at the bases of the first antennae, and only later breaks up into two pairs of ganglia. A certain amount of support is also afforded by the peculiar structure of the first antennae, which, as carriers of important sensory organs, do not develop in accordance with the fundamental type of the Crustacean limb, a point specially emphasised by CLAUS and BOAS. Such a heteromorphous structure of the antennule might, indeed, be secondarily acquired, and might be accounted for by its physiological significance already mentioned, as well as

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* A view first enunciated by HATSCHEK (Beiträge zur Entwickelungsgeschichte der Lepidopteren), and later accepted by GROBBEN for the Crustacea.

by its position at the anterior end of the body. The views of RAY LANKESTER and PACKARD are supported most strongly by KINGSLEY's statements concerning *Crangon* (No. 55): not only was the procerebrum observed to originate independently of the antennular ganglion, but the antennules and their pair of ganglia were found in a distinctly post-oral position. In accepting this view we should have, indeed, to assume, with RAY LANKESTER, a backward wandering of the mouth. We must, however, await further researches as to the structure of the Crustacean brain, and above all, as to the development of the whole region now under consideration, before forming a decisive judgment.

It is evident that, in a discussion as to the primary segmentation of the anterior region of the Crustacean body, the question of the morphological value of the first antenna comes to the front. Two alternatives are presented to us; we must either regard it as a true limb, although somewhat modified in shape, or else, with BOAS, deny that it has this significance, and consider it only as a stalked sensory organ (similar to the stalked eyes). Only in the latter case can we regard it as homologous with the primary cephalic tentacle of the Annelida. We, however, see many reasons for regarding the first antenna as a true body-appendage. We have only to recall the similarity between its position and development and those of the latter in the embryo, and its use for swimming purposes in the *Nauplius* stage and in many Entomostraca, in which the first antenna is sometimes diverted to other purposes (*e.g.*, climbing and sucking). It is only in the higher Crustacea that this limb is distinctly set apart as a sensory organ. If these considerations incline us to place the first antenna in the series of true trunk-limbs, we then have to ask whether the vestiges of the primary cephalic tentacle, so common among the Annelida, are not to be sought in some other structure. It is not difficult to assume this significance for the so-called *frontal sensory organs* (Fig. 123, *fs*, p. 269) found in the young stages of many Crustacea as paired peg-like or filamentous processes innervated from the procerebrum. This view gains in probability by a comparison with *Peripatus*, in whose embryos similar blunt processes have been observed, while the antennae of *Peripatus*, according to their development and their relation to the coelomic sacs, must be considered as modified trunk-limbs. If we held this view, to which, naturally, we can only ascribe a hypothetical value, we should be led to distinguish, with RAY LANKESTER, three sections in the anterior part of the Crustacean body which contains the brain. There would be one actual primary section, originally the only pre-oral section of the body, with the procerebrum, the eyes, and the frontal sensory organs, and two sections following posteriorly, trunk-segments drawn into the head (antennular and antennal segments), for which we must assume an originally post-oral position. We must, however, once more emphasise the fact, before accepting any one of these views, that in discussing these questions we are dealing entirely with hypothetical matters.

D. Sensory Organs.

Of the details of the development of the unpaired triple *Nauplius* or *Entomostracan eye** nothing is as yet known, but mention should

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* According to CLAUS (*Kaiserl. Akad. Wissensch. Anz. Wien*, 1891), the Nauplius eye is composed of three inverted cup-shaped eyes, in which the nerves enter the retinal cells from the side turned away from, while the rods are directed towards, the pigment cups. A certain similarity with the median eye of the Arachnoida is thus brought about. [BERNARD (The Apodidae) claims to have discovered paired rudiments for the Nauplius eye of *Apus*.—ED.]

be made of the observations of LEYDIG and GROBBEN, according to which this eye has a paired rudiment.

According to URBANOWICZ (No. 23), the eye in *Cyclops* is formed "of three ectoderm-cells, each of which secretes pigment and becomes a refractive sphere."

The development of the paired *compound eye* has been best studied in the Decapoda (BOBRETZKY, No. 41; REICHENBACH, No. 65; KINGSLEY, No. 52; HERRICK, Nos. 48 and 49; and PARKER, No. 62). It has also been observed in *Mysis* (NUSBAUM, No. 39), *Parapodopsis* (BOUTCHINSKY, No. 37a), and *Branchipus* (CLAUS, Nos. 8 and 9). The description of the development of the compound eye cannot be separated from that of the optic ganglion.

The simplest example of the development of a compound eye is that of *Branchipus*. The rudiment of the compound eye, as well as of the optic ganglion, can here be traced back to a pad-like growth of hypodermis, the superficial parts of which become transformed into the eye, while the deeper parts contain the material for the optic ganglion, which is connected with the brain. The several layers of cells which represent the rudiment of the eye, and which must be regarded as a simple thickening of the hypodermis, soon show an arrangement of the elements into a superficial layer (which yields the corneal cuticle and the crystalline cones) and a deeper pigmented layer for the formation of the retinulae, the latter layer being connected with the rudiment of the optic ganglion by fibrous strands. In the lateral parts of the whole rudiment there soon occurs a histological differentiation of the optic ganglion and of the ommatidia which compose the eye, whereas, in the anterior and more median portions, a proliferating hypodermis of embryonic character (Fig. 85) is retained until a later stage; this constantly yields new elements for the enlargement of the whole rudiment. Strictly speaking, two budding zones (*k'*, *k''*), which are distinct from, but in contact with one another, can be distinguished at this point; one of these (*k''*), by the production of new ommatidia, adds to the size of the eye itself, while the other and more proximal (*k'*) yields the elements corresponding to the optic ganglion. During these ontogenetic processes, the movable eye-stalks have arisen by simple outgrowth from the lateral parts of the head.

The development of the eye in the Schizopoda and the Decapoda is very similar to that in *Branchipus*. Here also the compound eye arises from a thickening of the hypodermis, which from the first is in close connection with the rudiment of the optic ganglion.

Even in early stages, the outer and anterior part can be distinguished as the rudiment of the eye (Fig. 80 *A*, p. 157, and Fig. 83, *o*, p. 163), and the inner, posterior part as that of the optic ganglion (Figs. 80, *go*, and 83, *o′*, *o″*). The latter is thus, from the very first, in close contact, not only with the rudiment of the eye, but, proximally, with that of the supraoesophageal ganglion.

The rudiment of the eye is thus only a part of the ectoderm (Fig. 86 *A*) which becomes multilaminar and produces from its superficial layers the cells of the cornea and crystalline cones, while the lower layers give rise to the retinulae and the pigment-cells. A basal membrane secreted on the inner surface of this hypodermis (Fig. 86, *mb*) yields the *membrana limitans* which bounds the eye on the side of the optic ganglion. Mesoderm-elements are deposited on this membrane from within, and these, in *Mysis*, yield the pigment of the innermost of the three pigment-layers. In *Mysis*, according to NUSBAUM (No. 39), differentiation occurs at the time when the stalked eye rises from its substratum, the first differentiation of the ommatidia appearing in that dorsally curved lamella which, by its curvature, causes the eye to separate from the food-yolk. In this lamella, a very regular arrangement of the cells both into horizontal layers and into vertical columns takes place early. The horizontal lamination separates the corneal cells from those of the crystalline cones, etc. The vertical arrangement gives rise to two alternating columns of cells, which we may distinguish as *ommateal* and *intermediate columns.* In each ommateal column, the most superficial transverse layer is formed by two corneal cells (CLAUS, No. 78) destined to secrete the corneal lens; below this comes the layer of the crystalline cone, also consisting of two cells. In accordance with this number of cells, GRENACHER was able to prove the origin of the crystalline cone from two separate segments, the

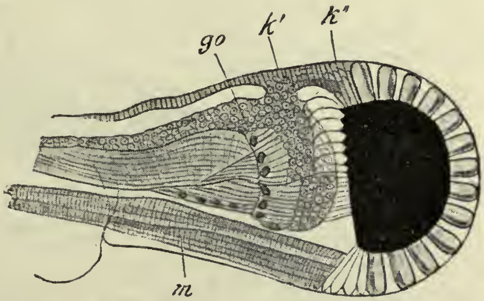

FIG. 85.—Left eye of a young *Branchipus*, seen from the ventral side (after CLAUS). *go*, optic ganglion; *k′*, budding zone for the optic ganglion; *k″*, budding zone for the ommatidia; *m*, muscle of the eye.

boundaries of which can be recognised in the adult crystalline cone. The cells in the lower layers of the ommateal column no doubt give rise to the elements of the retinulae, but NUSBAUM is inclined to derive these from the intermediate columns. CLAUS derives from these columns the anterior and posterior pigment-cells which surround the crystalline cone in *Mysis.* The observation of these processes is rendered difficult by the early deposition of pigment which is to be found within the rudiment of the eye in two layers, and in a third mesodermal layer below it.

FIG. 86.—Sections through the compound eye of the American Lobster (*Homarus americanus*) in three stages of development (after PARKER). *A*, transverse section through the optic lobe in a young stage. *B*, older stage when the optic rudiment (*r*) and the optic ganglion (*go*) are beginning to be separated by the development of a basal membrane (*mb*). *C*, cross section of still older stage. *c*, rudiment of the brain; *go*, optic ganglion; *mb*, basal membrane; *r*, rudiment of the eye (retinogen).

The account here given of the ontogeny of the eye in *Mysis* resembles that given by HERRICK (No. 48) in connection with *Alpheus*, and PARKER (No. 62) for *Homarus.* The optic lobes here develop, by proliferation of the ectoderm, into a multilaminar rudiment (Fig. 86 *A*). (HERRICK considers that indifferent elements out of the yolk also contribute to their formation). There then takes place a separation into a superficial and a lower part (Fig. 86 *B* and *C*). The first layer (*retinogen*) becomes the rudiment of the eye (*r*), while that of the optic ganglion (*go*) arises from the cell-mass of the lower layer (*gangliogen*). In later stages the two layers are separated by a cuticular basal membrane, through which strands of nerve-fibres pass. In the rudiment of the eye itself, which we have called the retinogen, the separate ommatidia are said to develop (HERRICK), the corneal cells forming into groups of two in the most superficial layer, and the crystalline cone-cells into groups of four in the subjacent layer, while, in the lowermost layer, the cells of the retinulae form bundles of seven each, these bundles reaching and enclosing the lowermost, pointed ends of the cells of the crystalline cone. The separate rudiments of the ommatidia are divided by numerous undifferentiated ectoderm-cells.

In this last point the accounts of PARKER and HERRICK differ. In *Homarus* it is said (PARKER) that the separate rudiments of the ommatidia lie close to one another, and are not separated by any kind of intermediate pillars. Three layers can be distinguished; from the outermost arise the corneal hypodermis-cells and the anterior pigment-cells (distal retinulae), from the median layer the cells of the crystalline cone, and from the lowest the actual retinulae.*

The paired lateral eye of the Isopoda also develops in a similar way. In BULLAR's account of *Cymothoa* (No. 81) the rudiment of the eye stands in close connection with that of the optic ganglion. The two proceed from one and the same ectodermal thickening. While the inner layers of this thickening become detached for the formation of the optic ganglion which is connected with the brain, a superficial hypodermal thickening becomes marked off by a pigmented basal membrane. This hypodermal thickening represents the rudiment of the eye, in which the separate ommatidia seemed to be marked off from one another by a strongly pigmented mantle of cells. The details of the development of the ommatidia were not followed in this case.

In the cases we have hitherto described, the development of the eye is comparatively simple, but in *Astacus* (REICHENBACH, No. 65) and *Crangon* (KINGSLEY, No. 52) complication occurs through an invagination which forms on the boundary between the rudiment of the eye and that of the ganglion. This invagination, which, according to REICHENBACH, is replaced at a certain stage of development by a more solid ingrowth, gives rise to the *optic fold* between the rudiment of the eye and the gangliogen; in this fold an inner and an outer layer are recognisable. Although REICHENBACH did not closely follow the future fate of the optic fold, it appeared probable to him that the outer layer enters into the formation of the eye and yields the retinular layer, while the inner fold enters into the formation of the optic ganglion. It was pointed out, especially by CARRIÈRE (No. 44), that in such a method of development of the retinular layer the position of its cells is reversed, their basal ends being directed towards the cells of the crystalline cone, and their upper ends towards the rudiments of the ganglion, and that we must thus assume a later re-arrangement in the retinular area, such as takes place among the Araneae, but has not yet been observed among the Crustacea. The suggestion made by PATTEN appears to us probable, viz.—that the optic fold has nothing to do with the formation of the eye, but merely yields the material

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* [*Cf.* PARKER, G. H., Retina and Optic Ganglia in Decapoda, *Mittheil. Stat. Zool. Neapel.*, xii., 1895.]

for the enlargement of the optic ganglion. If so, it would correspond to the proximal budding point (for the enlargement of the ganglion, Fig. 85, *k'*) in the eye-stalk of *Branchipus*. This last view has recently been accepted by KINGSLEY also, who originally thought that the layer of the crystalline cones and the retinular layer arose from the outer wall of the optic invagination.

The above view receives its chief support, as CARRIÈRE pointed out, from the position of a pigmented layer of mesoderm-cells, which, according to REICHENBACH, develops between the outer wall of the optic fold and its crystalline cone-layer, and which is, nevertheless, evidently identical with the layer of pigment-cells below the basal membrane of the eye, described above (p. 169) for *Mysis*.

With regard to the significance of the separate parts of the ommatidium, as to which GRENACHER and PATTEN have recently taken opposite views, attention should be drawn to PARKER's observations, which revealed a connection of the retinular cells with fine nerve-fibres, while the crystalline cone-cells, which doubtless reach to the basal membrane, end at that point. This is in agreement with the view of GRENACHER, who saw in the retinular cells the percipient elements, while PATTEN considered that the crystalline cone-cells known as retinophorae were the elements connected with the nerves.

In the development of the compound eye of the Cladocera, which was carefully described by GROBBEN (No. 11), special interest is awakened by the formation of an integumental fold which grows over the eye, cutting off a hemispherical precorneal space. The movement of the sunken eye is thus assisted. Similar conditions are found in *Apus*, *Estheria*, *Limnadia*, and *Limnetis*. The compound eyes, in these forms and perhaps also in the Ostracoda, may be regarded as movable stalked eyes with degenerated stalks which have sunk below the surface. Where, as in the Cladocera, an unpaired compound eye is found, this must be considered to have arisen by the fusion of paired rudiments.

An *auditory organ* was observed by REICHENBACH (No. 65) in *Astacus*, as a dorsal invagination in the basal joint of the antennule. Even in early stages, the ectodermal sensory epithelium, which probably yields the auditory ridges, is distinguished by the multilaminar and regular arrangement of its cells. NUSBAUM (No. 39) similarly was able to observe the origin of the auditory sac in *Mysis* in the endopodite of the last pair of pleopoda out of an ectodermal invagination.

E. Gills.

The branchiae first appear as simple outgrowths of the superficial body-epithelium (ectoderm), within which lacunar blood-spaces traversed by connective tissue-strands develop (REICHENBACH). We may with some probability regard all the branchial sacs or tubes which belong to the outer side of the basal joints of the limbs, and can thus be described as *epipodial gills* (p. 195), as homologous structures throughout the whole of the class Crustacea. We may also, perhaps, derive them from the branchial tubes of the Annelida. On the other hand, it must be pointed out that branchial outgrowths develop at other points also, *e.g.*, on the exopodite of the pleopoda (*Squilla*), or on the endopodite of the same limbs (*Siriella*), as dorsal appendages in certain Ostracoda (*Asterope*), as mantle-folds in the *Balanidae*, etc. These naturally cannot be homologised with the epipodial gills. The epipodial branchial sacs present in a single row in the Phyllopoda are replaced in the Decapoda by three rows of branched tubes, which, according to their exact points of attachment, are distinguished by HUXLEY as *podobranchiae*, *arthrobranchiae*, and *pleurobranchiae*. Instead of these, we find in the *Euphausidae* and *Lophogastridae* only a single row of dendriform branched tubes, so that CLAUS raises the question whether the three rows of gills of the Decapoda may not be derived from the principal branches of the Schizopodan gill which have shifted apart.

F. Intestinal Canal.

The intestinal canal arises here, as in most groups of animals, from three separate rudiments, the fore-gut and hind-gut arising as ectodermal invaginations (the stomodaeum and the proctodaeum), while the mid-gut is formed from the cells of the entoderm. Whereas the two former approach their adult form by a series of comparatively simple changes, the development of the latter is brought about by far more radical ontogenetic processes, on account of disturbances due to the presence of the food-yolk, these processes also varying in the different orders of Crustacea.

There is some variation among the sub-groups of the Crustacea with regard to the time of the appearance of the fore- and hind-guts. In the Entomostraca, the rudiment of the fore-gut, as a rule, appears first. This is also the case in *Asellus*, *Gammarus*, and *Mysis*, while, in *Oniscus*, the hind-gut develops first. In the Decapoda, the proctodaeal invagination usually appears first, a fact connected with the early development of the abdomen.

The position of this invagination with relation to the closed blastopore is of importance. In *Moina*, according to GROBBEN, the point at which the blastopore closes corresponds to the oral aperture, while in the Decapoda, it always lies close to the future anal orifice. According to REICHENBACH, in *Astacus*, it lies somewhat behind the point at which the anal aperture is forming, as is also the case in *Atyephyra* (ISCHIKAWA). The opposite, according to LEBEDINSKY, holds true for *Eriphia*. Here the proctodaeal invagination develops behind the blastopore. KINGSLEY, on the contrary, believes that, in *Crangon*, the proctodaeal invagination corresponds exactly to the point at which the blastopore closed, this being also maintained by Bobretzky for *Astacus* and agreeing with P. Mayer's account of *Eupagurus*. Hoek found that, in the free-living Copepoda, the point at which the blastopore had closed corresponded to the position of the future anal aperture, and Nassonow made the same observation in *Balanus*, so that, as a rule in the Crustacea, the position of the blastopore may be assumed to be in the neighbourhood of the anal aperture (p. 141).

The time at which the three rudiments unite to form a single canal varies according to the stage of development at which the larva leaves the egg. In the free-living Copepoda (*Cetochilus*), the intestinal canal is completed at an early stage, while in the Decapoda, communication is established between the fore- and hind-guts and the mid-gut usually at a later stage. The hind-gut here appears to show its adult structure sooner than the fore-gut.

We have as yet very little accurate information as to the manner in which the mid-gut develops in the Entomostraca. In *Moina*, the entoderm-cells first form a solid strand, a cross section of which reveals a radial arrangement of the cells, but no lumen (Grobben). In *Cetochilus*, on the contrary, the entoderm-sac which is formed by invagination seems to be transformed direct into the mid-gut. In many other Entomostraca, the mid-gut rudiment can be recognised as a central mass of cells filled with food-yolk (*Balanus*, Lang, Nassonow). In later stages, the nuclei of the entoderm-cells, with the protoplasm which surrounds them, migrate to the surface, and as the food-yolk is gradually assimilated, the cavity of the mid-gut appears within. This is also the case in *Palaemon* (p. 132). In the parasitic Copepoda also, the mid-gut, according to Van Beneden (No. 17), appears to develop in this way. The mid-gut, filled with food-yolk, is connected at its anterior end with the stomodaeal invagination, and at its posterior end with the proctodaeal invagination.

The development of the mid-gut is best known in the Decapoda. In *Astacus*, where the cells of the entoderm-vesicle absorb the whole of the food-yolk, without thereby disturbing the conformation of the vesicle, the epithelium of the mid-gut arises by the shifting of the nuclei to the surface of the yolk-bearing entoderm-pyramids, a separation of the cells from the food-yolk there taking place; as the entoderm-cells increase in number they become arranged into an epithelium which now covers the surface of the disappearing yolk (p. 130). At the same time, the whole rudiment of the mid-gut, by constriction from without, assumes a lobate form. Paired anterior lobes form which become connected with the median rudiment of the mid-gut, at whose posterior dorsal portion can be recognised another swelling, the rudiment of the dorsal caecum of the mid-gut. The development of the mid-gut epithelium just described first takes place at the point where the entoderm-vesicle and the rudiment of the hind-gut are in contact, and where soon an entodermal epithelial plate can be seen (Fig. 63 *B*, *ep*, p. 131). The same has been observed at the point from which the formation of the hepatic tubes commences. Separate centres of epithelial formation are to be found at the anterior, lateral and posterior parts of the mid-gut corresponding to the anterior, lateral, and posterior hepatic lobes of the adult animal; at these points, the epithelium soon grows out to form the primary hepatic tubes. The rudiment of the posterior pair of tubes seems from the first to be connected with the entoderm-plate described above. As the epithelium continues to grow over the rest of the entoderm-vesicle, the central part of the alimentary canal arises, receiving the efferent ducts of the mid-gut gland (liver); this central part, in the adult, is of no great extent. Its musculature arises by the deposition of mesodermal elements.

The stomodaeal invagination soon becomes divided into a narrower oesophageal portion and an inner and more swollen portion, the rudiment of the so-called stomach. In the latter can be recognised the rudiments of the tooth-plates as epithelial thickenings, and those of the gastrolith-sac as two diverticula diverging on the ventral side. The young *Astacus* hatches with two completely developed gastroliths (REICHENBACH). The mid-gut becomes connected with the fore- and hind-guts only at a late stage.

The mid-gut develops in a similar manner in those Decapoda in which the entoderm-sac does not retain its continuity, but breaks up into single cell-elements, which become distributed in the food-yolk (*Palaemon*, *Eupagurus*, *Eriphia*, *Atyephyra*, *Crangon*, etc.). In these also, the entodermal elements finally rise to the surface, and yield the mid-gut in the way described above. Here also the first appearance of this epithelium was observed in contact with the blind inner end of the proctodaeal invagination (Fig. 64 *C*, *ep*). Three pairs of originally distinct hepatic rudiments, however, appear to be added to it (*Crangon*, KINGSLEY).

The formation of the mid-gut in the Arthrostraca differs from the type above described as occurring in the Decapoda in that here the mid-gut epithelium does not proceed from elements scattered in the food-yolk, but from a paired lateral mass of cells which lies superficially on the yolk and gradually grows round it (p. 139, etc.), while within the yolk, vitellophags are found only in isolated cases (*Oniscus*, NUSBAUM); in other cases (*Porcellio*, Amphipoda), cell-elements are here altogether wanting. By the gradual circumcrescence of the yolk from the two sides by the paired entoderm-rudiment, the mid-gut vesicle closes, the very large primary hepatic sacs forming by constriction at its sides. These hepatic sacs give rise later, by longitudinal constriction, to four or six tubes. In some cases (*Oniscus*, *Caprella*, *Sunamphithoë*), the formation of the hepatic tubes precedes the development of the mid-gut vesicle. In most cases, the chief part of the entoderm is used up in the formation of the hepatic rudiment, only a small part entering into the formation of the central portion of the intestinal canal. The latter is almost exclusively composed of the fore and hind-guts, only a short tract in the immediate neighbourhood of the openings of the hepatic tubes being entodermal in origin. As diverticula of the posterior section of the mid-gut, there arise in *Gammarus* (Pereyaslawzewa) those paired tubes (*urinary glands*), the entodermal nature of which was recognised even in the anatomical researches of Nebeski. The homologising of these urinary tubes with the Malpighian vessels of the Insecta is on this account inadmissible, the latter belonging to the hind-gut, and therefore having an ectodermal origin.

The observations of Bullar (No. 81) on the development of the mid-gut in *Cymothoa* are in fairly close agreement with those of Nusbaum for *Oniscus*. There are, however, no so-called yolk-cells here inside the very considerable mass of food-yolk; the formation of the mid-gut proceeds from the inner cell-layer of the germ-band. The first trace of a separate entodermal rudiment is found in a paired mass of cells lying somewhat behind the stomodaeal invagination; this mass of cells gives rise to three pairs of hepatic tubes. At a later stage, a layer of cells connected with the epithelium of the hepatic tubes grows over the whole of the food-yolk. The rudiment of the mid-gut now consists of the yolk-vesicle thus formed and the hepatic tubes communicating with it. The anterior end of the yolk-vesicle is connected with the stomodaeal invagination. The proctodaeal invagination, on the contrary, is not in contact with the posterior end of the yolk-sac, but runs forward over its dorsal side so as to pass into it quite near the stomodaeal invagination. The yolk-vesicle appears now as a ventral diverticulum of the alimentary canal, but, as most of it undergoes absorption, it results that here also only quite a small part of the definitive intestinal canal near the points of entrance of the hepatic tubes belongs to the mid-gut (*cf.* p. 139 on *Ligia*).

The above description of the formation of the mid-gut in the Arthrostraca, founded on the observations of Bullar, Nusbaum, Pereyaslawzewa, and Rossijskaya, applies, according to Nusbaum, to *Mysis* also (Figs. 65 and 66, p. 135). The entoderm here originally lies as a mass of cells in the most posterior section of the germ-band (p. 134). The entoderm-cells soon increase in number, and spread out over the whole ventral surface of the embryo. At a later stage they also reach the lateral and dorsal parts, the food-yolk in this way becoming surrounded by a layer of entoderm-cells While this circumcrescence is going on in the posterior part of the embryo, the entoderm in the anterior part (behind the mandibular segment) forms two lateral grooves consisting of large granular cells (Fig. 66, *l*); these are the rudiments of the hepatic tubes, which become connected later on the ventral side by entodermal epithelium. Two longitudinal folds arise and fuse with the inwardly curving edges of the grooves, and thus separate the hepatic tubes from the middle portion of the intestinal canal. At the same time, the hepatic tubes become divided through longitudinal folding into four secondary tubes in the same way as in the Arthrostraca. It appears that, in *Mysis*, when the mid-gut vesicle forms, the whole of the food-yolk is not taken up into it, but part of it comes to lie in the cephalic region outside of the intestine, and thus in the body-cavity. The food-yolk has a similar position in *Moina*.

G. Heart.

In describing the development of the heart, we must take as our starting point the observations made by CLAUS (Nos. 8 and 9) on *Branchipus*. The somatic layer of the mesoderm here forms a cell-stratum originating on the ventral surface, and now divided into separate segments; this mesoblast gradually grows upwards under the lateral parts of the integument. The dorsal edge of these growing mesoderm-segments is formed by a single row of large cells (*cardioblasts*, NUSBAUM, Figs. 87, *c*, and 88 *A*, *c*), which later assume a crescentic shape (Fig. 88 *B*, *c*), so that a channel is now formed on each side. These semilunar channels, meeting and fusing in the middle line, give rise to a dorsal tube (Fig. 88 *C*, *c*). The latter is from the very first divided up into separate segments (chambers) corresponding with the primitive mesoderm-segments; the boundaries of these chambers persist as the lateral ostia. This origin of the heart seems distinctly to show that its lumen must be considered as a remains of the primary cleavage-cavity (BÜTSCHLI, SCHIMKEWITSCH).

The ostia develop at the boundaries of the mesoderm-segments. The cardioblasts become transformed into the muscle-cells of the wall of the heart. During their development, the latter have their lower ends connected with the dorsal portion of the intestinal muscle-layer. From this point, a horizontal septum stretches out towards the body-wall; this is the *pericardial diaphragm* (Fig. 88 *C*, *s*), which separates an upper portion of the coelom containing the heart from the rest of the body-cavity. This septum is found in all Crustacea.

The heart of *Oniscus* develops in a similar way by the fusing of two grooves which arise from a single row of cells on each side (NUSBAUM). The formation of the heart in the Amphipoda (PEREYASLAWZEWA, ROSSIJSKAYA) also passes through a similar stage. While, however, in *Oniscus*, the posterior parts of the body develop first, and the formation of the heart proceeds gradually from behind forward, in the Amphipoda, the heart begins to form in the middle region of the body. A vascular trunk arises simultaneously in front of the dorsal organ in the same way. The two rudiments only fuse after the dorsal organ has degenerated, that organ retarding the development of the single dorsal tube. In the Amphipoda the fusing of the two grooves takes place in such a manner that the ventral precedes the dorsal fusion. This leads us to the condition observed in the Decapoda.

In *Astacus*, the first rudiment of the heart is to be recognised as an accumulation of mesoderm-cells in the most posterior part of the embryonic disc (Fig. 63 *B*, *h*, p. 131), and thus behind the point from which the ventrally curved thoraco-abdominal region arises. In sections it can be seen that these mesoderm-cells unite to form a transverse plate which becomes opposed to the ectoderm on each side. The cavity found between the ectoderm and the plate of cardioblasts is the future lumen of the heart. This plate already shows slight pulsation, in which the ectoderm passively participates, before it curves round dorsally to form a tube (REICHENBACH). A similar condition is described by LEBEDINSKY for *Eriphia* (No. 57).

The heart of *Mysis* develops in a manner analogous with that of *Oniscus*. The heart here arises as a cavity in a kind of dorsal mesentery formed by the fusion of the lateral edges of the somatic mesoderm. Its formation proceeds from behind forward.

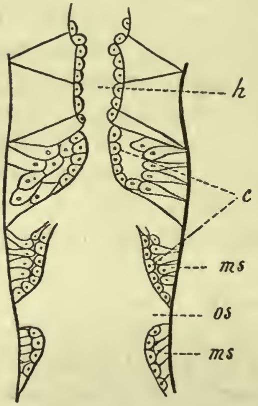

FIG. 87.—Dorsal aspect of a posterior segment in the body of a young *Branchipus* larva, showing the development of the heart (after CLAUS). *c*, cardioblasts; *h*, cardiac cavity; *ms*, mesoderm-somites; *os*, rudiments of the ostia.

As the primitive form of Crustacean heart we must assume a long dorsal vessel provided with numerous segmentally-arranged pairs of ostia; such a heart has been retained in the Branchiopoda (Fig. 95, *h*, p. 202), and also occurs in the Stomatopoda. The short, sac-like heart of the Copepoda and Cladocera is a degenerate form of this elongate type. Such degeneration may lead in small Entomostraca to the entire disappearance of the heart (many Copepoda and Ostracoda). In the same way the short sac-like heart of the Decapoda is probably to be derived from an elongate type of heart, such as is found in the Stomatopoda and Leptostraca. It seems probable, from CLAUS's researches on the vascular system of the Stomatopodan larvae with regard to the origin of the arteries, that the heart of the Decapoda corresponds to the most anterior portion of that of the Stomatopoda.

H. Glands.

Two pairs of glands which occur in the Crustacea must be regarded as modified segmental organs. These are the antennal gland (green gland) and the shell-gland. REICHENBACH (No. 65) and ISCHIKAWA (No. 51) have maintained that the former arises as an ectodermal invagination, while KINGSLEY (No. 55) has proved that, in *Crangon*, it arises from a collection of mesoderm-cells, and only secondarily does the vesicle open externally. The mesodermal origin of the shell-gland has been established in the case of the Cladocera by GROBBEN (No. 11) and LEBEDINSKY (No. 11a).

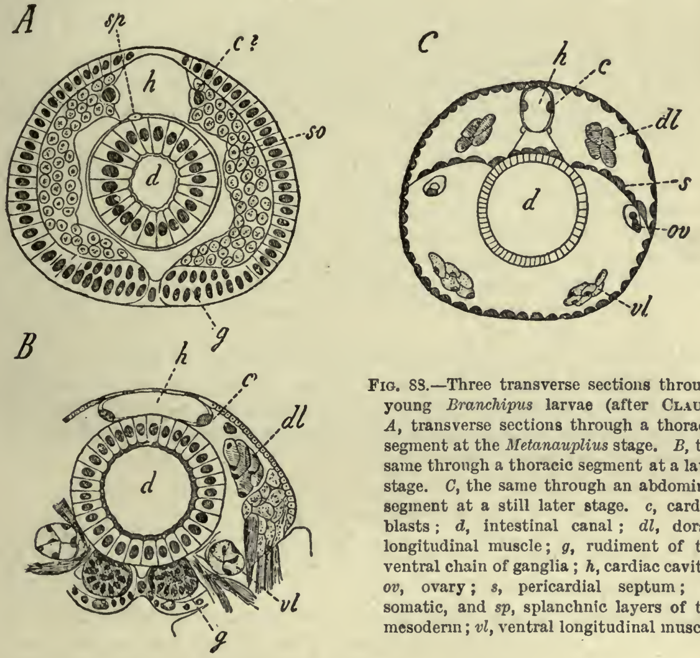

FIG. 88.—Three transverse sections through young *Branchipus* larvae (after CLAUS). *A*, transverse sections through a thoracic segment at the *Metanauplius* stage. *B*, the same through a thoracic segment at a later stage. *C*, the same through an abdominal segment at a still later stage. *c*, cardioblasts; *d*, intestinal canal; *dl*, dorsal longitudinal muscle; *g*, rudiment of the ventral chain of ganglia; *h*, cardiac cavity; *ov*, ovary; *s*, pericardial septum; *so*, somatic, and *sp*, splanchnic layers of the mesoderm; *vl*, ventral longitudinal muscle.

Our belief that these two glands, which formerly were often confused with one another, are the homologues of the Annelidan segmental organs, rests partly on the statements of LEYDIG and GEGENBAUR. This interpretation of the antennal gland is supported chiefly by the careful anatomical researches of GROBBEN, and by the agreement thereby revealed between the structure of this organ and the nephridia of *Peripatus*, so thoroughly investigated by SEDGWICK. According to GROBBEN, we must distinguish in the antennal gland (in the Entomostracan larva as well as in the adult Malacostracan) two sections—an "end-sac" and a much-coiled tubular portion which often enlarges before opening on the basal joint of the second antenna into a vesicle (urinary bladder). All these separate parts of the gland may become more complicated by the development of secondary diverticula. In recent researches, in which the indigo-carmine injections recommended by KOWALEVSKY were used, WELDON (No. 68),* working on *Palaemon serratus*, concluded that the structure

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* *Cf.* MARCHAL, *Compt. Rend.*, Tom. cx., cxi., and WELDON, *Quart. Journ. Micro. Sci.*, Vol. xxxii.

of this urinary organ was far more complicated than is generally believed. It had been thought probable, from investigation of *Peripatus*, that the "end-sac" of the antennal gland might be considered as the vestige of the coelomic sac of this segment. But Weldon found in *Palaemon* a large coelomic sac lying in front of the genital glands and not communicating with the rest of the body-cavity, but connected with two nephridial canals running forward to the right and left; these last widened out to form the urinary bladder. To this canal system, the "end-sac," which may be compared with the Malpighian glomerulus, is a lateral addition connected with the urinary bladder by five glandular tubes. As the relations of the body-cavity in the Crustacea are still far from clear, further investigation of this remarkable condition is very desirable. In the meantime, it is perhaps advisable to adhere to the views put forward by Grobben.

That the above pairs of glands and the parts of the mid-gut participating in the formation of the excretory products (in Copepoda and Amphipoda) are by no means the only excretory organs of the Crustacea is proved by the experiments of Metschnikoff and Kowalevsky (*Biol. Centralbl.*, Bd. ix.) mentioned above. These authors, by means of coloured injections, demonstrated the presence of small tubes in the thoracic limbs of *Mysis*, in which the colouring matter accumulated, and of cell-groups in a corresponding position in *Nebalia.*

Lebedinsky (No. 57) has described the development, in *Eriphia spinifrons*, of a "segmental organ," arising as a paired outgrowth of the somatopleura. The tube thus produced lengthens out anteriorly and forms a coiled canal, which enters into communication with an ectodermal invagination in the coxal joint of the first pair of maxillipedes.

I. Genital Organs.

Our knowledge of the development of the genital organs in the Crustacea is as yet very fragmentary. The rudiments of the genital glands belong in all cases to the mesoderm. Grobben (No 21) found that, in *Cetochilus*, the genital rudiments are paired in the *Nauplius* stage, and lie ventrally to the intestinal canal. Only later do they shift dorsally to a position above the intestine, where they unite to form a single gland. Each of the genital rudiments consists of a large special genital cell, and of adjoining mesoderm-cells which yield the envelopes and efferent ducts.*

In *Moina*,† probably in connection with its paedo-parthenogenesis, the genital rudiments can be recognised as unpaired genital cells as early as the time when

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* [Hacker (*Archiv. f. mikr. Anat.*, Bd. xlix., p. 35; "Die Keimbahn von Cyclops") traces the rudiment of the genital gland to a single cell, which is completely isolated at the thirty-two-celled stage, and which can be identified from the first cleavage which divides the egg into two cells, one of which is purely somatic, while the other (the "Körnchenzelle") gives rise to a certain number of blastomeres (three), but always retains its individuality, and finally divides into the primitive entoderm and the primitive genital cell.—Ed.]

† In *Daphnia similis*, Lebedinsky (No. 11a) was unable to distinguish the genital cells at as early a stage as is possible in *Moina*. Even in the *Nauplius* stage, the genital rudiments were indistinguishable.

the germ-layers separate. A cell-mass arising from these by division shifts within the embryo, and there forms an unpaired plate lying dorsally above the rudiment of the mid-gut; this plate only secondarily divides into two halves. The above mass of cells is invested later with a mesodermal envelope.

The statements of CLAUS (No. 9) in connection with the development of the genital organs in *Branchipus* are of importance. The rudiment of the genital glands is here a paired strand lying in the three or four anterior segments at the sides of the alimentary canal, and recognisable even in early stages. The first development of the efferent ducts, however, takes place at a later stage of sexual differentiation (p. 200), and proceeds from a transformation of the twelfth and thirteenth post-cephalic segment into two pairs of genital swellings. The latter, in the female, join in the median line, while in the male they remain separate. In both sexes the genital swellings of the posterior segment are grown over by those of the anterior segments. The fused swellings then appear, in the female, as a broad median prominence, or in the male as paired lateral prominences. The cell-material found in the genital swellings is utilised in such a way that the mesoderm-cells yield the efferent apparatus (oviduct and uterus—seminal duct and seminal vesicle) as well as the accessory glands, while an ectodermal ingrowth on the second pair of swellings becomes, in the female, the short external portion of the uterus (vagina), and, in the male, the long protrusible copulatory organ (cirrhus).

In the Decapoda, the genital rudiment has only been observed in the latest stages of embryonic life. BOBRETZKY and REICHENBACH (No. 65) conjecture that it is represented by two cell-strands which lie above the intestinal canal. According to BOBRETZKY, these lie in the mid-gut region below the pericardial septum, whereas REICHENBACH observed the rudiment in the posterior segments in the hind-gut region.

NUSBAUM (No. 39) found the genital rudiments, in *Mysis*, as a paired group of cells lying behind the hepatic rudiment. When the hepatic tubes develop, this rudiment shifts towards the dorsal side, and later probably fuses to form an unpaired rudiment lying between the heart and the intestine. It appears doubtful whether a few large cells observed in the ectoderm at the time when the germinal layers form, and which later lie in the abdomen, are really, as authors maintain, to be identified as the genital rudiment.

Although, for general reasons, we feel inclined to attribute the genital rudiments to the mesoderm, PEREYASLAWZEWA and ROSSIJSKAWA (Nos. 70 and 73) derive the genital cells in the Amphipoda from the wall of the mid-gut (!). According to these authors, a few entoderm-cells leave the mid-gut epithelium (in *Orchestia*, the hepatic tubes also), and, surrounded by a mesodermal envelope, become the rudiment of the genital glands. It is well known that such an origin was asserted for these glands in *Peripatus* by SEDGWICK.

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II. Metamorphosis.

1. The Nauplius Stage.

The most typical feature of the metamorphosis in the Crustacea, and therefore, perhaps, the most convenient one with which to commence our study, is the so-called *Nauplius stage.* In those cases in which the young animal is hatched at a later stage of development (*e.g.*, in the Cladocera, the Arthrostraca, and most Decapoda), the *Nauplius* stage is thrown back among the series of embryonic stages; nevertheless, we commonly find that this stage is indicated by a period of rest, such as an ecdysis of the Nauplius integument (p. 118).

The Nauplius body (Fig. 89) is as a rule oval, the anterior end being the more rounded, and the posterior the narrower end of the body. In other respects, there is great variety in the shape of the body. Dorsally compressed, laterally compressed, long, and even broad *Nauplii* are to be found. The possession of three pairs of limbs—the future first antennae (*a′*), second antennae (*a″*), and mandibles (*md*)—points to the fact that, in the *Nauplius*, we have an already segmented larval form. This segmentation is, however, not externally recognisable in the body of the *Nauplius*, although the limits of the segments may be indicated in the ontogenetic stages which lead up to the *Nauplius* (free-living Copepoda, Cirripedia). Typically, the *Nauplius* has no shield-like reduplication of the dorsal integument, but such a fold (which usually only appears at a later stage) may be distinctly recognisable in individual cases (Cirripedia, Fig. 102 *A*), or at least may be indicated by a slight fold in the integument of the dorsal surface. The posterior end of the body is still without the paired furcal processes, but is armed with paired setae (furcal setae). The most anterior pair of limbs, the first antennae (*a′*), are uniramose, and consist of few joints or are still unjointed. They serve for locomotion, and are also of importance as bearing sensory organs. The two pairs of limbs which follow these are developed in the form of biramose swimming limbs. The first of these, the second antennae (*a″*), lie at the sides of the mouth, and are distinguished by a strong, hook-like, masticatory process springing from the basal joint. The third pair of limbs, the mandibles (*md*), also function principally as locomotory organs. A masticatory blade is not, as a rule, developed on the basal joint, indeed, this structure, so characteristic of the appendage in the adult, is hardly indicated, although it may in some cases occur here. The U-shaped antennal gland (*at*) opens externally on the basal joint of the second antenna. The oral aperture which lies between the two antennae is overhung by a large upper lip (labrum), and leads into the alimentary canal, in which can be distinguished a short oesophagus, a widened mid-gut, and a hind-gut. The anal aperture may be wanting in the first *Nauplius* stages (*Cetochilus, Cyclops*). It has been observed in many cases that this aperture originally opens on the dorsal surface (Cirripedia, Fig. 103, p. 212; *Cetochilus*, Fig. 111 *B*, p. 233; embryonic stage in the Cladocera, Fig. 72, p. 147), the aperture shifting later to the posterior end of the body between the furcal processes. The nervous system retains its original connection with the ectoderm, and consists of the supraoesophageal ganglion, circumoesophageal commissures, and the first pair of ganglia of the ventral cord. The second antennae are innervated from a pair of ganglia lying behind the mouth (Claus, Dohrn), an arrangement which is retained by the Phyllopoda in the adult. As a sensory organ, there is the unpaired Nauplius eye, which lies in the frontal region, and is composed of three parts. The most developed muscles are those of the limbs, which are attached to a point in the mid-dorsal region. The heart is not yet developed.

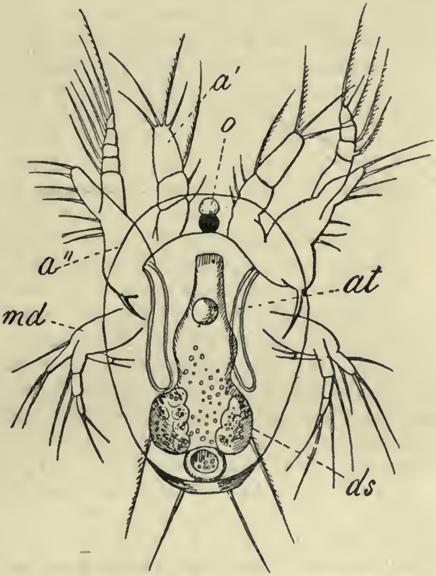

Fig. 89.—*Nauplius* of *Cyclops* (after Claus). a', first antenna; a'', second antenna; *md*, mandible; *o*, Nauplius eye; *at*, antennal gland; *ds*, mid-gut with excretory cells.

Although there is no external segmentation in the Nauplius body, we can nevertheless recognise in it the following segments:—An anterior pre-oral or primary *cephalic segment*, a posterior terminal or *anal segment* at the posterior end of the body, and the true *trunk-segments* which lie between these. As members of the last group, we recognise the section of the body belonging to the second antenna and the mandibular segment. We have, however, already pointed out (p. 165) that the region of the first antenna possibly also corresponds to a trunk-segment, which became early specialised and lost its independence. The cephalic and terminal segments stand in a certain contrast to the trunk-segments, in so far as only the latter have rudiments of limbs. The posterior portion of the Nauplius body contains anteriorly a budding zone from which new trunk-segments are continually being produced, while its posterior extremity eventually becomes the anal segment (telson) of the adult.

The typical form of *Nauplius* above described undergoes many variations in detail, some of which will be described later. In most cases, at the *Nauplius* stage, not only the above-named trunk-segments are perceptible, but also the rudiments of other segments behind these. Such a stage, indicating as it does a higher grade of segmentation of the body, is more correctly described by CLAUS' name of *Metanauplius.* This name denotes all those larval stages following upon the *Nauplius* stage, which, while retaining the general characters of the *Nauplius*, show an advance upon it in segmentation by the possession of trunk-segments bearing limbs behind the mandibular segment. Such a widening of the conception of the *Nauplius* appears the more admissible as O. F. MÜLLER founded his hypothetical genus *Nauplius* on a *Cyclops* larva with four pairs of limbs, while to the younger stage with three pairs of limbs he applied the name *Amymone.* After it had been discovered that MÜLLER's genus belonged to the series of ontogenetic stages of *Cyclops* (*Jurine*), the name "*Nauplius*" was adopted for all similarly-shaped Crustacean larvae.

The *Nauplius*, in accordance with the views of FRITZ MÜLLER (No. 16) was for a time regarded as a larval form of great significance (HAECKEL, DOHRN, No. 9), as it was thought to represent the common racial form of all the Crustacea. In what way this racial form was to be connected with the lower groups of animals was not so clearly stated. It was, however, thought that the nearest relations of the hypothetical ancestral form were to be sought among the Rotifera or the Annelida. The first to oppose the prevalent view was HATSCHEK (No. 15), who pointed out the resemblance in body-structure existing between the Crustacea and Annelida, and urged that the common ancestral form of the Crustacea must have had a body already composed of many segments, and that such a racial form could be directly deduced from the Annelida. This view received great support when the structure of the two pairs of excretory glands (shell- and antennal glands) was better known; the homology of these glands with the segmental organs of the Annelida had already been asserted by LEYDIG and GEGENBAUR. Very gradually the following view has been adopted and is now generally accepted (DOHRN, No. 11), viz.—that the *Nauplius* does not represent a stage in the direct ancestral line of the Crustacea, but is a caenogenetic, adaptively modified larval form in which the following Crustacean characters are early developed: the form of the limbs, the strong cuticularisation of the surface of the body, and in connection with this, the development of hair-like processes, the absence of ciliated epithelia, the disappearance of the coelomic sacs, and the development of a lacunar body-cavity. The *Nauplius* thus shows typical Crustacean characters in its structure and in its histological constituents, while in its body-segmentation it stands at a level which can best be compared with that of a polytrochan Annelid larva. The *Nauplius*, therefore, is a larval form which is secondarily modified by its early adoption of the Crustacean manner of life, but which, phylogenetically, arose at a comparatively late stage.

One of the principal reasons advanced for considering the *Nauplius* to be the racial form of the Crustacea was the common occurrence of this larval form in the most varied groups of Crustacea. This general occurrence of the *Nauplius* in the ontogeny of all Crustacea shows that the hypothetical common ancestor had already passed through the stage at which the *Nauplius* was acquired, and that therefore the modification in the ontogeny of the Crustacea just described took place in very early times. This appears the less surprising when we realise how greatly the ontogeny of a form is influenced by variation affecting the adult. Only in so far as the wide occurrence of the *Nauplius* larva justifies us in forming conclusions as to the ontogeny of the racial form of the Crustacea, can a certain phylogenetic significance be ascribed to it (HATSCHEK, Lehrbuch der Zool., p. 25).

The further development of the *Nauplius* stage is accomplished in the Entomostraca, *e.g.*, in the Phyllopoda and also in some Copepoda, by a series of very gradual changes of shape through many moults, the adult condition being reached by a continuous increase in the number of body-segments and of pairs of limbs, the growth of the dorsal shell-fold, the appearance of the lateral eye, and other transformations occurring one after the other. While, in these lowest forms, the course of metamorphosis is comparatively simple, it becomes more complicated among the Malacostraca, where independent larval forms, notably the *Zoaea*, are intercalated. These do not belong to the direct series of transformations between the *Nauplius* and the adult form, but are distinguished by secondarily acquired peculiarities, resulting in a great increase in number of larval forms. (For the metamorphoses of the Malacostraca, see p. 246.)

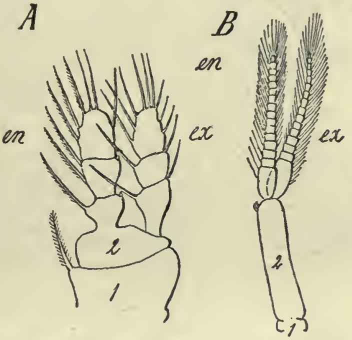

FIG. 90.—*A*, thoracic limb of a Copepod (after CLAUS). *B*, abdominal limb of *Gammarus locusta* (after BOAS). *1*, first, *2*, second joint of the protopodite; *en*, endopodite: *ex*, exopodite.

2. Typical Form of the Crustacean Limbs.

In the two posterior pairs of Nauplius appendages, we have a very primitive form of Crustacean limb. With the exception of the first antenna (antennule) which shows an altogether heteromorphous structure, all the Crustacean limbs can be traced back to a fundamental type corresponding to the biramose second and third pairs of Nauplius limbs. We can always distinguish a proximal section as the stem of the limb or *protopodite* (HUXLEY), which splits into two distal branches, the inner being, as a rule, called the inner branch, or *endopodite* (Fig. 90, *en*), and the outer the outer branch, or *exopodite* (*ex*). While the exopodite and the endopodite undergo considerable variation, developing as lamellate appendages or adopting some altogether different form, or breaking up into a very varying number of separate joints, the protopodite is in most cases composed of two joints (Figs. 90, 91, *1*, *2*). The first of these joints (the proximal joint) (*1*) was called the *basal joint* by Claus, and the *coxopodite* by Huxley, while the second (the distal joint) (*2*) is known as the *stem-joint* (Claus) or *basipodite* (Huxley). It should be mentioned that in many cases (especially in the Malacostraca), the joints of the endopodite seem to form a direct continuation of the protopodite (Fig. 91 *B*), while the exopodite appears like a lateral appendage. This condition cannot, however, be regarded as primitive.

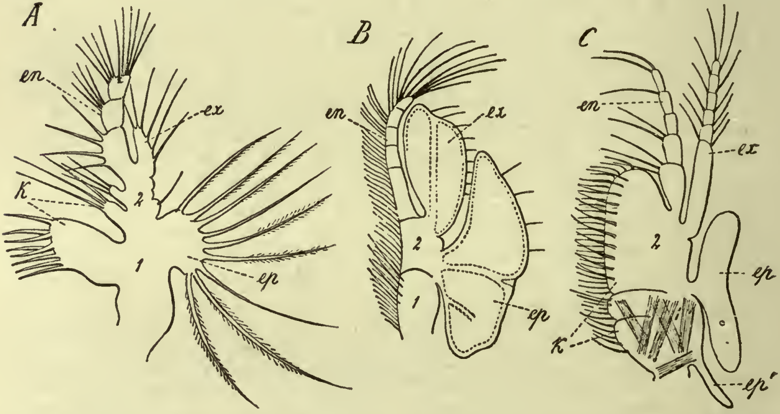

Fig. 91.—Three Crustacean limbs (after Claus). *A*, maxilla of *Calanella*. *B*, thoracic limb of *Nebalia*. *C*, first maxillipede of an advanced *Penaeus* larva. *1*, first, *2*, second joint of the protopodite; *k*, masticatory processes of the same; *en*, endopodite; *ex*, exopodite; *ep*, epipodial plate; *ep'*, rudiment of a branchial tube.

The close proximity of the ventrally placed Crustacean limbs allows mutual inter-action of the two members of one and the same pair, and we therefore often find, on the inner side of the endopodite and protopodite, processes of very various kinds which act mechanically upon any foreign bodies (particles of food) that may come between the two approximated limbs. Such processes have received the general name of *endites*, but when found on the protopodite they may bear more special names (Fig. 91, *k*), being known as masticatory hooks, lamellae, or lobes, or else as *masticatory blades.* We have already observed the development of such a masticatory hook on the protopodite of the second antenna (Fig. 89, p. 191).

Another component of the Crustacean limb which, however, is not always developed, is to be found on the external side of the protopodite, and is in most cases connected with the movement of the surrounding water and has a secondary respiratory function. Such appendages, several of which may occur together, we shall call *epipodites* (Fig. 91, *ep*), whether they are developed as lamellae (epipodial plate, *ep*) or as branchial sacs or tubes (ep^1) provided with a rich circulation of blood (p. 172). The epipodial appendages, as a rule, belong to the coxopodite or basal joint.

In the following pages we shall have to refer to the many modifiations and degenerations which these separate constituents of the Crustacean limb undergo. Of the two extreme types, the elongate form of limb appears to be the more specialised and to have developed very gradually, while the lamellate, broadened form, such as occurs in most Phyllopodan limbs and in the thoracic limbs of *Nebalia*, probably represents the more primitive type.

It has not yet been satisfactorily demonstrated in what manner the separate parts of the leaf-like Phyllopodan limb can be homologised with those of the schematic Crustacean limb above described. RAY LANKESTER's explanation seems to have a certain degree of probability. According to this author, among the six endites belonging to the inner side, the fifth represents the endopodite (Fig. 92, en^5), and the sixth the exopodite (en^6). This view is supported by the observations of CLAUS (Nos. 20 and 21), which show that, in the developing limb of *Branchipus*, these two lobes were the first to become distinct. The fan-like plate (*ep*), which arises much later, is to be regarded as an epipodial appendage as well as the branchial sac (ep^1). The breaking up of the stem of the limb into separate joints shown in Fig. 92 is exceptional among the Phyllopoda.

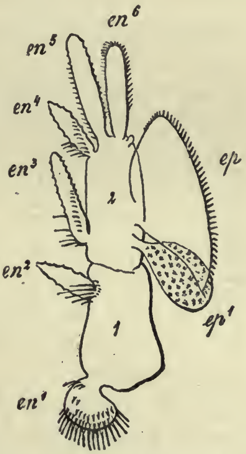

FIG. 92.—Second thoracic limb of *Apus cancriformis* (after RAY LANKESTER). *1*, first, *2*, second stem-joint; en^1, en^2, en^3, en^4, en^5, en^6, the six endites; *ep*, epipodial lamella; *ep′*, branchial sac.

We feel tempted to deduce the typical biramose form of the Crustacean limb direct from the bilobed Annelidan parapodium. Such a deduction is supported by the fact just mentioned that the separation of the exopodite and endopodite takes place unusually early in the limb-rudiment in *Branchipus* (CLAUS). Whilst, however, the Annelidan parapodia are processes of the lateral sides of the body, the limbs of the Crustacea have shifted ventrally and have become approximated, a fact which indicates that we must imagine, as the intermediate form between the Annelida and the Crustacea, an animal which crept on the sea-bottom. The mutual action of the limbs and the development of endites connected with this is thus a new acquisition peculiar to the Crustacea. On the other hand, the epipodial appendages may with some probability be deduced from the dorsal cirri of the Annelida, although this view meets with a difficulty in the late appearance of these structures in the ontogeny of the Crustacea. We must not, however, forget that the respiratory requirements only, as a rule, increase when a certain size of body is attained, and that this appears to explain why small Crustacean larvae (as well as adults of small size) have no branchial appendages.

3. Phyllopoda.

A. Branchiopoda.

The larvae of the Branchiopoda, after hatching, bear a general resemblance to the *Nauplius*, but the body is divided into an anterior cephalic section carrying the Nauplius limbs and a posterior abdominal section. Since the rudiments of a number of body-segments are to be found in the latter, this larval stage of *Branchipus* must be described as a *Metanauplius* (Fig. 93). This stage is very little modified in the various Branchiopodan genera. The rudiment of the dorsal shell-fold is, as a rule, still wanting, only developing at a later stage. The further metamorphosis is exceedingly simple, new segments being successively yielded by the posterior end of the body, and the limbs budding out in the same order. An exception to this regular course of development is found in the limbs of the maxillary region which, in keeping with their slight development in the adult, appear late. While the segmentation of the body thus gradually approaches that of the adult, the paired compound eyes develop as well as the shell-fold, which latter must be counted as belonging to the maxillary region, the internal organs develop, and the three pairs of Nauplius limbs degenerate in size and become modified.

As an example of the development of this group we may take that of *Apus*, which is so well known through the investigations of ZADDACH (No. 31), BRAUER (No. 18), and especially of CLAUS (Nos. 20 and 21). The *Metanauplius* of *Apus* (Fig. 93 *A*) is more or less oval in shape, narrowing posteriorly; when it leaves the egg it still retains the original dorsal curvature of the body (BRAUER) but soon straightens out. The only internal organs which can be recognised are the Nauplius eye and the intestine which widens anteriorly and opens out in a depression at the posterior end of the body. The three pairs of limbs are of the typical Nauplius form. The first antennae (*1*), which are inserted at the sides of the large, helmet-shaped upper lip, are simple unjointed rods each carrying two large setae at the tip. The second antennae (*2*) are large biramose swimming limbs, each carrying a movable masticatory hook on the basal joint. The endopodite of each of the second antennae is small and has setae at its end, while the five-jointed exopodite has five swimming setae on its inner side. The mandibles (*3*) are smaller than the second antennae, but agree with them in general structure. The masticatory hook is wanting in the mandibles; the future masticatory blade (often the sole representative of the mandible in the adult) is visible at this stage merely as a slight swelling on the inner side of the protopodite. The endopodite and exopodite are unjointed and carry setae at their tips. The anterior or cephalic region of the body, which carries the Nauplius limbs, is bounded posteriorly by a small dorsal prominence, in which we recognise the first rudiment of the dorsal shield. At the middle of this anterior dorsal region there is a more or less round, sharply circumscribed point, the rudiment of the nuchal gland so widely distributed among the Phyllopoda (p. 151). In the posterior, thoraco-abdominal region, five consecutive thoracic segments have begun to form as transverse swellings (*I–V*).

After the first moult (Fig. 93 *B*), the form of the body is essentially changed by the broadening of the anterior region and the elongation of the narrow, cone-like, posterior section. The dorsal shield now covers the tergum of the first thoracic segment. The Nauplius limbs retain essentially the same character. The endopodite of the second antenna is now two-jointed. On the basal joint of the mandible (*3*), a strong masticatory blade has developed with teeth on its inner edge, this being covered by the now relatively small upper lip. Behind the mandibles, the first pair of maxillae have begun to appear as simple plates (*4*). In the anterior thoracic region, two to four lobed rudiments of limbs can be made out. The number of thoracic segments is increased to eight by the addition of new rudiments. At the posterior end of the body, the large furcal processes have developed. Other points of interest in this stage are: the development of the frontal sensory organs as styloid filaments (*fs*) near the Nauplius eye, the rudiments of the hepatic outgrowths at the wide anterior part of the mid-gut, the greater distinctness of the antennal gland in the basal section of the second antenna, and the rudiment of the shell-gland in the ventro-lateral part of the dorsal shield.

The third larval stage (after the second moult), reveals lobed rudiments of limbs on the six anterior thoracic segments; on the seventh segment, a non-lobate rudiment is found, and behind this, the rudiments of two or three more segments. Behind the first pair of maxillae, the rudiment of a second pair can be distinguished as a transverse prominence. The shell-gland is distinctly visible in the lateral part of the dorsal shield, which has now slightly increased in size. At this stage the heart can already be made out, reaching from the maxillary region posteriorly to the sixth thoracic segment. As the segments develop posteriorly, new chambers are added to the heart (Fig. 87, p. 178).

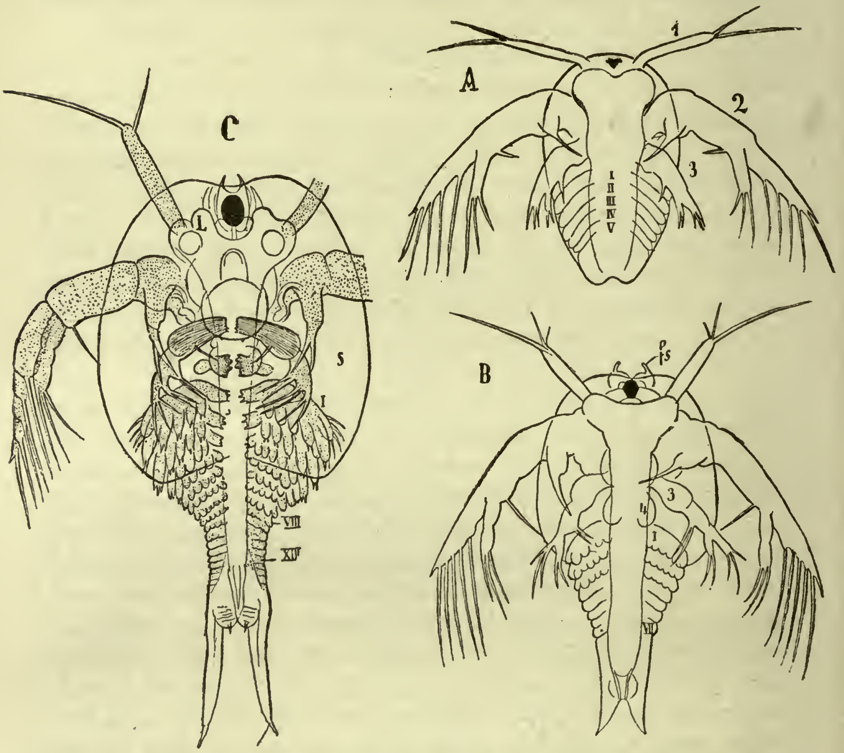

Fig. 93.—Three larval stages of *Apus cancriformis* (after Claus, from Lang's *Text-book*). *A*, larva just hatched (*Metanauplius*). *B*, second larval stage with the anterior maxillae and seven (or eight) thoracic segments. *C*, fourth larval stage with about fifteen thoracic segments. *1*, first, *2*, second antenna; *3*, mandible; *4*, first maxilla; *I.–XIII.*, first thirteen trunk-segments; *fs*, frontal sensory organ; *s*, dorsal shield; *L*, liver.

In the fourth larval stage (Fig. 93 *C*), further rudiments of limbs are seen in the act of forming on the thoracic segments; on the seven anterior segments these are distinctly lobate, on the next two, indistinctly lobate, and on the three or four following, they are unlobed. The thoracic shield (*s*) and the furcal processes have increased considerably in size. As important new rudiments, we have those of the paired eyes, which are situated dorsally above and behind the Nauplius eye, and in which the deposition of pigment has commenced These rudiments and those of the developing optic ganglia become more and more distinct during the subsequent stages.

At the fifth stage, there are nine distinctly lobate pairs of limbs, a tenth rudiment indistinctly lobate, and four following these not as yet lobate. Six more rudiments of segments are discernible behind these. At this stage, the formation of the heart and the branching of the liver by means of secondary diverticula progress gradually. In the later stages which succeed one another through numerous moults, the form of the adult is gradually approximated by the appearance of fresh segments and limbs, by the increase of the dorsal shield, which gradually covers almost the whole of the dorsal region, and by the lengthening of the furcal processes. At the same time a degeneration of the Nauplius limbs takes place, the first antenna remaining as a small two-jointed stump, and the second as a still smaller unjointed vestige; of the mandibles, only the basal joint is retained with its now strongly-developed masticatory blade. The distal part of this latter limb is visible in the later larval stages as a gradually diminishing mandibular palp, which finally disappears. This degeneration of the limbs is accompanied by a change of the method of progression. In the first stages, the larva jerks itself forward by the powerful strokes of the second antennae, but now it moves more regularly by the gentler swimming action of the numerous rowing limbs.

The above description applies to *Apus cancriformis*. The development of *Apus productus*, made known to us by BRAUER (No. 18), is quite in agreement with the above account. The egg, however, is here considerably larger and the development more abbreviated. The number of moults and of separate ontogenetic stages is smaller. The second antennae, as early as the fourth stage, cease to act as rowing organs, and at the sixth stage are greatly degenerated. The *Metanauplius* which hatches out of the egg has not only a large number of segments, but already shows the rudiments of the paired eyes.

The *Metanauplius* of *Branchipus* is somewhat longer, and the thoraco-abdominal section of the body is more sharply separated from the cephalo-thoracic section. The maxillary segments and the first two thoracic segments, with the rudiments of the corresponding thoracic limbs, can be recognised, as well as the commencement of the metameric segmentation of the rest of the body (CLAUS, No. 20). The gradual development of these larvae, as well as that of *Artemia,* follows a course similar to that of *Apus,* if we bear in mind the differences caused by the absence of a dorsal shield and the consequent cramped position of the shell-gland, whose opening was found by CLAUS (No. 21) on the second maxilla. The course of development of the compound eyes can here be followed very clearly; these, together with the optic ganglia, originate from a proliferation of hypodermis at the sides of the cephalic segment (p. 168). In this hypodermal growth, a separation into layers takes place, the inner layer being transformed into the ganglion, while the superficial layer yields the actual compound eye. A lateral outgrowth of this part of the head leads to the development of the eye-stalk, which later becomes a movable, jointed appendage (CLAUS). The method of development of the stalked eyes in this form affords the most weighty objections to the view that these organs are structures homologous with the limbs (p. 165). Until the stage at which the full number of segments and limb-rudiments is attained (first period of development), the antennae and the mandibular palps retain the larval character of the *Metanauplius* stage. Only in the subsequent period of sexual differentiation, in which the genital segments develop in a manner characteristic of the two sexes, do the muscles of the swimming antennae and the mandibular palps degenerate. The mandibular palps altogether disappear, while the second antennae shift to the

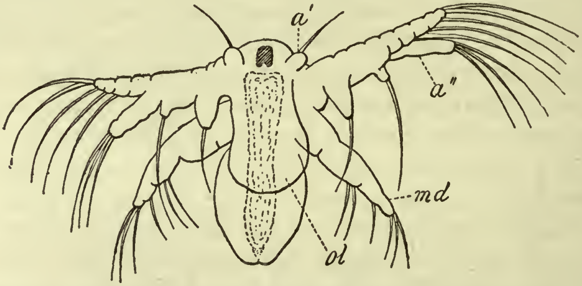

FIG. 94.—So-called *Nauplius* stage of *Estheria ticinenis* (after G. FICKER). *a'*, first, *a''*, second antenna; *md*, mandible; *ol*, upper lip.

frontal surface and become transformed into the so-called cephalic horns, varying in the different species. At the same time, a sensory organ (Claus, No. 21) develops between the forehead and median eye; this must not be confounded with the paired frontal organ. It consists of an accumulation of club-shaped terminal nerve-cells which contain peculiar three-pronged, strongly refractive deposits. It corresponds to the nuchal organ described by Leydig in connection with the Cladocera.

The development of the *Estheridae* also does not deviate in any essential point from that described for *Apus* and *Branchipus*. The so-called *Nauplius* stage (Fig. 94) is still entirely devoid of the shell-fold which, in the adult *Estheria*, is bivalve. It is distinguished from the corresponding stage of *Branchipus* only by the remarkably large upper lip (*ol*) and the rudimentary condition of the first antenna (*a′*), which is a hemispherical swelling provided with a long seta (Ficker, No. 22). At a later stage, the two maxillary segments and six distinctly separate limb-segments, still, however, quite devoid of their limb-rudiments, can be recognised. At the posterior end of the body, the furcal processes have already developed. The rudiments of the paired eyes and of the ganglia belonging to them can be made out. At this stage the rudiment of the shell first appears as a paired outgrowth of the dorsal integument of the maxillary region (Fig. 96, *s*). Within this rudiment can be recognised the as yet slightly developed shell-gland. The later stages are chiefly characterised by the growth of the shell, the increase in number of segments and limbs, the changes which take place in the Nauplius limbs, and the gradual diminution of the upper lip. In these stages (Fig. 95), the larva strikingly resembles an adult Cladoceran. The head, which is not yet covered by the shell-valves, has a pair of small antennules beset with olfactory filaments (*a′*), and large swimming antennae (*a″*) recalling in a striking manner by their structure the corresponding limbs in the *Daphnidae*. The mandibular palp (*md*) is much reduced. The shape of the shell-gland (*sd*), and the form of the posterior section of the body (post-abdomen), with its furcal hooks and two large sensory setae, so strikingly recall the Cladocera that we cannot doubt that the latter group has been derived from the *Estheridae* by a diminution of the number of segments and limbs, and a degeneration of the heart to a short sac (Claus, No. 8).

In its larval development, *Limnadia* closely resembles *Estheria* (Lereboullet, No. 26). Here also the two shell-valves develop as originally distinct outgrowths of the dorsal integument of the maxillary region (Fig. 96, *s*), fusing in the median line only at a later stage. Although here, as in the Cladocera (Grobben), the two halves of the shell at first develop separately, we must, nevertheless, trace them back to an originally single dorsal shield, like that of *Apus*.

In the youngest larval stages of *Limnetis* (Fig. 97) observed by Grube (No. 23), the shape of the body is very remarkable. In the number and structure of the limbs, this larva agrees with the so-called *Nauplius* of other Branchiopoda, but it is distinguished by a flat, circular, and somewhat transversely broadened dorsal shield. There is a correspondingly large and transversely broadened upper lip on the ventral side. At the anterior cephalic region there are one unpaired and two paired lateral conical projections. The flat dorsal shield is replaced by a bivalve shell only at a somewhat late stage.

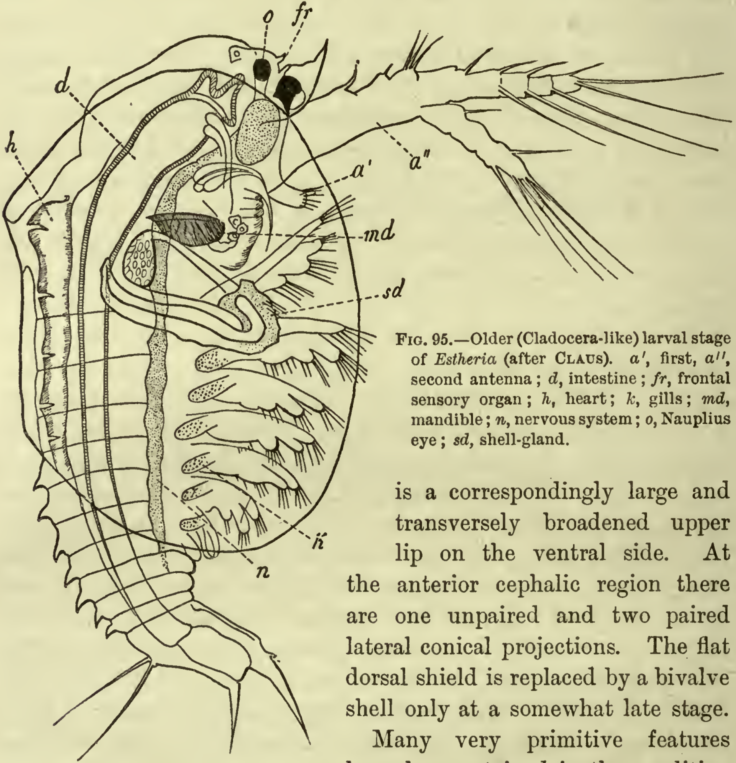

Fig. 95.—Older (Cladocera-like) larval stage of *Estheria* (after Claus). *a'*, first, *a''*, second antenna; *d*, intestine; *fr*, frontal sensory organ; *h*, heart; *k*, gills; *md*, mandible; *n*, nervous system; *o*, Nauplius eye; *sd*, shell-gland.

Many very primitive features have been retained in the condition of the body among the numerous forms of the Branchiopoda. As such we may assume the presence of many body-segments, the comparatively homomorphic development of the limbs, the origin of the antennal nerves from a pair of ganglia lying in the oesophageal commissure, the presence of separate ganglia in each maxillary segment, the ladder-like development of the ventral chain of ganglia, the presence of a long chambered dorsal vessel, and perhaps also the lamellate character of the limbs. The fact that the great groups of the Malacostraca through their most primitive member (*Nebalia*) join on to the Branchiopoda, will still further incline us to see in the latter the now living representative of a series of forms which are least removed from the hypothetical ancestor of the Crustacea (Dohrn, No. 9). On the other hand, we must not forget that the existing Branchiopoda (Phyllopoda) in many respects seem undoubtedly to have undergone great secondary modification. In the first place we must here recall the reduced form of the oral limbs (mandibles and maxillae). With regard to these we shall have to turn to the larvae of the Copepoda and the Malacostraca, so as rightly to complete the picture of the hypothetical racial form. Nevertheless, in forming a judgment of the phylogenetic relations of the Crustacea, we shall often have to return to the Phyllopoda as a very primitive group.

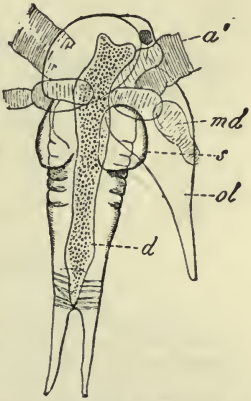

Fig. 96.—Dorsal aspect of the larva of *Limnadia* (after Lereboullet). a'', base of the second antenna; *d*, intestine; *md*, mandible; *ol*, upper lip; *s*, rudiment of the right shell-valve.

B. Cladocera.

Whereas the Branchiopoda pass through a metamorphosis characterised by many moults, larval ecdyses are altogether wanting in their relations, the Cladocera, the young animal leaving the egg with a shape resembling that of the adult. The whole modelling of the body is here shifted back to the embryonic stages, among which a distinct *Nauplius* stage can be recognised; this is in many cases even marked by a moult—development of the Nauplius cuticle—(Fig. 72, p. 147).

Special peculiarities of shape, however, are met with in the newly-hatched young of the remarkable genus *Leptodora*. Whereas the young coming from the summer egg resemble the adult in shape (P. E. Müller), the larva hatched from the winter egg resemble an advanced *Metanauplius* (Fig. 98), and have therefore another stage to pass through (G. O. Sars, No. 29). The body in this *Metanauplius* is long, without outwardly recognisable segmentation, and ends posteriorly in the two furcal processes. The first antennae (a') are short and club-shaped, the second (a'') long biramose swimming appendages, which however are devoid of the special masticatory hook found in the Branchiopodan *Nauplius.* The mandibles (*md*) consist of the basal blade and a long unjointed oar-shaped palp. The oral aperture is overhung by a large upper lip (*ol*). In the thoracic section of the body the rudiments of six pairs of limbs (p^{I}–p^{VI}) are visible in the form of transverse swellings. In the cephalic region, the Nauplius eye alone is recognisable, the compound eyes developing at a later stage. Further metamorphosis takes place by the development of the limbs and of the body-segments, the growth of the dorsal shield, the diminution of the upper lip, the degeneration of the mandibular palp, and the acquisition of the characteristic curvature of the body. The Nauplius eye persists in the generation coming from the winter egg, whereas it is wanting in individuals developing from summer eggs.

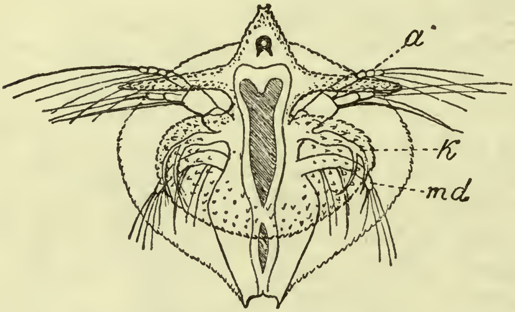

Fig. 97.—*Nauplius* stage of *Limnetis brachyura* (after Grube). *a''*, second antenna; *k*, masticatory process of the same; *md*, mandible.

The genus *Leptodora*, in the metamorphosis of the winter eggs and in the Branchiopoda-like *Metanauplius* stage, as well as in many other respects, has thus retained primitive characters among the Cladocera.

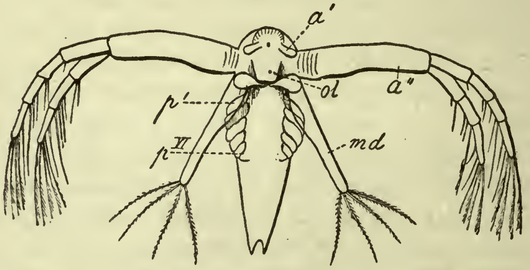

Fig. 98.—*Metanauplius* stage of *Leptodora hyalina* developed from a winter egg (after G. O. Sars). *a'*, first, *a''*, second antenna; *md*, mandible; p^{I}–p^{VI}, rudiments of the first six pairs of thoracic limbs; *ol*, upper lip.

The summer and winter eggs differ not only with regard to the development of the embryo, but in other points as well. It has already been indicated (p. 114) that, in *Bythotrephes* and *Leptodora*, the type of cleavage of the summer egg differs from that of the winter egg. Sars (No. 30) has pointed out in this connection that the embryos that develop (in ephippia) in the winter eggs remain during the whole duration of development enveloped in the egg-integument ("chorion"), while the summer eggs throw off the very thin vitelline membrane before reaching the last stage of development.

The number of pairs of thoracic limbs which we found as rudiments in the *Metanauplius* was six, and this must be considered as the primitive number in the Cladocera. This number is also retained in the *Sididae.* In the embryo of *Lynceus* six pairs appear as rudiments, but the last of these degenerates later (Claus, No. 8).

4. Ostracoda.

The Ostracoda, which are provided with a bivalve shell, often impregnated with calcareous salts, undergo more or less marked metamorphosis. These animals were probably derived from Phyllopodan ancestors by a process of degeneration tending in a definite direction, the number of segments being reduced, and the powers of locomotion diminished. In *Cypridina*, the *Cytheridae*, and the *Halocypridae*, whose development is as yet unknown to us, the metamorphosis appears to be to some extent abbreviated, since the larva when hatched has almost the form of the adult; the *Cypridae*, on the contrary, undergo a metamorphosis, passing through many moults from the *Nauplius* stage to the adult form. This metamorphosis has been observed by Claus (Nos. 32 and 34) in the cases of *Cypris fasciata*, *C. ovum*, and *C. vidua.* Reckoning by the number of consecutive moults, there are here nine different stages, some of which, however, differ only slightly.

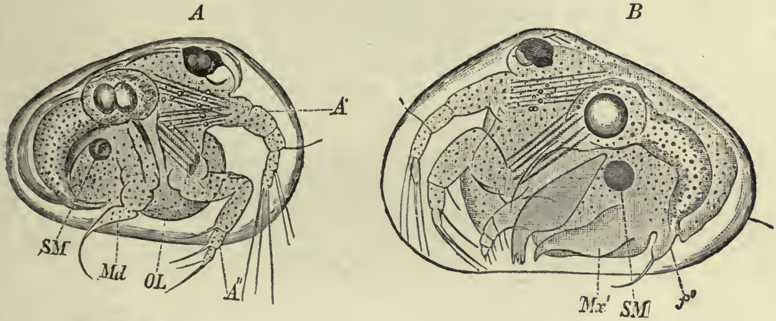

Fig. 99.—Two larval stages of *Cypris* (after Claus, from Balfour's *Text-book*). *A*, *Nauplius* stage. *B*, second larval stage. *A'*, first, *A''*, second antenna; *f''*, first pair of feet; *Md*, mandible; *OL*, upper lip; *Mx'*, first maxilla; *SM*, adductor muscle.

The *Nauplius* (Fig. 99 *A*) resembles the Phyllopodan larva at the same stage in that the three pairs of limbs are used as locomotory organs, and in the possession of a large helmet-shaped upper lip (*OL*), but in having a well-developed bivalve shell provided with an adductor muscle (*SM*), it already shows a typical Ostracodan feature, the development of which has evidently been shifted back secondarily to this early stage. Further metamorphosis takes place, as in the Phyllopoda, by the gradual development in regular order of the posterior pairs of limbs, the growth of the posterior section of the body and of the corresponding internal organs. In accordance with these changes in the body, a change in the shell (observed by Zenker, No. 35) takes place. In the *Nauplius*, the anterior half of the shell is remarkably developed. Its greatest height, as well as its greatest breadth, lies anteriorly to the middle of the body. The anterior section of the shell appears sharply inclined, while the posterior end of the shell runs out more gradually to a point. As the posterior part of the body develops, the posterior halves of the shell also increase in size (Figs. 99–101). An exception to the rule that the limbs appear in order from before backward is found in the second maxillae which are somewhat retarded, not appearing until after the limbs which lie posteriorly to them have developed. There is here a recurrence of a feature found in the Phyllopoda and a few Copepoda (*Cyclopidae*, *Harpactidae*).

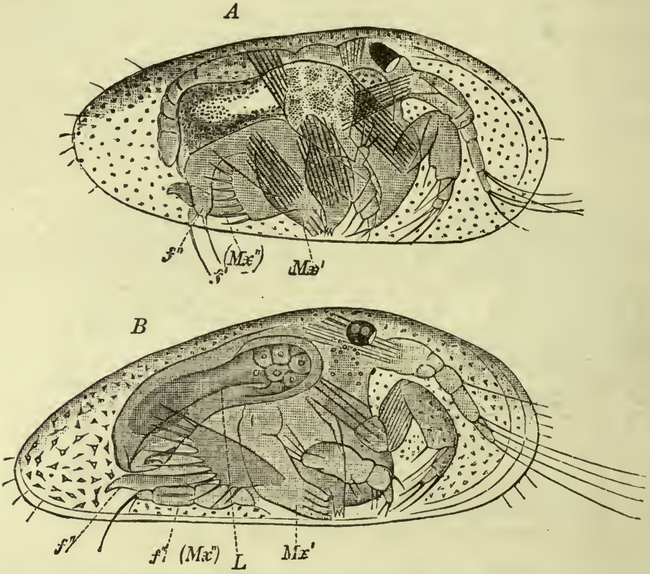

Fig. 100.—Two further stages of development of *Cypris* (after Claus, from Balfour's *Textbook*). *A*, fourth stage. *B*, fifth stage. *Mx'*, first maxilla; *Mx''* and *f'*, second maxilla; *f''*, first pair of feet; *L*, liver.

The *Nauplius stage* (*first free larval stage*, Fig. 99 *A*) is, as already mentioned, distinguished by the presence of a bivalve shell provided with an adductor muscle (*SM*). At its highest point is found the Nauplius eye, which is here very large and provided with paired lenses. The alimentary canal, which consists of oesophagus, mid-gut, and hind-gut, is still without hepatic appendages. The oral aperture is overarched by a large upper lip (*OL*). The three pairs of limbs differ somewhat in shape from those of the Phyllopodan *Nauplius*, being here developed as uniramose crawling limbs. The first two pairs already approach the adult form. The first antenna (*A′*) is bent inwards, and consists of four joints, the three terminal joints being beset on their upper surfaces with rowing setae. The second antenna (*A″*) already shows the characteristic knee-like bend inwards. The mandible (*Md*) has still the form of a three-jointed crawling limb, its tip ending in a large hooked seta. The future masticatory blade is at this stage merely a small serrated process of the basal joint.

In the *second larval stage* (Fig. 99 *B*) which follows, the mandible loses the primitive character just described. Besides this, behind the mandible, two more rudiments have arisen, those of the first maxilla (*Mx*) and of the first pair of feet (*f″*). The body has correspondingly lengthened. The basal joint of the third limb is now transformed into a large triangular masticatory blade (mandible) toothed on its inner edge, the rest of the limb persisting as a four-jointed mandibular palp. Attached to the basal joint of the latter can be recognised the first rudiment of a hand-shaped appendage beset with setae (exopodite). The next rudiment (that of the first maxilla) is a leaf-shaped curved plate (*Mx′*), while the first ambulatory limb (*f″*) is an unjointed climbing organ provided with a terminal hook.

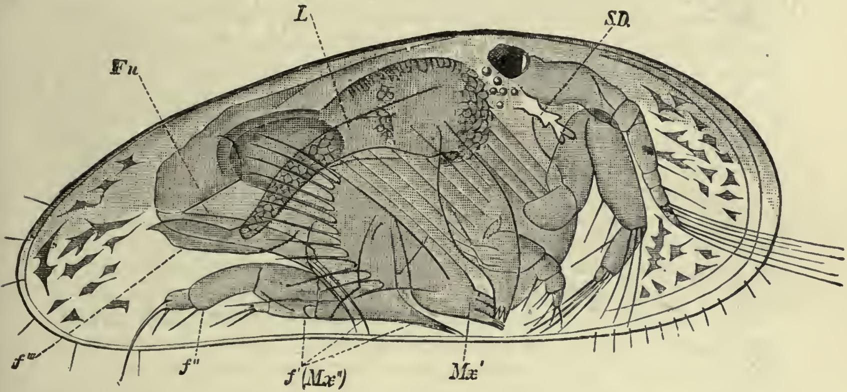

FIG. 101.—Sixth larval stage of *Cypris* (after CLAUS, from BALFOUR's *Text-book*). *Mx′*, first, *Mx″*, and *f′*, second maxilla; *f″*, *f‴*, first and second pairs of feet; *Fu*, caudal fork; *L*, liver; *SD*, shell-gland.

In the *third stage*, the maxilla approaches its adult form, two strong, toothed, masticatory blades and the rudiment of a third being discernible. The rudiment of the movable gill-plate (exopodite) beset with hairs can also now be recognised. In the following *fourth larval stage* (Fig. 100 *A*) there is no essential alteration in the antennae and the mandibular palp beyond a richer provision of setae; on the other hand, on the first maxilla (*Mx′*) four masticatory blades have developed, the upper one (endopodite) already showing the formation of a terminal joint. Behind these limbs a new rudiment (Mx'') can be made out occupying the space between the first maxilla and the first pair of feet; this is the rudiment of the second maxilla which arises as a curved triangular plate after the first pair of feet has already appeared. The second pair of feet is still wanting, but the posterior end of the body is now marked by the development of two furcal setae.

The *fifth larval stage* (Fig. 100 *B*) is distinguished by the further development of the second maxilla (Mx''), which now appears as a four-jointed limb directed backwards and carrying on its basal joint a projecting masticatory blade. It is an interesting fact that these limbs, during the ontogenetic stages of *Cypris*, not only resemble legs, but function as such, a condition which is retained throughout life in the *Cytheridae*. The two furcal appendages at the posterior end of the body are now more distinctly marked. Among the internal organs we must mention the development of the hepatic tubes (*L*), which extend into valves of the shell, and the first appearance of an organ lying below the eye and regarded by CLAUS as the shell-gland (Fig. 101, *SD*).

The *sixth stage* (Fig. 101) is characterised by the appearance of the last (second) pair of feet (f'''). The second maxilla has become transformed by the increase in size of its masticatory blades and the diminution of its leg-like palp. The anterior pair of feet, until now somewhat undeveloped, has several joints. The posterior (last) pair of feet essentially resembles the rudiments of the limbs which precede it as found in earlier stages. The caudal fork already approaches its adult form and terminates in two strong hooked setae.

In the *seventh stage*, which in the structure of the limbs shows the adult condition, the rudiments of the genital apparatus are recognisable. Among the alterations which have taken place in the limbs, the development of a small leaf-like appendage (exopodite) on the basal joint of the second maxilla, and the segmentation of the last pair of feet, deserve special mention.

In the *eighth stage*, the development of the genital rudiment progresses, the way being prepared for the development of sexual differentiation, while the ninth and tenth seem to be stages for the development of sexual maturity.

The *Cytheridae*, according to ZENKER, hatch at a stage more or less comparable with the fourth stage of the *Cypridae*. Besides the two pairs of antennae, the mandibles and the first maxillae have appeared and are somewhat advanced in development. The rudiments of the two pairs of feet seem to be present behind the above. The mandibular palp still functions as a locomotory organ.

In *Cypridina*, whose eggs, like those of the *Cytheridae*, pass through their embryonic development between the valves of the mother, the shell undergoes changes of shape resembling those pointed out in connection with the young form of *Cypris*. The compound paired eyes appear early. Embryos just before hatching possessed the furcal pro-appendages, but were without the three posterior pairs of appendages (the first pair of feet, the cleaning foot, and genital prominence). It is probable that the larva leaves the egg very nearly resembling the adult in shape (CLAUS, No. 33).

In the *Halocypridae* also metamorphosis has almost disappeared, the young when hatched being apparently already provided with all the limbs, and only being distinguished from the adult by the immature condition of the sexual organs, the small number of furcal hooks, and the slight development of the sexual characters (Claus).

5. Cirripedia.

The Cirripedia, which have been modified in a remarkable manner in connection with their attached mode of life, have often been placed in close relationship with the Copepoda, in accordance with the views of Claus (No. 8). We must, however, in consequence of the presence of the so-called *Cypris* stage (with a bivalve shell) which occurs in their metamorphosis and brings about the transition from the free to the attached life, assume for them a similarly-shaped ancestral form, which we must then seek among the Phyllopoda. Since the correspondence in structure and development between the Cirripedia and the Copepoda may also be explained as the result of adaptation in a similar direction (convergence), and as, on the other hand, the shell in the Copepoda has undergone great reduction, these two orders of Crustacea appear to us to be independent derivatives of the primitive Phyllopodan stock.

The metamorphosis of the Cirripedia begins with a true *Nauplius* stage, characterised by the possession of the so-called frontal horns* and of a usually triangular dorsal shield. The series of *Nauplius* stages proceeding one from the other through several moults, ends in a *Metanauplius* in which can be recognised the rudiments of the paired eyes, a fourth pair of limbs, and the subsequent six pairs of thoracic limbs. Another moult and the larva appears in the *free-swimming Cypris stage* which, after attachment, prepares for the transition into the adult. This latter proceeds, after a further moult, from the *attached Cypris stage* (*pupa*).

A. Thoracica.

The series of *Nauplii* belonging to the *Balanidae* (Fig. 102 *A*) are, as a rule, simpler in shape than the much larger spined *Nauplius* of *Lepas*, so that we shall commence with a description of the former. The body shows no trace of external segmentation, and is covered dorsally by a flat, triangular or somewhat oval shell, which, at

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* We must here point out that the possession of frontal horns is not a universal distinctive feature of the Cirripedian *Nauplius*. Such horns are, for instance, wanting in the *Nauplius* of *Laura Gerardiae* (p. 229), and in a Rhizocephalan, found by Sluiter, parasitic on an Ascidian (*Sphaerothylacus polycarpae*). They are also wanting in that remarkable pelagic larva, of whose systematic position we are still doubtful, which was obtained at Mindanao and at first thought by Willemoes-Suhm to be the larva of *Limulus*, but was later considered to be a Cirripede larva (No. 63).

the lateral angles of its frontal margin, is produced out to form the "frontal horns" (*h*). The posterior end of this dorsal shell appears at first to be rounded, but at a later stage may have a pair of spines directed backwards and upwards. Each of the frontal horns contains a style-like process (Claus, No. 8), while in the sheath that covers this are found the openings of two large and several smaller unicellular glands (Fig. 102 *B*, *dr*, Claus, No. 8; Willemoes-Suhm, No. 62). This is probably a protective apparatus and not a sensory organ. The posterior end of the body (thoraco-abdominal section, Fig. 102 *A*, *t*) projects freely out beyond the

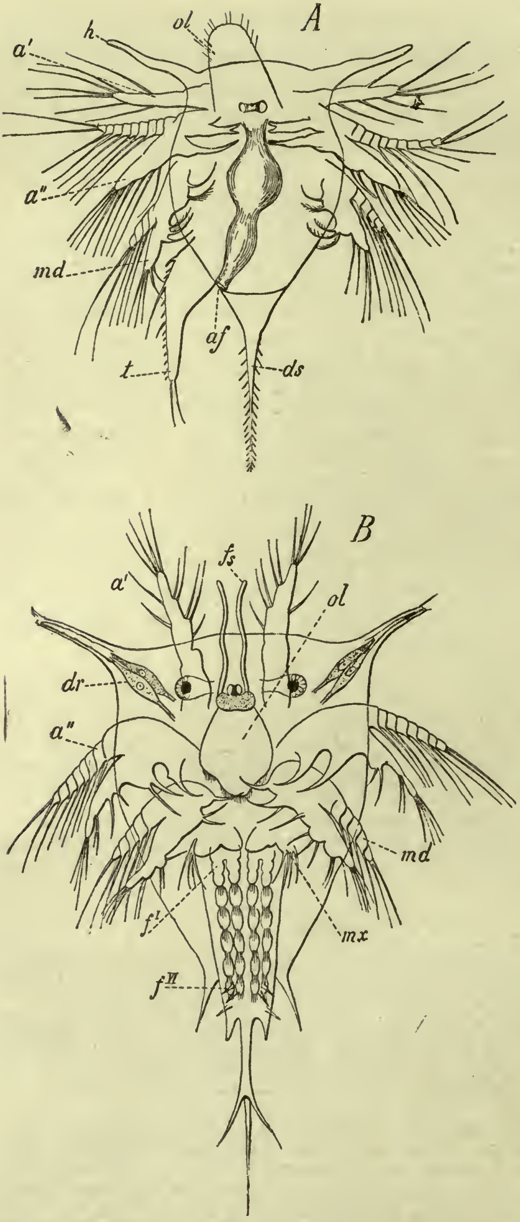

Fig. 102.—Larval stages of *Balanus* (after Claus). *A*, older *Nauplius* stage. *B*, *Metanauplius*. a', first, a'', second antenna; *af*, anus; *dr*, glandular cells of the frontal horns; *ds*, dorsal caudal spine; f^{I}–f^{VI}, first six pairs of thoracic limbs; *fs*, frontal sensory organ; *h*, frontal horns; *md*, mandible; *mx*, rudiment of the maxilla; *ol*, upper lip; *t*, thoraco-abdominal appendage.

dorsal shield and terminates in a caudal fork. The anal aperture (*af*) lies somewhat far forward on the dorsal side of this part of the body. Between it and the posterior edge of the dorsal shield there arises from the dorsal side of the thoraco-abdominal section a large spine running backwards and ending in a sharp point (the so-called caudal spine, *ds*).

In later stages, on the ventral side of thoraco-abdominal region, in front of the caudal fork, are found a pair of thorn-like processes repeating the shape of the larger caudal fork, and in front of these another smaller pair. These thorn-like processes which, in some forms, are still more developed, may produce the appearance of segmentation on the thoraco-abdominal section, but cannot be regarded as indicative of a true segmentation of that region of the body.

In the anterior region of the body, the unpaired Nauplius eye which is closely applied to the brain is always distinctly perceptible. The oral aperture is overhung by a large helmet-shaped upper lip (*ol*), which, by its form, recalls the upper lip of the Phyllopodan larva. The limbs show the structure typical of the *Nauplius* stage, and, in the first stages, often appear only indistinctly jointed, while in the later stages the joints are more numerous and more distinct. The most anterior limb (a', first antenna) is invariably uniramose, and its distal portion is beset with swimming setae. The second and third limbs (a'', *md*) are biramose. The longer exopodite consists of a large number of closely crowded joints beset with swimming setae; the shorter endopodite has fewer joints. The protopodite in both these limbs carries several masticatory hooks directed towards the oral aperture.

The later stages are characterised by the gradual increase in size of the body, by the appearance of the above-mentioned spinous processes on the dorsal shield and in the thoraco-abdominal region, and above all by the presence of a paired frontal sensory organ (*fs*), which here develops in the form of two filamentous processes inserted near the Nauplius eye. Among the internal organs, besides those already mentioned (eyes, brain, glandular tubes of the frontal horns), we should note the muscles for moving the limbs, the thoraco-abdominal appendages, and the alimentary canal. The latter consists of a short oesophagus, a wider mid-gut, and a hind-gut opening through the dorsal anal aperture. As to the presence of the antennal gland (in the basal joint of the second pair of limbs) which occurs in the Entomostracan *Nauplii*, nothing is as yet known.

The *Nauplii* of the *Lepadidae*, when hatched, seem closely to resemble the *Nauplii* of the *Balanidae* in shape, differing only in this one respect, that the long frontal horns are bent backwards. Soon after hatching they undergo a first moult, after which the spine-like thoraco-abdominal appendage (ventral spine) and the dorsal caudal spine first attain their full length. During later moults, the *Nauplius* grows to a great size (12 mm. long), and is then distinguished by a number of accessory structures. In *Lepas fascicularis*, seven moults take place before the *Metanauplius* stage is reached. These later stages (Fig. 103) show the thoraco-abdominal appendage (*t*), and the dorsal caudal spine (*ds*) drawn out as long, pointed processes beset with small hooks. A similar process (*d*) has arisen at the central point of the dorsal shell; this process, which runs obliquely backwards, is known as the dorsal spine. At the margin of the dorsal shield also, besides the frontal horns, eight large spine-like processes can be recognised, the first pair lying anteriorly between the frontal horns, and the others being distributed laterally and posteriorly. Both the dorsal shield and the larger processes are further beset with a series of minute spines, which are wanting only on the frontal horns. Many of these minute spines, as well as the marginal spines of the dorsal shield, are found to be perforated and connected with the ducts of unicellular integumental glands. On the ventral side of the thoraco-abdominal appendage, two more posteriorly-placed, immovable thorns can be distinguished, and, anteriorly, six pairs of larger movable spines (*x*), which do not appear simultaneously but successively, each new moult developing a fresh pair, until, after the last moult, the full number of six is attained. The conjecture, made with some hesitation by

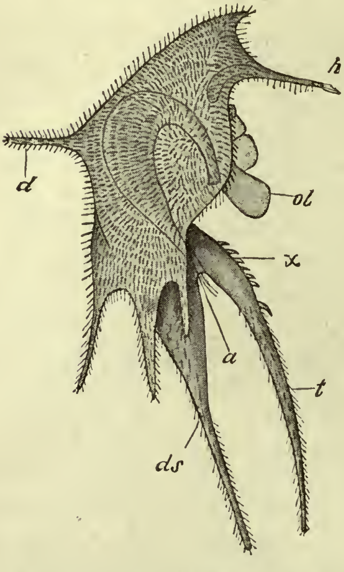

FIG. 103.—Larva of *Lepas australis* (*Archizoaea gigas*) (after DOHRN). *a*, anal aperture; *d*, dorsal spine; *ds*, dorsal caudal spine; *h*, frontal horns; *ol*, upper lip; *t*, thoraco-abdominal appendage (ventral spine); *x*, paired movable spines.

Dohrn (No. 42) and Willemoes-Suhm (No. 62), that these pairs of spines correspond to the rudiments of the six pairs of thoracic limbs in the *Cypris*-like larva appears to us somewhat plausible. This last stage would then have to be assumed to be the *Metanauplius* stage.

For more recent observations on the larvae of the *Lepadidae* we are above all indebted to Willemoes-Suhm (No. 62). Dohrn (No. 42) has minutely described a large *Nauplius* larva—probably to be referred to *Lepas australis* under the name of *Archizoaea gigas.* These stages have, however, absolutely nothing to do with the *Zoaea* larva of the Malacostraca. The development of long spine-like processes is a protective adaptation often occurring in pelagic animals (*cf.* the skeletons of the Radiolaria and the spines of the *Pluteus* larvae).

In the whole series of *Nauplius* stages, except the last, there is no essential alteration apart from the increase in size of the body and the above-mentioned development of thorn- and spine-like processes. In the last stage which immediately precedes the *Cypris* stage (*Metanauplius*, Fig. 102 *B*), important new rudiments of organs appear. With respect to the general form of the body, it should be emphasised that the lateral parts of the dorsal shield now already begin to bend downwards, and, covering the body laterally, foreshadow in position the valves of the shell in the *Cypris* stage. The three anterior pairs of limbs still bear a general resemblance to the typical Nauplius limbs, but already, within the first pair (first antennae), the rudiment of the sucking disc so important in the *Cypris* stage can be made out (Krohn, No. 50; Willemoes-Suhm, No. 62; Claus, No. 8). This fact affords a direct proof that the adhesive antennae of the later stages are actually derived from the most anterior pair of Nauplius limbs (Krohn, No. 50; Fr. Müller). Behind the mandible is to be seen the slightly developed rudiment of the fourth pair of limbs; it is, however, probable, as we shall see further later, that we have here the rudiments of two consecutive pairs of limbs (*mx*) (Metschnikoff, No. 53; Claus, No. 8). The thoraco-abdominal region of the larva has increased considerably in size; in it, beneath the Nauplius cuticle, can be recognised the rudiments of the six pairs of swimming limbs (f^{I}–f^{VI}) of the larva (thoracic limbs), as well as the caudal processes of the short abdomen (furcal processes) (Krohn, No. 50; Claus, No. 8). Another important point is that in this stage, near the Nauplius eye, the paired, movable compound eyes (Fig. 102 *B*) already appear as rudiments. In this *Metanauplius* stage, therefore, all the more important organs and limbs of the *Cypris*-like larva are formed, and the larva itself, by the casting of the Metanauplius integument, emerges from the preceding stage.

The *free-swimming Cypris stage* (Fig. 104), which is only of short duration, derives its name from the bivalve shell that envelops the whole body. The actual segmentation of the body and the inner organisation have nothing in common with the Ostracoda. In respect to these the larva at the *Cypris* stage already very nearly approaches the adult. The two shell-valves which can be brought together by an adductor muscle, are directly continuous dorsally. The dorsal border appears arched, whereas the ventral edge is flattened. Anteriorly they are rounded, but run out to a point posteriorly. In the anterior section of the valves, near the ventral side, a small projection may be remarked on which can be recognised the frontal horn of the *Nauplius*. The ventral margins of the shell are closely approximated in the middle of their length. Posteriorly, a fissure opens between them for the passage of the swimming limbs of the larva (*rf*), and there is also an anterior aperture through which the first antennae, the adhesive organs (*l*), are protruded. The latter limbs, in the free *Cypris* stage, are used for the occasional attachment of the larva, which precedes and prepares the way for the final attachment. They consist at this stage of four joints, the basal joint joining the body by a broad base, and carrying various chitinous ingrowths (apodemes) for the attachment of muscles. The second joint, which is lengthened like an arm, is bent at an angle to the basal joint. The short third joint carries at its outer side the adhesive disc, at the centre of which the duct of the cement-gland opens, while the truncated fourth joint seems to be provided with one ordinary and one large olfactory seta (CLAUS, No. 39; WILLEMOES-SUHM, No. 62).

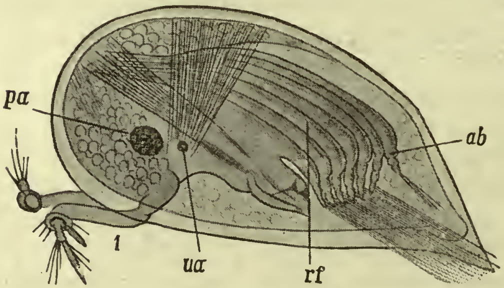

FIG. 104.—*Cypris*-like stage of *Lepas fascicularis* (after CLAUS, from LANG'S *Text-book*). *ua*, Nauplius eye; *pa*, paired eye; *rf*, thoracic (swimming) limbs; *ab*, abdomen; *l*, first antenna.

The cement-gland (Fig. 105, *cd*) shows various degrees of development in the *Cypris* larva. In the pupal stage which follows, it shifts to the base of the eye-stalk formed from part of the head of the larva, and here takes the form either of a closely-packed coiled gland (*Lepas pectinata*), or else of widely scattered cells connected only by the efferent duct. On account of its structure, the cement-gland must be regarded as an accumulation of unicellular glands on a much-branched common duct, the single glandular cells being sessile on this duct, like grapes.

We are still very much in the dark as to the genesis of this gland and its morphological derivation. Attempts have been made to derive it from one of the two typical pairs of Crustacean glands (antennal and shell-glands), although such a homology is attended by considerable difficulty on account of the aperture of the gland occurring on another limb. CLAUS (No. 8) finds, within the shell-fold of the free-swimming *Cypris* stage of *Lepas australis*, a coiled gland-like cell strand, and is disposed to homologise this with the shell-gland of other Entomostraca, while he conjectures that the cement-gland which is recognisable in later stages is derived from this cell-strand. WILLEMOES-SUHM, on the contrary (No. 62), found, even in the *Nauplius* stage, a paired glandular mass lying at the sides of the upper lip, out of which, according to him, the cement-gland develops. While authorities thus hold conflicting views, we shall do well for the present to regard the cement-gland as a peculiar structure found in the Cirripedia, and to abstain from attempting to homologise it with the glands of other Crustacea.

A great change occurs in the structure of the limbs which surround the oral aperture of the *Nauplius*. The second antennae seem altogether to disappear (if they are not to a certain extent, as PAGENSTECHER (No. 58) conjectured, retained in the palp-like appendages of the upper lip). The actual mouth-parts, together with the upper lip, are already shifted on to a slightly projecting oral cone, and appear in the form of three pairs of truncated rudiments, in which we recognise the future mandibles, the first maxillae, and the lower lip which results from the fusion of the second maxillae. In what way these mouth-parts are derived from the limbs of the *Metanauplius* stage is still far from clear. The most probable view appears to us to be that of CLAUS (No. 8), according to which the mandibles are derived from the basal joints of the third pair of Nauplius limbs, while the outer segment of the rudimentary limbs following these in the *Metanauplius* (Fig. 102 *B*, *mx*) yield the first maxillae. The under lip, on the contrary, is said to rise from a rudiment on the inner side of this limb. We should thus have to assume that, in this imperfectly developed limb, we have the rudiments of the first and second pairs of maxillae crowded together. METSCHNIKOFF (No. 53) also derives two pairs of limbs from this rudiment, but identifies them with the mandible and maxilla of the adult Cirripede, the third Nauplius limb as well as the second being supposed to vanish completely. In the more posterior section of the body, we find six pairs of swimming limbs (*rf*), which, in their structure, strikingly recall the thoracic limbs of the Copepoda, and are also similarly used as swimming feet. Each of these consists of a two-jointed basal segment provided with an exopodite and endopodite, each of these, again, being composed of two joints and clothed with long swimming setae. Posteriorly, the body terminates in a short abdomen (*ab*) composed of four segments, the last of which ends in two furcal appendages bearing long setae.

With regard to the internal organs, it should be mentioned that, at this stage, sac-like outgrowths of that enlargement of the intestinal canal which is called the stomach begin to appear: these develop into the so-called liver; further, that the rudiment of the ovaries is to be seen in the shape of paired tubes situated ventrally in the cephalic region.

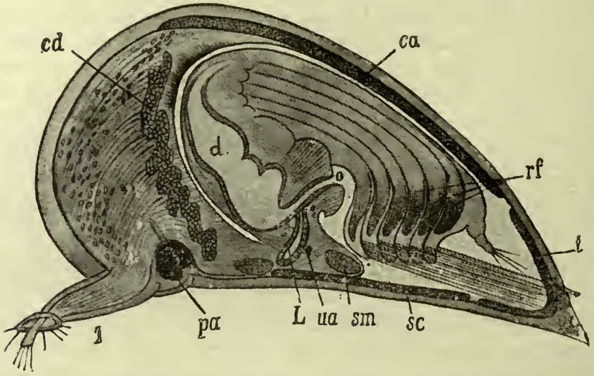

Fig. 105.—Pupa of *Lepas pectinata* (after Claus, from Lang's *Text-book*). *ua*, Nauplius eye; *pa*, paired eye; *rf*, thoracic limbs (with the tendril-like—cirriform—feet beginning to form inside); *o*, mouth; *d*, intestine; *L*, liver; *sm*, adductor muscle; *sc*, scutum; *t*, tergum; *ca*, carina; *cd*, cement-gland; *l*, first antenna with the sucking disc.

The free-swimming *Cypris*-like larva, after becoming finally attached, gives rise to the *fixed Cypris-like larva* (Fig. 105) of the Cirripedia. As, at this stage, the larva ceases to feed and loses all power of locomotion, while important external and internal changes are going on in the body beneath the cuticle of the *Cypris* stage (as if beneath a pupal integument), this stage has been well called the pupal stage (*Cypris*-like pupa). From this, by the casting of the cuticle of the *Cypris*-like stage, proceeds the young Cirripede. For details as to the processes through which these transformations are brought about, we are indebted chiefly to the observations of Darwin (No. 40), Pagenstecher (No. 58), and Claus (Nos. 39 and 8).

The larva attaches itself firmly with the sucking discs found on the first antennae and by means of a sticky fluid secreted by the cement-gland. At first the whole of the ventral surface is in contact with and parallel to the surface of attachment (Fig. 106 *A* and *B*). The changes which first attract attention are certain processes of growth by means of which different parts of the body approach the final shape. For example, the mouth-parts at the top of the buccal cone, which until now were very rudimentary, become distinctly developed; in the *Lepadidae* the principal feature in this process is the great increase in size of the upper lip. The thoracic limbs also elongate and become (Fig. 106 *B*) the rudiments of the tendril-like feet (*rf*). All these parts develop under the somewhat loose Cypris cuticle. The long tendril-like feet naturally have not the room necessary for development in the short envelope of the thoracic limbs of the *Cypris* stage, and therefore become much curved, and even press back into the thorax (Fig. 105). The abdomen degenerates almost completely, while from its base (genital segment) the unpaired penis projects as an outgrowth.

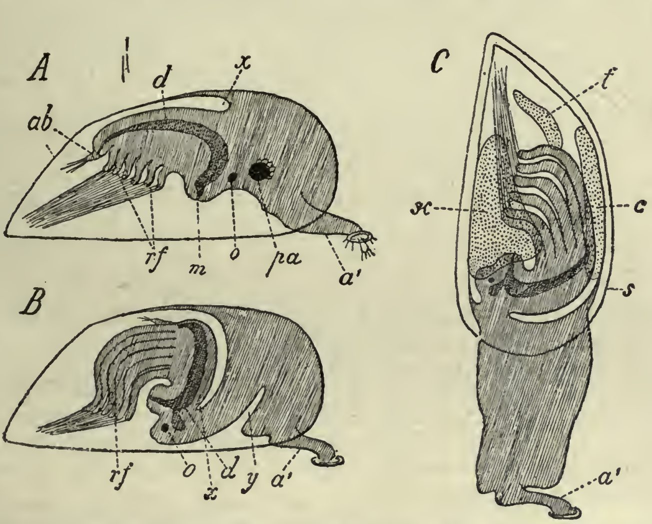

Fig. 106.—Diagrammatic illustration of the metamorphoses of *Lepas*. *A*, *Cypris*-like stage. *B*, attached pupa. *C*, young *Lepas* stage, still surrounded by the loosened Cypris shell (*s*). *a′*, first antenna; *ab*, abdomen; *c*, carina; *d*, intestine; *m*, mouth; *o*, unpaired eye; *pa*, paired eye; *rf*, thoracic limbs; *s*, Cypris shell; *sc*, scutum; *t*, tergum; *x*, reflection of the dorsal integument; *y*, ventral fold.

While these processes of growth are taking place, the whole thorax undergoes a significant change of position (Fig. 106 *A* and *B*). Whereas, in the earlier stages, the thorax lay almost parallel to the ventral surface, it now rises into a more perpendicular position with regard to that surface, so that the anal aperture no longer lies behind the oral aperture, but above it. Simultaneously with this change of position, a sharper distinction arises between the thorax and the cephalic region, the point (x) at which the wall of the thorax unites with the surface of the mantle shifting ventrally (*cf.* the position of x in Fig. 106 *A*, with its position in Fig. 106 *B*).

Meanwhile many changes take place in the anterior cephalic region of the pupa, these being preparatory to its transformation into the stalk of the adult form. The broad basal joint of the adhering antenna first completely fuses with the head and is taken up into the latter, so that the adhesive antennae of the adult Cirripede each consist of only three joints. Further, somewhat behind this point, a deep infolding of the surface of the body occurs (Fig. 106 *B*, y), so that that portion of the head which forms the stalk is at this stage sharply bent on itself.

This fold arises by the withdrawal of the stalk-integument from the cuticle of the *Cypris* larva. Some of the important organs of the larva, however, which are not to be taken over into the adult, remain attached to that cuticle. The chief of these are the paired eyes (the Nauplius eye, however, passes over into the adult Cirripede and is retained throughout life), and the chitinous processes called by Darwin the apodemes, which served for the attachment of the antennal muscles and are cast off in the moult which follows. These details are not represented in the figure.

The most important change which now follows is in the position of the larva and the lengthening of the stalk which is connected with it. By an opening out of the fold above mentioned, the larva now rises from the surface of attachment, its ventral surface standing at right angles to the latter. At the same time the stalk passes out from between the shell-valves of the *Cypris* stage (Fig. 106 *C*), and lengthens to form the adult peduncle.

Darwin (No. 40) pointed out the fact that the part by means of which the attachment of the larva at first takes place does not correspond to the frontal extremity of the body, but to the most anterior portion of the ventral surface. Only after the upright position has been assumed does the frontal extremity come into contact with the surface of attachment, to which it is glued by a secretion. In *Crytophialus*, on the contrary, and also in *Alcippe*, *Lithotrya*, and *Anelasma*, this part is not firmly attached, but grows out further. This further growth can only take place when the substratum can give way correspondingly.

In *Anelasma*, the substratum is affected by simple pressure, but in the other forms just mentioned by a boring action of the stalk.

The passage of the stalk out of the Cypris shell is rendered possible by the fact that the latter at this stage surrounds the body very loosely. Whereas, in the *Cypris* stage, the whole of the cephalic region is contained within the bivalve shell, in the adult, the anterior part of that section (the stalk) is not covered by the shell, here, as in the Cladocera, only that part of the head which carries the mouth-parts being included within the shell. We may imagine this change to have arisen at the time when the stalk grew out by a secondary flattening out of that anterior part of the mantle-fold which, in the Cirripede pupa, covered the most anterior part of the head.

The adult Cirripede shell now appears more distinctly beneath the Cypris shell, and in it can be made out the first rudiments (primary valves, DARWIN) of the five calcareous plates (scuta, terga, and carina, Fig. 106 *C*, *sc*, *t*, *c*). These primary valves are distinguished by their sieve-like sculpturing, which is caused by the boundaries of the matrix-cells remaining evident in the calcareous secretion. The surfaces of the valves are covered by a thin cuticle. The primary valves do not directly increase in size, but new calcareous layers are continually being secreted below them, and these attain a size greater than that of the original valves. In a superficial view of the primary valves, they are now seen to be surrounded by concentric lines representing the subjacent calcareous layers. By this method of increase of the valves, the non-calcareous parts of the shell which spread out between the valves become more and more circumscribed, but in some cases these intermediate spaces are retained to a considerable extent (*Conchoderma*). It should be mentioned that in those forms which have a large number of valves, only the five primary valves are at first formed.

The metamorphosis of the *Balanidae*, in the first stages, resembles that of the *Lepadidae*. Here also the *Cypris* pupa gives rise to a young form attached by a short fleshy stalk. Only later does the broad base characteristic of the *Balanidae* develop and form that external secondary mantle-fold, within which the upper part of the mantle which carries the scuta and terga appears like an operculum. The first rudiments of the shell are here membranous, and the sculpturing mentioned above, which is characteristic of the *Lepadidae*, is wanting.

While the external form of the adult is reached in this manner, the inner organs are also undergoing important changes, some of which are as yet little understood. Some organs are cast off at ecdysis (paired eyes, antennal apodemes), others simply degenerate (antennal muscles). Meantime the hepatic outgrowths appear in the intestinal canal. The cement-gland increases considerably in size, and the genital organs show special development. The ovaries undergo their characteristic displacement, shifting to a position within the stalk.

The moult which follows, and in which the cuticle of the *Cypris* stage is cast, closes this period of development. In the moult, the outer cuticle of the two shell-valves is cast first, the thorax and the inner mantle-cavity losing their cuticle later.

In most of the Thoracica, metamorphosis seems to run the course above described. Only in individual cases is it more abbreviated. Thus, according to Koren and Danielssen (No. 48), the larvae of *Anelasma squalicola* pass through the greater part of their metamorphosis within the mantle-cavity. Kossmann, however, describes the *Nauplii* of these forms whose larvae, according to the above authors, when hatched, are provided with six pairs of limbs. Pagenstecher has rightly connected this feature with the attachment of *Anelasma* to sharks. Still more abbreviated is the metamorphosis of *Scalpellum Strömii*, the *Cypris* stage of which, surrounded by the Nauplius cuticle, was found by Hoek (No. 45) even within the egg-envelope.

B. Abdominalia.

The metamorphosis of *Alcippe*, a form which bores into the columella of the shells of *Fusus* and *Buccinum* (especially when these are inhabited by Pagurids) seems to agree in essentials with that of the Thoracica. The *Nauplii* were first described by Hancock. The *Cypris* stage described by Darwin (No. 40) is distinguished by the possession of six pairs of thoracic limbs, a fact worth mentioning in contrast to the reduced number and shape of these limbs in the adult; only four pairs of these are retained, the first as a palp, the second biramose, and the third uniramose.

In *Kochlorine*, which bores into the shell of *Haliotis*, Noll (No. 56) found two kinds of larval forms, a small form provided with adhering antennae, but without a mantle, and a larger form having a bivalve shell and resembling the *Cypris* stage. It is probable that the metamorphosis here is closely related to that of the nearly allied genus *Cryptophialus*.

The metamorphosis of *Cryptophialus*, first described by Darwin (No. 40), is greatly abbreviated. The egg here passes almost direct into the *Cypris*-like larval form. There first arises from the oval egg a larva in which two processes can be recognised as the rudiments of the adhering antennae. A third process indicates the posterior end of the body. At a later stage, the adhering antennae are approximated, while the body assumes generally a more pointed egg-like shape. From this stage the *Cypris* form emerges, in which can be distinguished the mantle-fold, the paired eyes, and the well-developed adhering antennae. The rudiments of the thoracic limbs are here wanting, but three pairs of setae are found on the abdomen. These larvae creep about by means of the adhering antennae in the mantle-cavity of the mother, and finally change into the adult form. For the development of the stalk in these forms, see p. 218.

C. Rhizocephala.

The free-swimming stages of the Rhizocephala (*Nauplius* or *Cypris* stage) were early observed by Fr. Müller (Nos. 54 and 55), Kossmann (No. 49), and others. The later transformations, on the contrary, which bring about the transition from the *Cypris* stage to the parasitic form, were first observed by Delage (No. 41) in the case of *Sacculina carcini.* We shall, therefore, in our description, follow the statements of Delage.

The *Nauplius* of *Sacculina carcini* leaves the egg with a more or less compact form, but by a moult which follows soon after hatching attains a greater length (Fig. 107 *A*). Otherwise it shows the normal Cirripede type. The two frontal horns with their glands (*gl*) are well developed, as also are the filamentous frontal organ (*fs*) and the Nauplius eye (*ua*), lying close to the brain. As a remains of the labrum a projection is found which is known as the *rostrum*; on the other hand, the oral aperture, the intestinal canal, and the anal aperture are wanting. The intestinal canal is here replaced by a large accumulation of food-yolk. The Nauplius limbs (*1*, *2*, *3*) are developed in the typical manner, but the protopodites of the two posterior pairs are without the masticatory hooks usually found on them. A median mass of cells lying within the body between the brain and the rostrum is assumed by Delage to be the ovary (*ov*).

Fritz Müller asserted the presence of a broad, oval, dorsal shield in the *Nauplius* of *Sacculina.* Kossmann, however, has pointed out that Müller's figures are of larvae about to undergo ecdysis, in which the Nauplius cuticle is no longer in contact with the body.

The most important change found after a third moult is the further growth of the thoraco-abdominal region of the *Nauplius*, in which the six thoracic segments, with the rudiments of their limbs, soon appear distinct from the abdomen. At the same time the most anterior limbs begin to assume the character of the adhering antennae (*Metanauplius* stage).

By the fourth moult the *free Cypris* stage (Fig. 107 *B*) is reached. In this moult the biramose limbs of the Nauplius stage are entirely cast off, and not only do the chitinous envelopes of these limbs adhere to the cast skin, but it appears that even some of the soft parts are thrown off in the moult. The *Cypris* stage in which, as in the former stages, there is no trace of an alimentary canal, closely resembles in form the similarly-named stage in the Thoracica. The bivalve shell has almost the same shape; the segmentation of the thorax, the form of the swimming limbs (*I–VI*) are in agreement.

The abdomen (*ab*) is very rudimentary, consisting of a single joint bearing two furcal appendages. The first antenna (*1*) is without sucking disc and cement-gland. It consists of three joints: a basal joint which is broadened and connected with the chitinous apodemes, a long middle joint, and a short, terminal joint provided with three hooked setae. The Nauplius eye (*ua*) persists, but the paired eyes are absent. Among the internal organs present at this stage, we note the very distinct ovarian cell-mass (*ov*), the strongly-developed musculature, the persistence of the glands of the frontal horns (*gl*), and the accumulations of pigment and of food-yolk (*f*).

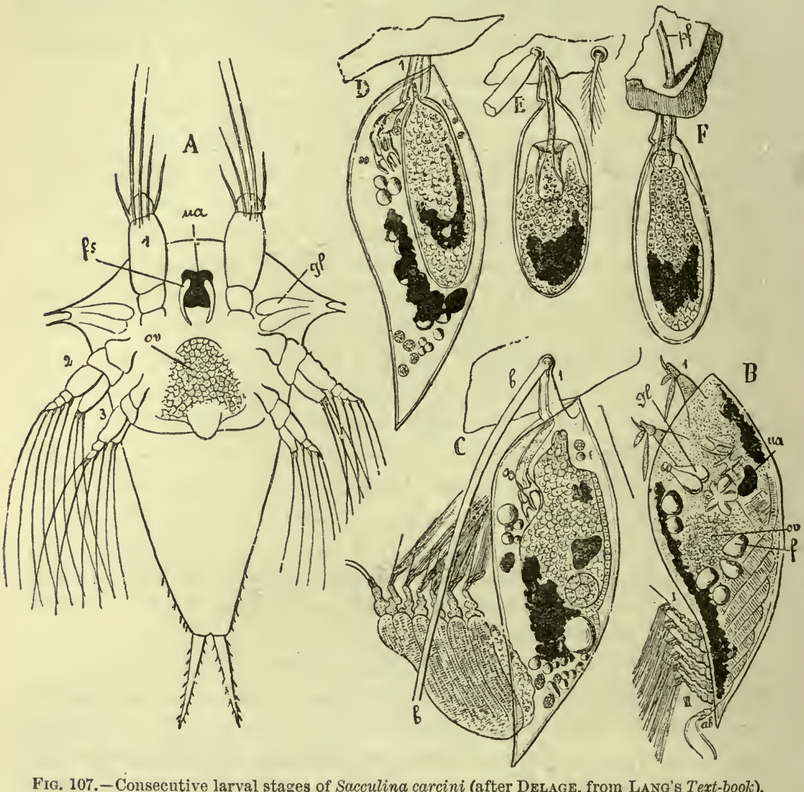

FIG. 107.—Consecutive larval stages of *Sacculina carcini* (after DELAGE, from LANG'S *Text-book*). *A*, *Nauplius* after the first moult. *B*, free-swimming *Cypris* stage. *C*, *Cypris* stage after the larva has become attached to a seta (*bb*) of the host. *D*, formation of the *Kentrogon* larva. *E*, the *Kentrogon* larva after the Cypris shell has been thrown off and the arrow has formed. *F*, the arrow has bored through the chitinous cuticle of the host. *1*, *2*, *3*, the three pairs of Nauplius limbs; *I-VI*, thoracic limbs; *ab*, abdomen; *bb*, seta of the host; *f*, fat globules; *fs*, frontal sensory organ; *gl*, glands of the frontal horns; *ov*, rudiment of the ovary; *pf*, arrow; *ua*, Nauplius eye.

The next stage which we may compare with the pupa of the Thoracica is called by Delage the *Kentrogon* stage. In this stage the attachment of the larva to the body of the host (*Carcinus maenas*), and its passage into the body-cavity of the latter are accomplished. After the free *Cypris*-like larva has swum about for three or four days, it seeks out a host, a young shore-crab (from 3 to 12 mm. broad), and attaches itself to one of the integumental setae (*bb*), one of the adhering antennae (*1*) of the *Cypris* larva surrounding such a seta near its point of insertion (Fig. 107 *C*). The point at which the larva attaches itself is not, as we should expect, *a priori*, on the ventral surface of the abdomen (of the host), but seems to be indiscriminately chosen. Fixation often takes place on the back of the host, or on one of the legs. The next change to take place may be described as a moult in which many important parts of the body are cast off (amputated). First the soft contents of the adhering antennae are drawn in, the apodemes (chitinous tendons of the antennal muscles) being at the same time expelled from within the body. These latter remain attached for a long time to the envelopes of the adhering antennae, which are also retained for some time (Fig. 107 *D*), as they are of importance in bringing about the attachment of the larva to the host. While the soft parts are everywhere withdrawn from the chitinous envelope, the thorax is protruded far beyond the shell-valves and *amputated in toto* (Fig. 107 *C*). This can only be accomplished by a somewhat extensive rupture of the body-wall, and, through this, remnants of internal organs are thrust out into the larval shell and lost. Thus a great part of the pigment found in the larva, as well as remains of food-yolk, are thrown out, the frontal glands and the whole body musculature undergoes degeneration, and the masses of detritus thus produced, together with the Nauplius eye, are now eliminated. The remainder of the body left after the separation of all these organs draws together to form a solid oval sac (Fig. 107 *D*), which soon becomes surrounded with a chitinous envelope. This latter is closely contiguous to the sac; only at its most anterior end, that turned towards the adhering antennae, it can be noticed that the soft body seems to lie naked against the inner sides of those organs. The newly-formed envelope is in this region probably exceedingly delicate, and very closely apposed to the inner surface of the antennae. The layers into which the contents of the sac break up are at this stage not at all clear. A superficial ectodermal cell-layer can, however, be distinguished from the inner mass which, in all probability, is mesodermal, and the chief constituent of which is the cell-mass of the ovary. Besides remains of pigment and food-yolk, other mesodermal elements no doubt enter into the formation of this second layer, from which are to be derived the rudiments of the testes as well as the musculature and other organs of the adult *Sacculina*. It is important to bear in mind that the encysted sac thus produced has been derived, after the expulsion of the whole thorax, exclusively from the cephalic section of the *Cypris* larva.

The soft body of the sac-like larva now begins to develop a small fine point at its anterior end (Fig. 107 *D*), which protrudes into the inner cavity of the antenna used for attachment, and this is followed by the secreting of a new chitinous envelope at the surface of the soft body (second moult of the *Kentrogon* stage, Fig. 107 *E*). As the new cuticular layer thickens considerably over this anterior point, it forms the arrow-like tube which characterises the *Kentrogon* stage. This tube, increasing in length and becoming somewhat bent, invaginates the anterior surface of the sac (Fig. 107 *E*). At this stage the cast off Cypris shell is either only very loosely attached to the sac, or is even completely severed from it.

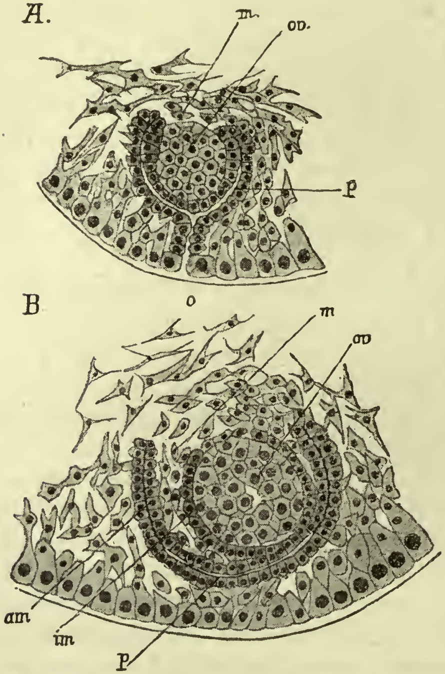

Fig. 108.—Two sections through the nucleus of a *Sacculina interna* (after Delage). *A*, younger stage. *B*, older stage. *am*, outer mantle-layer; *im*, inner mantle-layer; *m*, mesoderm-cells; *o*, aperture of the perivisceral cavity; *ov*, rudiment of the ovary; *p*, perivisceral cavity.

The protrusion of the arrow now takes place (Fig. 107 *F*, *pf*), the invagination just described being re-evaginated. The arrow first enters the inner cavity of the adhering antenna, and thence, conducted by the latter, passes into the soft articular membrane of the seta to which the *Cypris*-like larva attached itself. Through this membrane the arrow bores, thus establishing a communication between the inner cavity of the sac and the body-cavity of the host. During these processes the soft inner body becomes surrounded with another very delicate cuticle (third moult of the *Kentrogon* stage).

There is at this point a gap in our knowledge of the development of *Sacculina*. There can, however, be no doubt that the soft body of the larva passes through the canal of the arrow, so as, in this way, to reach the body-cavity of the host. The *Sacculina* thus becomes an endoparasite (*Sacculina interna*).

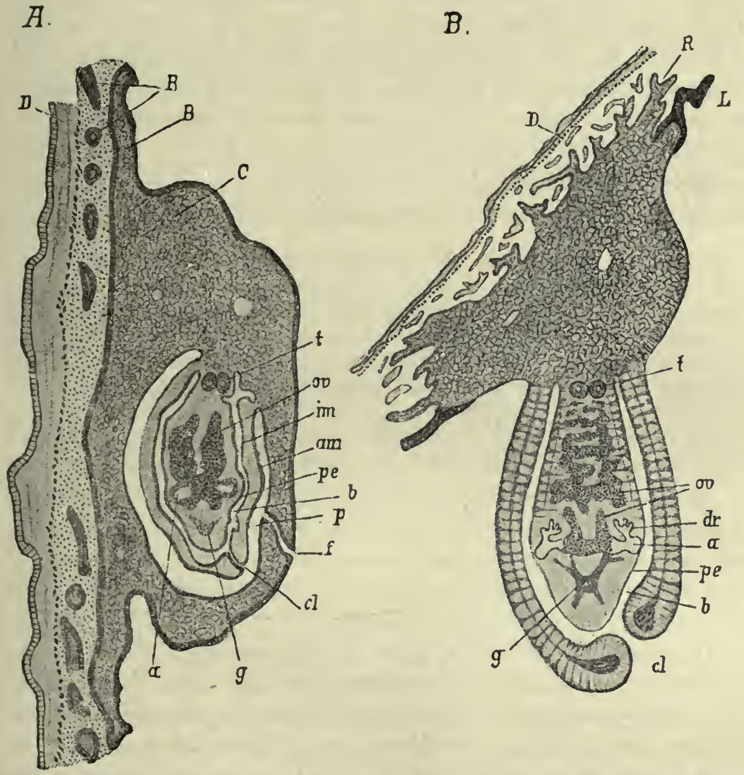

Fig. 109.—Longitudinal sections through two stages of development of *Sacculina carcini* (after Delage). *A*, *Sacculina interna*. *B*, *Sacculina externa*. *a*, atrium (widening of the oviduct); *am*, outer mantle-layer; *b*, brood-cavity (mantle-cavity); *B*, basal membrane; *C*, central tumour; *cl*, cloacal opening; *D*, intestinal wall of the host; *dr*, glands of the ovarian sac; *f*, aperture of the perivisceral cavity; *g*, ganglion; *im*, inner mantle-layer; *L*, body-wall of the host; *ov*, ovary; *p*, perivisceral cavity; *pe*, perivisceral ectodermal layer; *R*, root-processes (some in cross section); *t*, rudiment of testes.

Sacculina interna. The endoparasitic larva now wanders from the point at which the attachment of the *Cypris* larva occurred, further into the host, until it reaches the ventral side of the intestinal canal where its final fixation takes place. At the same time it sends out an exceedingly wide-spread network of rootlets which penetrate throughout the whole body of the host, covering superficially all the organs and only leaving the heart and the gills unaffected. At the point where the actual *Sacculina* lies, all the rootlets gather together to form a plate (*basal membrane*, Fig. 109, *B*), in the middle of which can be seen a swelling (*central tumour*, Fig. 109, *C*). The body rudiment of the Sacculina lies sunk in this central tumour as its so-called *nucleus*. The rootlets, the basal membrane, and the central tumour show essentially the same histological structure. They consist of a superficial epithelium (ectoderm) and an inner cavernous tissue composed of star-like anastomosing cells of connective tissue.

The *nucleus* (Fig. 108) is completely sunk in the central tumour, and therefore lies in a cavity which is called by DELAGE the *perivisceral cavity* (*p*), and which opens externally through one small aperture. Even this aperture closes (Fig. 108, *B*), to re-appear later in the form of a transverse fissure (Fig. 109, *f*, *fente de sortie*). The point at which the nucleus is in contact with the wall of the perivisceral cavity is now known as the stalk (peduncle) of the nucleus.

In the nucleus itself, a superficial ectodermal layer can be distinguished (Fig. 108 *A*) which, near the stalk, passes into the wall of the perivisceral cavity. The inner mass of the nucleus at this stage consists almost exclusively of the rudiment of the ovary (*ov*); but in the stalk there are some mesoderm-cells which are of importance in connection with the development of the testes, the musculature, the connective tissue, &c.

Delamination next takes place in the ectodermal layer of the nucleus, which divides into two layers that shift apart (Fig. 108 *B*). Into the space between the two layers, some of the mesoderm-cells just mentioned wander to yield the musculature of the mantle. The two layers of ectoderm which have thus arisen are known as the *outer* (*am*) and *inner* (*im*) *mantle-layers*, on account of their relation to the future mantle of the *Sacculina*. A second similar process of delamination now takes place in the inner mantle-layer, an inner ectodermal layer surrounding the central part of the nucleus being thus split off. The latter, as surrounding the future visceral sac, is distinguished as the *perivisceral ectodermal layer* (*pe*). Between it and the inner mantle-layer there now appears a cavity lined with chitin (Fig. 109, *b*); this is the so-called *brood-cavity* (*cavité incubatrice*).

We thus see that, by changes in the nucleus, the most important parts of the body of the adult *Sacculina* begin to be formed; viz., the inner visceral sac, the brood-cavity, and the mantle-fold which surrounds it. The visceral sac is not completely encircled by the brood-cavity, for, at the point of attachment of the sac, the inner mantle-layer passes over into the perivisceral ectodermal layer; this transition point is the so-called *mesentery*, which DELAGE assumes to have a ventral position in the body.

Having now obtained a general idea of the development of the form of the body in *Sacculina*, we must add a few words as to the rise of its most important organs. In the mantle region the changes are not great. In the late stages, the mantle-cavity breaks through into the perivisceral cavity, and thus arises the *cloacal aperture* (Fig. 109, *cl*), which lies almost opposite the stalk of the *Sacculina*, but somewhat to the left side of the body. While the ectodermal cells of the mantle lengthen to form transverse connective fibres (Fig. 109 *B*), the mesoderm-cells change into longitudinal muscle-strands and the sphincter of the cloaca.

More important alterations occur in the region of the visceral sac. The *ganglion* (*g*) here forms by an immigration of ectoderm-cells, in which not only the perivisceral ectodermal layer, but also the inner mantle-layer (by means of the mesenterial margin?) are said to take part. Whereas, in earlier stages, the whole inner space of the visceral sac was almost exclusively occupied by the ovarian rudiment, numerous *mesenchyme-cells* now wander from the stalk into the perivisceral sac, surround the ovary, forming a peritoneal envelope around it, and fill the space between the body-wall, the ganglion, and the ovary. The ovarian rudiment simultaneously breaks up into two lateral lobes connected by a commissure. The manner in which the short oviduct arises is not quite clear, but DELAGE believes that he can trace it back to a paired lateral ectodermal invagination. This latter, widening inwardly, gives rise to the so-called atria (*a*), on whose walls the *glands of the ovarian sac* (cement glands, *dr*) appear as lateral outgrowths. The *vasa deferentia* arise in the same way through ectodermal invaginations near the stalk of the visceral sac, while the actual testes (*t*) are derived from mesoderm-cells which become attached to the ends of these ducts.

After the *Sacculina*, completely enclosed within the central tumour (in the perivisceral cavity), has in almost every respect attained the grade of development of the adult, it rises to the surface of the central tumour, passing out through the widened opening of the perivisceral cavity (Fig. 109 *A*, *f*). The fold by which this cavity was formed now draws back to the base of the stalk and soon entirely disappears. An increase in size takes place in the *Sacculina* after leaving the central tumour, and this causes constant pressure on the ventral wall of the abdomen of the host (Fig. 109 *B*, *L*) leading to gangrene of the part thus affected, and to the consequent formation of an opening through which the body of the *Sacculina* passes out freely, its stalk still connecting it with the basal plate and the network of rootlets within the host.

The *Sacculina* is, by these processes, changed into a *Sacculina externa* (Fig. 109 *B*). The parts that lie outside of the host now become strongly chitinised, there is further increase in size, and the stage of sexual maturity is reached.

The metamorphosis of *Sacculina* above described is without doubt one of the most remarkable processes of transformation in the animal kingdom. The intercalation of a temporary endoparasitic condition must no doubt be referred to the protected position thus obtained, and, indeed, the whole process of development of this form has undergone marked coenogenetic changes. Although, considering the unusual simplification in structure of the *Kentrogon* larva, we may not be ontogenetically justified in tracing back the various parts of the adult body to those of the *Cypris*-like larva, the consideration of other forms (*e.g.*, *Anelasma*) leaves us not a moment in doubt as to how the body of the adult *Sacculina* is to be interpreted. Such consideration would lead us to compare the peduncle of the *Sacculina*, running out at its base into root-like processes, to the stalk of the *Lepadidae*, the mantle of the *Sacculina* to the shell of the latter, and the brood-cavity of *Sacculina* to the mantle-cavity of the *Lepadidae*. The cloacal aperture would then correspond to the shell-cleft in the latter family. This interpretation is supported most of all by the similar position of the ovarian sacs in these cavities. It becomes probable, on comparison with *Anelasma*, that Delage's definition of the mesenterial margin as the ventral side of the *Sacculina* is actually correct.

Frequent attempts have recently been made to oppose the Rhizocephala to all other Cirripedia as an independent group (sub-order). On the other hand, it must be pointed out that they, in the *Nauplius* and the *Cypris* stage, show such complete agreement with other Cirripedes that too great stress must not be laid on changes of structure which have evidently arisen secondarily as the result of parasitic life.

D. Ascothoracida.

This group comprises a few forms (*Laura Gerardiae*, *Synagoga mira*, *Petrarca bathyactidis*) which live parasitically in Anthozoa, and *Dendrogaster astericola*, an endoparasite in the Asteroidea (*Solaster*, *Echinaster*). In the most important features of their organisation, these forms are true Cirripedes, although they claim a special position within that group. *Laura Gerardiae*, thanks to the researches of LACAZE-DUTHIERS (No. 51), is the member of this group which we know best. The animal is surrounded by a large mantle which here shows direct relation to the shell-valves of the *Cypris* stage; each half contains between its two lamellae not only the hepatic outgrowths of the intestinal canal, but also the ovaries. The body proper appears very much reduced, but is still distinctly segmented, the mouth-parts are adapted for sucking, the six (or five) pairs of thoracic limbs have degenerated, and the abdomen is short. It should be mentioned as a characteristic of the group that the first antennae are here never used, as in other Cirripedes, for the attachment of the body. For the general morphological elucidation of these forms indeed, we must compare them not with the adult *Lepas*, but rather with the free-swimming *Cypris* larva.

Very little has been made known, up to the present time, of the ontogeny of these forms. The cleavage of the egg in *Laura* seems to resemble that in *Balanus*. The *Nauplii* of *Laura* show very little similarity with the typical Cirripede *Nauplius*, on account of the absence of the very characteristic frontal horns. A small form observed by LACAZE-DUTHIERS, and no doubt representing a stage in the course of development of *Laura*, may possibly be regarded as a complemental male. The *Cypris* stages of *Dendrogaster* (Fig. 110), however, are known (KNIPOWITSCH, No. 47), the metamorphosis in this form appearing to be abbreviated, no free *Nauplius* stage being passed through. The larva, in which an anal aperture, as in the adult, is wanting, bears a general resemblance to the *Cypris* stage of the Cirripedia. Both the single and the compound eyes are, however, wanting. A very large olfactory filament (*a′*) is developed on the first antenna. There are five biramose pairs of thoracic limbs; the first abdominal segment carries the rudiment of a penis (*p*). The abdomen, (*ab*) which is distinguished by its length, consists of five joints and the furcal appendages.

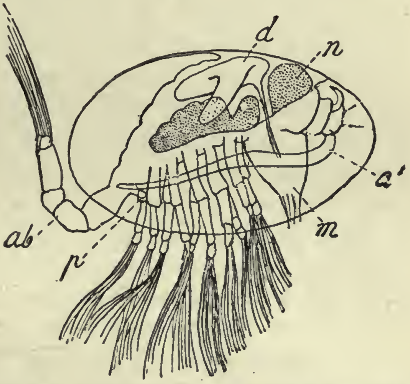

FIG. 110.—Free-swimming *Cypris* stage of *Dendogaster astericola* (after KNIPOWITSCH). *a′*, first antenna; *ab*, abdomen; *d*, intestine; *m*, buccal cone; *n*, nervous system; *p*, rudiment of penis.

E. The Morphological Derivation of the Complemental Male.

The sexual differentiation of the Cirripedia is very complicated and difficult to explain. As a rule the Cirripedia are hermaphrodite. We shall not err if, considering the almost universal separation of the sexes in all other Crustacea, we regard this hermaphroditism as secondarily acquired in consequence of the attached manner of life. We must assume that the free-swimming ancestors of the Cirripedia were of separate sexes, and that hermaphroditism was only gradually acquired after the fixed sedentary mode of life had become fully established as a characteristic of this group. While, in the *Balanidae* and Rhizocephala, hermaphroditism has become the exclusively prevailing condition, there is a tendency in many groups of the *Lepadidae* to retrogression in the direction of the separation of the sexes. Male forms here appear either side by side with hermaphrodite individuals, being then called *complemental males*, or else, in cases of the complete separation of the sexes, in company with true females. These complemental males are always smaller than the hermaphrodite individuals or the females; they are found attached parasitically to the bodies of the hermaphrodites or females. In isolated cases, the shape of the body in the male deviates only slightly from that in the hermaphrodite (*Scalpellum villosum* and *S. Peronii*), but in other cases there is striking sexual dimorphism in this respect, the male undergoing a process of degeneration in which the calcareous portions of the skeleton, the limbs, the mouth, and the alimentary canal have been lost, thus sinking to a very low grade of organisation, and becoming actually a dwarf or complemental male. The following degrees of degeneration of the male are found in the genus *Scalpellum* (Hoek, No. 46).

I. True hermaphrodite forms (*Scalpellum balanoides*, Hoek).

II. Large hermaphrodite forms with small complemental males.

(*a*) The males resemble the hermaphrodites in structure.

The division into capitulum and peduncle is recognisable, mouth and alimentary canal are present (*Scalpellum villosum*, *S. Peronii*).

(*b*) The males have degenerated; they are without mouth and intestine; without a shell, or have only a vestigial shell; without a peduncle (*Scalpellum vulgare*, *S. rostratum*).

III. Separate sexes. The female is large and resembles the hermaphrodite individuals of the other species. The male is very small (*Scalpellum ornatum*, *S. regium*, Hoek, etc.).

The Abdominalia (*Alcippe*, *Cryptophialus*) show a differentiation akin to that of this last group. Here also we find separation of the sexes with highly developed sexual dimorphism. The complemental males appear very much reduced. They have no tendril-like feet, no mouth, and no alimentary canal. In other respects, if we take into account the reduction that has commenced, their structure can be traced back to that of the female.

A condition resembling that above described for *Scalpellum* is found in the genus *Ibla*. In *Ibla quadrivalvis*, side by side with the hermaphrodite form, there is a small complemental male with a large peduncle, but a very reduced capitulum and a diminished number of thoracic limbs, while in *Ibla Cumingii* a similar male is found side by side with a true female, complete separation of the sexes being here obtained.

It follows from the above that, in accordance with HOEK (No. 46), in tracing the sexual condition of the Cirripedes, we start from the hermaphrodite form, proceeding to others with dwarf males in company with hermaphrodite individuals, and reach finally a complete separation of the sexes in which marked sexual dimorphism has secondarily developed. The series of complemental males, as well as the dwarf males, would thus be derived from the hermaphrodite form by the degeneration of the female genital rudiment. It is perhaps difficult to imagine how the want of complemental males can in the first instance have made itself felt in hermaphroditic forms. But we must bear in mind that, according to F. MÜLLER, cross-fertilisation appears to be the rule even among the true hermaphroditic *Lepadidae*. This cross-fertilisation is of the greatest importance in securing the vitality of the race; but owing to the fixed mode of life of the Cirripedia there is some danger that it may not take place. All such danger is precluded by the development of these dwarfed forms living semi-parasitically on the larger hermaphrodites. The dwarfs, by the atrophy of their ovaries, have become males, and by the attachment to the hermaphrodites ensure cross-fertilisation. We must regard this condition as a partial retrogression in the direction of separation of the sexes, which has again been reached in individual cases in the further course of this development.

The view sketched above is in opposition to that of CLAUS (No. 8), according to which the sexually distinct forms (*e.g.*, *Alcippe* and *Cryptophialus*) have retained the primitive condition. From this originally dioecious condition, by a transformation of the females into the large hermaphrodite form, the condition found in most *Lepadidae* was developed, while the males were only retained in isolated species as complemental males. Consequently the males would be a vestigial remainder from those times when hermaphroditism had not yet become the rule among the Cirripedia. The occurrence of dwarf males side by side with hermaphrodite individuals in a number of forms would be easily explicable by this ingenious theory (not, however, in *Scalpellum villosum* and *S. Peronii*). HOEK, however, has pointed out in opposition to it, that, in this case, the dwarf males ought to show a greater resemblance in structure to the *Cypris* form than they actually do show. The dwarf males in reality appear to be connected by gradual transitions with the complemental males of *Scalpellum villosum* and *S. Peronii*, which latter forms are evidently to be derived from the hermaphrodite form.

The view held by CLAUS would apply to the Rhizocephala if the statements of FR. MÜLLER and DELAGE were to prove true that complemental males occur in these forms which, throughout life, do not develop further than the *Cypris* pupa. But this last view, which rests upon the discovery in the cloacal aperture of a young *Sacculina externa* of an attached dead Cypris envelope, must still be considered doubtful, and has actually been denied by GIARD.

6. Copepoda.

The Copepoda are very numerous and rich in varieties of form, in spite of the simplicity of their body segmentation; they nevertheless show morphological characters which, in relation to those of the hypothetical ancestor of the Entomostraca, must be regarded as decidedly degenerate. Among these we must reckon the small size of the body and the comparatively small number of its segments, the reduced form or entire absence of the heart, the want of separate respiratory organs (branchiae), the loss of the paired lateral eyes, which are retained only in the families *Corycaeidae* and *Pontellidae*, and perhaps also the slight development of the dorsal shield. On the other hand, there are certain indications that the Copepoda ought to be counted among the most primitive of existing Crustacea. Among these characters we should specially mention the use of the two pairs of antennae as locomotory and clasping organs, the very primitive structure of the mouth-parts in the free-living forms (occurrence of a biramose mandibular palp, the segmentation of the first maxilla, Fig. 91 *A*, p. 194), and the metamorphosis which, in the free-living forms, shows very primitive features.

With regard to the segmentation of the body, we must distinguish as the most anterior region of the body a simple cephalic region carrying the antennae and the mouth-parts. The latter consist of three pairs of appendages (mandibles, first and second maxillae), the last pair separating into two appendages (the exopodite which shifts forward is called the first maxillipede, the endopodite which shifts backwards yields the second maxillipede). The thoracic region consists of five segments provided with biramose swimming limbs (Fig. 90 *A*, p. 193); the last of these segments may be vestigial, whilst the anterior segment often fuses with the cephalic segments, this union giving rise to an anterior region known as the cephalo-thorax. The abdomen consists of five segments, the most anterior of which alone carries the rudiment of a limb (genital prominence). A fusion of the two anterior abdominal segments usually gives rise, in the female, to a double genital segment which bears the genital aperture.

In a few *Pontellidae*, the cephalo-thoracic region, by the appearance of demarcations between the segments, becomes subdivided into regions (each consisting of two segments). This peculiarity stands almost alone in the whole series of Crustacea. Such a segmentation can only be regarded as a secondary re-appearance of the long-lost independence of the cephalic segment. It has, nevertheless, a certain interest.

A. Gnathostomata.

The metamorphosis of the free-living Copepoda is accomplished as a very gradual transition from the *Nauplius* to the adult form through many moults. There is, however, at a certain period, a more sudden change of shape, and this enables us to separate the course of metamorphosis into two periods, the first comprising the series of *Nauplius* and *Metanauplius* forms, while the second is distinguished by a name taken from the metamorphosis of the *Cyclopidae* as the series of *Cyclops*-like larval forms. In the first series, the Nauplius limbs show a general resemblance to the primitive form, the abdomen is not yet distinctly marked off, and the furcal processes have not yet developed. In the second series, these last advances in development are made, while the antennae and mouth-parts approach the adult form.

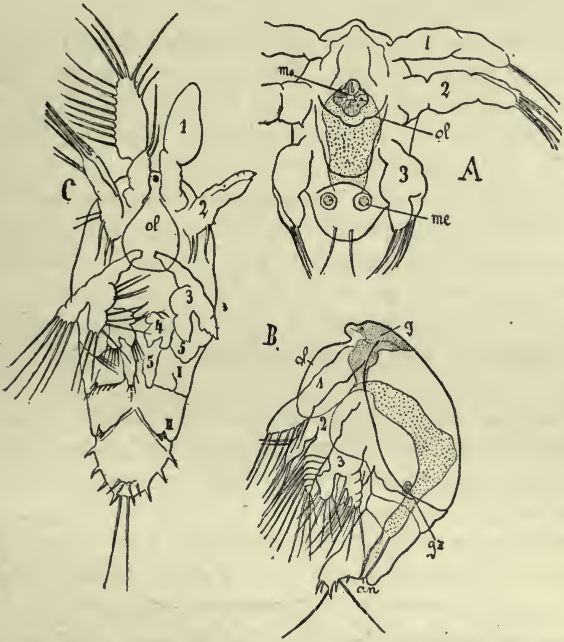

Fig. 111.—Larval stages of *Cetochilus septentrionalis* (after Grobben, from Lang's *Text-book*). *A*, *Nauplius*. *B*, *Metanauplius*. *C*, older *Metanauplius*. *1* and *2*, first and second antennae; *3*, mandible; *4*, maxilla; *5*, *5*, exopodite and endopodite of the second maxilla (=first and second maxillipedes); *I*, *II*, first and second pairs of thoracic limbs; *an*, anus; *g*, brain; *gz*, genital cells; *m*, mouth; *me*, primitive mesoderm-cells; *ol*, upper lip.

The development of the free-living Copepoda has been specially investigated by Claus (Nos. 64 and 67). We take, as the foundation of our description, the metamorphosis of *Cetochilus*, which has been minutely described by Grobben (No. 73). The free-living Copepod leaves the egg as a strikingly unspecialised *Nauplius* (Fig. 111 *A*).

The body, which is usually oval (only in individual cases long, transversely broadened or barrel-shaped), shows no traces of external segmentation, and carries on its ventral side the large upper lip (*ol*), as well as the three typical pairs of Nauplius limbs (*1*, *2*, *3*). The anterior limb (first antenna) is uniramose, the next (second antenna) biramose and provided with a masticatory hook on the protopodite. The mandible in *Cetochilus* is without such a masticatory process, and is a simple biramose swimming limb. The limbs are beset at their ends with long setae.

In the alimentary canal we can distinguish a stomodaeum, a long enteron, and a proctodaeum. The latter, in *Cetochilus*, in the first *Nauplius* stage, is still found as a solid ingrowth of the ectoderm, the anal aperture not yet having broken through. The nervous system is still connected for its whole course with the ectoderm. As a sensory organ, we find the Nauplius eye. The coiled antennal gland, which is probably developed at this stage, functions as excretory organ, besides which the cells of the enteron seem to have undertaken an excretory function; urinary concretions have, at least, been proved to exist in certain projecting cells in the enteron of the *Nauplius* of *Cyclops* (Leydig, Fig. 89, *ds*, p. 191).

The terminal region of the *Nauplius* is sharply bent ventrally, and provided with two setae. We here find, internally on each side, a large mesoderm-cell (*me*); these are assumed by Grobben to be primitive mesoderm-cells.

Later Nauplius stages are distinguished by the greater length of the body and by the outgrowth of its posterior region. During this latter process, the more strongly chitinised integument of the dorsal parts becomes marked off as the cephalo-thoracic shield by the development of a fold at its margin. The proctodaeum has now become perforated, a distinct dorsally-placed anal aperture being apparent. The brain is connected behind the Nauplius eye with a paired ectodermal growth, in which can be recognised the rudiments of paired lateral eyes and their optic ganglia (secondary brain); these, at a later period, become vestigial. The rudiment of the genital organs is to be recognised in large mesoderm-cells lying one on each side of the alimentary canal (Fig. 111 *B*).

There now appears, behind the mandible, a small biramose limb, the rudiment of the first maxilla (*4*), and the larva passes into the *first Metanauplius stage* (Fig. 111 *B*).

A *later Metanauplius stage* (Fig. 111 *C*) reveals three more rudiments of limbs, viz., the second maxillae (*5*), from the two branches of which the so-called maxillipedes of the Copepoda are derived, and the first two pairs of thoracic limbs (*I*, *II*). This stage still has a distinct Nauplius appearance. The body has grown in length, but still, when seen from the side, shows the characteristic ventral curvature. The posterior end of the body is still without the furcal processes. The two pairs of antennae have not essentially changed from their condition in the former stage, except in the increased number of their setae. The masticatory hooks are still present on the basal joints of the second antennae. In the mandible (*3*) a large masticatory blade can be seen projecting from the basal joint. The first maxilla (*4*) is like a small lobed plate, while, in the second maxilla (*5*), indications of the separation of the exopodite (so-called anterior or outer maxillipede) from the endopodite (so-called posterior or inner maxillipede) are to be seen. The rudiments of the two anterior pairs of thoracic limbs are found as bilobed swellings (*I*, *II*). At this period, several moults take place, no essential change occurring in the shape of the larva, beyond the appearance behind the second thoracic segment of the rudiment of a third. The whole series ends by a moult through which the larva passes on into the series of *Cyclops*-like stages.

The first of these stages, which, in accordance with the accepted terminology of the Copepodan metamorphoses, we shall call the *first Cyclops stage* (more correctly named *Cetochilus stage* by Grobben), reveals essential changes of form. The body is no longer flexed ventrally, but is straight. Its most posterior region is sharply marked off from the anterior portion of the body by a constriction; the furcal appendages and the rudiment of a fourth thoracic segment have developed. The limbs approximate in shape to those of the adult, although they have not so many joints. The first antenna has passed from the short leaf-shape into the long, cylindrical, oar-like form; it stands out laterally from the body, and consists of many joints. The second antenna has remained biramose, but has lost its masticatory process; on the mandible, the masticatory blade has greatly increased in size. The maxilla is larger and more richly jointed, the maxillipedes have become transformed into large prehensile organs. The two anterior pairs of thoracic limbs have developed as swimming limbs; the basal segment of each already consists of two joints, but the two rami are still unjointed; the third pair of thoracic limbs, on the contrary, can only be recognised as a pair of bilobed rudiments.

Among the transformations which take place in the internal organs during the *Cyclops* stages, we must mention the degeneration of the paired optic rudiment and of the secondary brain. Now for the first time the nerves which run to the paired frontal organs are distinctly recognisable. The antennal gland degenerates, while the *shell-gland*, which opens externally at the base of the anterior maxillipede, becomes functional in its stead. The anal aperture no longer lies dorsally, but shifts to the posterior end of the body between the two furcal appendages. The genital organs show an advance by an increase in number of genital cells and by the development of the efferent ducts. The paired genital rudiments now meet above the intestine and fuse to form a single gland. The heart develops between the first and second thoracic segments out of a paired rudiment of mesoderm-cells.

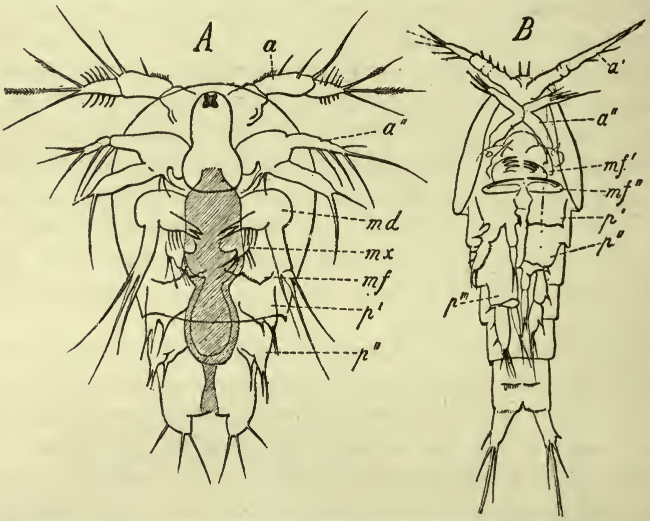

Fig. 112.—Two stages of development of *Canthocamptus staphylinus* (after Claus). *A*, *Metanauplius* stage. *B*, *Cyclops* stage with three pairs of swimming limbs. *a'*, first antenna; *a''*, second antenna; *md*, mandible; *mx*, maxilla; *mf*, second maxilla (rudiment of the two so-called maxillipedes); *mf'*, first so-called maxillipede; *mf''*, second so-called maxillipede; *p'*, *p''*, *p'''*, first, second, and third pairs of thoracic limbs.

In the *second Cyclops stage* (Fig. 112 *B*), there first appear the rudiments of the limbs of the fourth thoracic segment and the delimitation of the fifth thoracic segment. Thus we find, at this stage, behind the cephalo-thorax, four free thoracic segments, and, following these, the as yet unsegmented abdomen. Of the thoracic limbs, the three anterior pairs are well developed. In the *third Cyclops stage*, the fourth pair of thoracic limbs has attained full development and the first abdominal segment has formed; in the following *Cyclops* stages, the gradual segmentation of the abdomen takes place, as well as the complete transition of the limbs to their final shape. Besides the formation of a more richly segmented body, in the families of the *Cyclopidae* and *Corycaeidae*, the (inner) accessory branch of the second antenna is lost as early as the first *Cyclops* stage, and the mandibular palp degenerates.

The metamorphosis of the *Calanidae* (*Cetochilus*), which has here been considered as the type, is distinguished by the regular development of the limbs from before backwards, but in the *Harpactidae* (Fig. 112) and *Cyclopidae* an exception to this regular order is found in the second maxilla (*mf*), which in the later *Nauplius* stages has, indeed, begun to form, but is still in an exceedingly rudimentary condition, so that the pair of limbs which follow it precede it in development. We have here a parallel to the condition of the maxilla in the Phyllopoda.

B. Parasita.

The free-living Copepoda are connected with the more specialised parasitic genera by many transitional forms which mark the various degrees of parasitism, and we consequently also find various stages in the transformation and degeneration of the segmentation of the body. It may be laid down as a general rule that the female, on account of the part played by her in reproduction, shows a greater tendency to adopt the parasitic mode of life, and consequently to undergo degeneration of the locomotory organs, obliteration of the boundaries between the segments and deformation of the body. Thus, even in the little modified *Sapphirina*, we find that the females become parasitic in the respiratory cavity of the Tunicata, or in the umbrellar cavity of *Diphyes*, while the males are always found swimming freely about. An extreme example is found in *Lernaea* (Fig. 114 *A* and *B*), the metamorphosis of which ends in a *Cyclops*-like free-swimming stage, during which copulation takes place; the female afterwards becomes attached to a fish (often one of the *Gadidae*), and undergoes great deformation of the body (Fig. 114 *C* and *D*). Heteromorphism of the sexes develops in this group, in so far as the male is only slightly removed in the segmentation of its body from the later *Cyclops* stages, while the female is greatly transformed in accordance with her parasitic habit. The same is the case in the *Philichthyidae* and the *Chondracanthidae*. In some forms, on the contrary, the male also departs from the *Cyclops*-like shape of the later larval stages by a secondary transformation. Whereas, in the *Caligidae* and *Dichelestiidae*, the two sexes are not strikingly different in shape of body or size, in the Lernaeopoda (Fig. 115 *D* and *E*), the heteromorphous development of the two sexes takes place in a way different from that shown in *Lernaea*. The males here participate in the degeneration of the body-segments as a result of their parasitic life, and they further undergo arrest of growth, so that an enormously large female is contrasted with a dwarf male. This kind of heteromorphous development of the two sexes must be regarded as an excessive adaptation to the different sexual functions, which is rendered possible by parasitic life.

The parasitic forms can be deduced from the free-living forms by imagining that the latter have, in consequence of parasitism, undergone certain changes. Thus the parasitic Copepoda first passed through *Metanauplius* and *Cyclops* stages to a stage approaching the shape of the free-living form, and then, through a series of further stages, attained parasitic deformation. The metamorphosis of the parasitic Copepoda has thus been lengthened by the addition of final parasitic stages. The first two series of stages, however, seem to be correspondingly shortened. The larvae of the parasitic Copepoda frequently do not hatch in the *Nauplius* form, but in an advanced *Metanauplius* stage, or even in the *Cyclops* stage (Fig. 73, p. 148; *Chondracanthus*, *Tracheliastes*, *Achtheres*, *Anchorella*, *Brachiella*, etc.). On the other hand, the metamorphosis may be shortened by the suppression of the later *Cyclops* stages, since, in cases of the most specialised parasitic forms, the very first *Cyclops* stage passes at once into the parasitic form (*Chondracanthus*, *Lernaeopodidae*).

A further distinction between the metamorphosis of the parasitic Copepoda and that of the free-living forms arises from the circumstance that, even in the larval condition, a sedentary manner of life (on the gills of a host) is adopted, and that, in keeping with this, there is a development of a peculiar attaching organ (the frontal band of the larvae in the *Caligidae*, *Lernaea*, and *Lernaeopoda*) and of resting stages with reduced limbs (so-called pupal stages).

It would take us beyond the limits we have assigned to ourselves to give a complete enumeration of the very scattered notices of individual larval forms among the parasitic Copepoda, especially as there are still many gaps in the observations made on the development of these forms. We must content ourselves with selecting a few of the more important forms, of whose metamorphosis a more accurate knowledge has been obtained. We must here, in the first place, separate those larvae which apparently are not provided with the larval adhering apparatus (frontal band) from those in which such an organ has been observed.

In those families in which the adult retains more or less of the body segmentation of the free-living Copepoda (*e.g.*, *Corycaeidae* and the *Notodelphyidae*, which latter is placed among the Gnathostomata), the metamorphosis appears not to differ essentially from that above described for free-living forms. In the

Chondracanthidae, on the contrary, we find the above-mentioned abbreviations of metamorphosis. The young larvae which hatch from the egg of *Chondracanthus gibbosus* already show behind the Nauplius limbs the rudiments of two other pairs of limbs, and must therefore be described as *Metanauplii* (Claus, No. 71). The youngest parasitic females remain essentially at the level of development of the first *Cyclops* stage. Of the four distinct thoracic segments seen at this stage, only the two anterior ones carry bilobate rudiments of limbs without setae, while the posterior region of the body (abdomen) is small and divided into two parts. No further *Cyclops* forms follow these first stages, but while the small male remains during life at this grade of development, the female undergoes a secondary transformation, the region of the third and fourth thoracic segments increases in size and forms the main portion of the body. The large thoracic region now becomes transformed in an extraordinary manner, dorsal and ventral swellings and lateral projections appearing as secondary outgrowths on each of the thoracic segments (except the first).

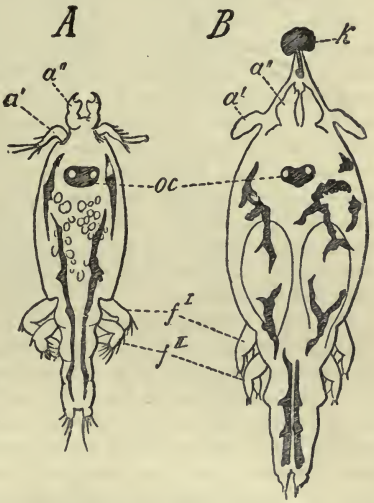

Fig. 113.—Two larval stages of *Lernaea branchialis* (after Claus). *A*, first *Cyclops* stage. *B*, so-called pupal stage. a', first antenna; a'', second antenna; f^{I}, first, f^{II}, second pair of thoracic limbs; *k*, adhesive mass; *oc*, eye.

Somewhat similar phenomena are found in the family of the *Philicthyidae*. Here the larval form which hatches from the egg in the genus *Lernaeascus* is a *Nauplius* with a large provision of food-yolk, whose second antennae are without masticatory hooks, the adhering apparatus (frontal band) being absent, as in the *Metanauplius* of *Chondracanthus*. The parasitic form arises from a *Cyclops* stage in which the thorax and abdomen are distinctly segmented, but only the two anterior thoracic segments show a well-developed rudiment of a swimming limb, while the third thoracic segment has only the vestigial remains of a limb. The male retains the shape of one of these developmental stages, while the female is parasitically transformed, the thoracic region lengthening, while a peculiar development of asymmetrical rows of chitinous scales makes its appearance (Claus, No. 69).

In the family just described, the ascending series of larval forms does not appreciably rise above the level of the first *Cyclops* stage, but in the *Dichelestiidae*, where the body of the adult undergoes less modification, the later *Cyclops* stages are also passed through. The young which hatch from the egg are true *Nauplii*. The frontal band appears to be wanting (?) in the larvae of this group.

An adhering apparatus of this kind is found in the larvae of the *Caligidae*, which, in their earlier stages, strikingly resemble the *Cyclops* stage (pupae) of *Lernaea* (Claus, No. 70, see below). The later larvae, which more nearly resemble the adult in form, but are still distinguished by the possession of the frontal band, were described by Burmeister as distinct forms under the name of *Chalimus*. Later, however, F. Müller proved that these forms belong to the ontogeny of *Caligus*, as had already been conjectured by Kroyer.

The *Lernaeidae* are very interesting with respect not only to the parasitism of the larval forms, but to the deformation that occurs in the body of the female after copulation. The metamorphosis of *Lernaea branchialis* has been made known by Metzger and Claus (No. 70). It is probable that the larva which hatches from the egg is a *Nauplius* resembling that of *Achtheres*, in which the segmentation of the body of the first *Cyclops* stage appears to be commencing beneath the cuticle. In these stages there is a free-swimming period, during which a search is made for the first host (*Platessa flesus*). The youngest forms found attached to the gills still show in all respects the segmentation of the first *Cyclops* stage (Fig. 113 *A*). They correspond to the first stage of development of *Achtheres*. The cephalo-thoracic region is followed by three free thoracic segments and a posterior unsegmented region carrying the furcal processes. Two pairs of well-developed swimming limbs (f^{I}, f^{II}) can be recognised, one attached to the cephalo-thorax and the other to the first free thoracic segment, as well as a third pair of truncated limbs (on the second free segment). The mouth-parts are already of the true Siphonostomatous type. The upper and lower lips (labrum and paragnatha ?) have fused to form a sucking tube which contains the stylet-shaped mandibles, while the pointed palp-like maxillae are attached to its sides. The first antennae (a') are beset with setae, the second antennae (a''), as well as the anterior maxillipedes, are changed into hooks for attachment. The posterior maxillipedes have completely degenerated, a point in which this larva differs from that of *Achtheres*.

The later *Cyclops* stages which succeed each other (Fig. 113 *B*) show decided adaptation to parasitic life. A hardened mass of secretion (k), projecting from the head and comparable to the frontal band of the larva of *Caligus*, brings about the attachment of the larva to the gills of the host; this permanent attachment precedes the degeneration of the locomotory organs. Almost all the limbs, and especially the swimming limbs (f^{I}, f^{II}), are now unjointed and truncated; they have no setae and are immovable. These stages in which independent movement is lost have also received the name of pupal stages. In this pupal condition the segments of the body and the pairs of limbs which were still wanting are developed. A stage can be distinguished with three pairs of swimming limbs and four free thoracic segments; at this period, in the male, the posterior maxillipede, until now suppressed, becomes distinct; then a further stage is developed with four pairs of swimming limbs; this last stage leads through another moult to the free-swimming stage in which copulation takes place (Fig. 114 *A* and *B*). Apart from the slight segmentation of the abdomen, the body shows the full development attained by free-living Copepoda. The first antennae (a') are now jointed and beset with setae and sensory filaments, the four pairs of swimming limbs (f^{I}, f^{IV}), with their clothing of setae, are adapted for active swimming, while in the structure of the second antennae (a'') and of the mouth-parts, the Siphonostomatous type is marked. The female (Fig. 114 *B*) is distinguished by a great lengthening of the genital segments, which gives the whole abdomen the appearance of a long, vermiform appendage. The female genital organs are not yet sufficiently developed for the production of eggs capable of fertilisation; the receptaculum seminis, on the other hand, with the two pores (g) for the reception of the seminal masses from the spermatophores, has attained full development. This free-swimming copulatory *Cyclops* stage is the last stage of the male, the fertilised female, however, seeks a new host (one of the *Gadidae*), in which she undergoes marked transformation of the body (Fig. 114 *C* and *D*). The genital segment, which has enlarged for the development of the eggs, is now a large doubly-curved portion of the body, the small abdomen, with its truncated furcal appendages, forming its termination. The cephalothorax is changed by the addition of three horns which function as barbed hooks, carrying at their points fork-like outgrowths. During these transformations, the limbs are all retained, but are to a certain extent transformed by strong chitinisation.

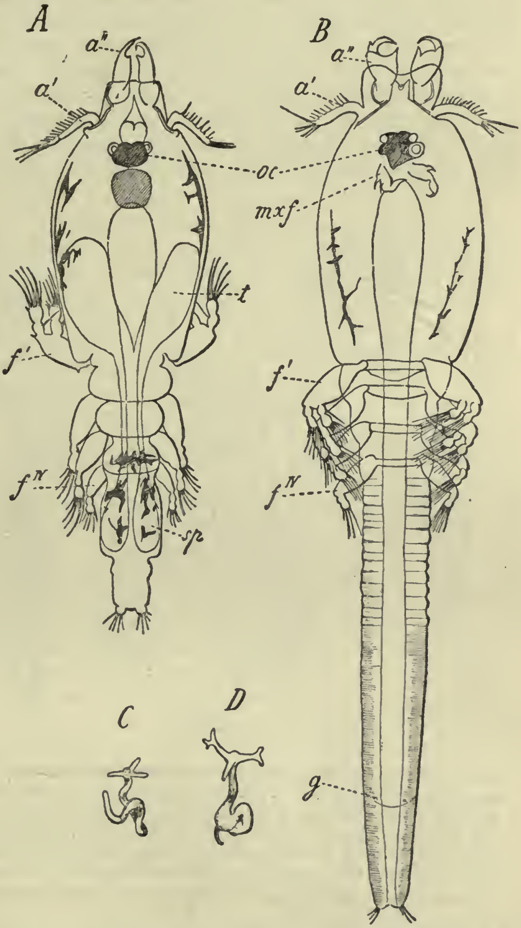

Fig. 114.—Sexually mature stage of *Lernaea branchialis* (after Claus). *A*, male. *B*, female at the copulatory stage. *C* and *D*, later condition of the female transformed by parasitism, slightly magnified. a', first, a'', second antenna; fI–fIV, first four pairs of thoracic limbs; *g*, opening of the receptaculum seminis; *mxf*, maxillipede; *oc*, eye; *sp*, spermatophoral sac; *t*, left testis.

The remarkable form *Sphaeronella Leuckartii*, which is parasitic in the brood-cavity of *Amphithoë*, is connected with *Lernaea* by its metamorphosis. Salensky (No. 80) found in *Sphaeronella* an extremely degenerate pupal stage following the first free-swimming *Cyclops* stage. Neither segmentation nor limbs were recognisable in the sac-like body which was attached by a larval adhering apparatus to the epimeral plates of the host. This stage led, through gradual transitionary stages, to the adult form.

The metamorphosis of the *Lernaeopodidae* is best known through the works of Kollar (No. 77), v. Nordmann (No. 79), Claus (No. 66), Vejdowsky (No. 81), and others. Its course in the various forms seems to show great agreement, so that *Achtheres*, described by Claus, may be selected as a type. The young animal which hatches from the egg (Fig. 115 *A*) exactly resembles a *Nauplius*, swimming about with difficulty by means of its two anterior pairs of limbs (first and second antennae). Closer examination, however, reveals the fact that the body which is hidden within the Nauplius cuticle already shows that degree of organisation characteristic of the first *Cyclops* stage. Not only the mouth-parts, but two pairs of thoracic swimming feet (p^1, p^2), lie hidden within the Nauplius integument. The mandibles (*md*) and first maxillae (*mx*) lie as small stumps at the sides of the upper lip, which enters into the formation of the adult rostrum. The position of the two maxillipedes (pm^1, pm^2) is of interest, in so far as it proves distinctly that they develop as the exopodite and endopodite of one and the same limb (second maxilla). Besides the above organs, we recognise the future adhering organ in the form of a spirally-coiled filament ending in a spherical swelling which grows out from a highly-refractive frontal process (*z*). Claus considers that this apparently homogeneous filament is a tube filled with a fluid secretion, and is the duct of a glandular mass which secretes a cementing medium. This first stage which seems to cover the whole series of *Nauplius* stages, undergoes ecdysis after a few hours, the larva which follows possessing the organisation of the first *Cyclops* stage (Fig. 115 *B*). It

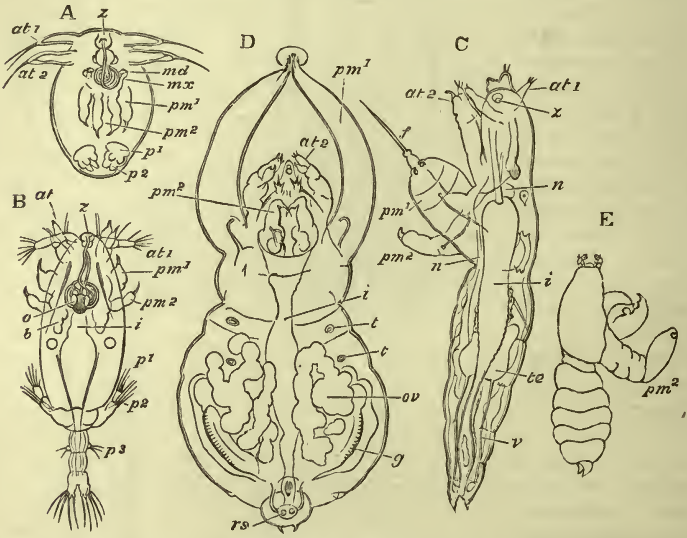

Fig. 115.—Metamorphosis of *Achtheres percarum* (after Claus, from Balfour's *Text-book*). *A*, so-called *Nauplius* stage. *B*, first *Cyclops* stage. *C*, older stage of the male larva. *D*, sexually mature female. *E*, sexually mature male. at^1, at^2, first and second antennae; *md*, mandible; *mx*, maxilla; pm^1, pm^2, first and second maxillipedes; p^1, p^2, first and second swimming limbs; *z*, frontal organ; *i*, intestinal canal; *o*, Nauplius eye; *b*, glandular body; *t*, organ of touch; *ov*, ovary; *f*, spine derived from the fused maxillipedes; *g*, cement gland; *rs*, receptaculum seminis; *n*, nervous system; *te*, testis; *v*, vas deferens.

has a long cephalo-thorax, followed by three free thoracic segments and an unsegmented abdomen. In the thoracic region, two pairs of well-developed swimming limbs (p^1, p^2) and a third rudimentary pair (p^3) can be recognised. The first antennae (at^1) are cylindrical three-jointed limbs beset with setae. The second antennae are still biramose (at^2), but are already changed into the adhering organs of the larva, the longer branch ending in a hook bent like a claw, while the shorter branch is beset with papillae. The upper lip has united with a channelled lower lip (derived from the paragnatha?) to form a conical sucking proboscis, from the outer sides of which project the short, conical mandibles, representing the transition from the masticatory jaws of the *Cyclopidae* to the piercing stylets of the Parasita; here also the palp-like first maxillae are found. These are followed by the two pairs of maxillipedes transformed into adhering hooks (pm^1, pm^2), the outer one already assuming a more forward position, and the inner one lying more posteriorly. Among the internal organs, the intestine, the Nauplius eye shifted far back, and two bean-shaped bodies (b, glands?) at the sides of the latter can be recognised.

It is probable that the larva, after a short life of free activity in the water, becomes attached as early as this stage to the mucous membrane of the jaw of the perch (v. NORDMANN). The peculiar adhering organ, however, appears to become free, and to be used for its special purpose only after a further moult. In this and two other attached stages, which probably follow through further moults, the mandibles shift to a position within the sucking proboscis, while a reduction in the setae on the swimming feet probably takes place. These stages, however, did not come under observation, but in a somewhat later stage which was observed (Fig. 115 *C*), there was already considerable approximation in the structure of the body to the adult *Achtheres*. The body has now become almost vermiform, the first thoracic segment having separated from the head and having united with the four following segments to form a sac-like region, at the end of which the small, pointed, furcal appendage can be recognised. The antennae and the mouth-parts already essentially resemble the corresponding parts of the adult. The frontal adhering organ, with the exception of a vestige of its basal section (z), has vanished; on the other hand, a new provisional adhering organ in the shape of a stiff filament (f) has arisen on the outer (anterior) maxillipede (pm^1); this filament starts from the tips of the fused outer maxillipedes. It is an interesting fact that at this stage sexual differentiation begins to be noticeable. Smaller individuals (young males) have remarkably strong outer maxillipedes (pm^1), which are only united at the point of insertion of the adhering filament, and carry a strong terminal hook. When this filament is thrown off in the next moult, these structures give rise to the anterior maxillipedes of the male, which remain distinct and function as hooks for attachment (Fig. 115 *E*). The posterior maxillipedes (pm^2) are also very large and each carries a small anchoring hook. In the female, on the contrary, the anterior maxillipedes (pm^1) are rather long and retain the fused condition, ending in a sucking disc (Fig. 115 *D*); the posterior maxillipedes can in the same way be distinguished from those of the male by a large, hook-like, terminal joint With regard to the inner anatomical peculiarities of this larval form, we must first mention the degeneration of the Nauplius eye, which, indeed, is not universal among the parasitic Crustacea. The Nauplius eye is retained in the dwarf males of *Chondracanthus* and of *Lernacopoda*, as well as in many females (*e.g.*, *Chondracanthus cornutus*). In the posterior cephalic region of the larvae under consideration, at the sides of the intestine, there are two pairs of glands derived from the bean-shaped bodies above mentioned ; these glands, whose efferent ducts open out at the base of the maxillipedes, yield a stiff secretion. Between these glandular bodies a dorsally-placed, pulsating organ can be noticed ; this is probably a short, sac-like heart. A similar organ has been observed in *Tracheliastes* by VEJDOWSKY, and in the larva of *Lernaea* by HESSE. The rudiments of the genital organs are already clearly recognisable. At the next moult the animal becomes sexually mature. The male does not increase in size, but, in the female, the posterior region of the body becomes very much enlarged.

C. Branchiura.

The Branchiura are usually considered to be nearly related to the Copepoda. This supposed relationship is based principally on the similarity existing between the swimming limbs of *Argulus* and those of the free-living Copepoda, and on the structure of the mouth-parts, which, according to the investigations of CLAUS, are very like those of the parasitic Copepoda (Siphonostomata). Hook-shaped mandibles and stylet-like maxillae can be distinguished. These appear to be enclosed in a proboscis formed by the fused upper and lower lips, together with lateral parts which must be regarded as derived from the mandibles. These are followed by two pairs of maxillipedes which serve as adhering organs. The view that these latter are the two rami of the second maxilla which have become independent receives special support from the position of the ducts of the shell-gland, discovered by CLAUS on the basal portion of the second maxillipede. Such a derivation of the maxillipedes would constitute a fresh link between these forms and the Copepoda. *Argulus*, indeed, shows in the structure of the genital organs, as well as in other points of its organisation, some remarkable peculiarities, and by the possession of paired, movable, lateral eyes and of branched, hepatic tubes approaches the Phyllopoda, so that we must probably consider the Branchiura as an offshoot from the common ancestor of the Copepoda.

The eggs, which are rich in food-yolk, and in which the germ-band attains a ventral curvature, are attached by the female in rows to stones, etc. The young, when hatched (CLAUS), already greatly resemble the adult in shape (Fig. 116), having the same body-segmentation as well as the same number of limbs (apart from the maxillae).

The shield-like anterior portion of the body (cephalo-thorax) consists of the cephalic segments fused with the most anterior limb-bearing segment which carries a pair of swimming limbs. Three free thoracic segments follow, each having a pair of swimming limbs, and these again are followed by an unsegmented abdomen with terminal furcal appendages (in the young form). In the adult, these latter have shifted dorsally. The young are further distinguished from the adult by the small extent of the cephalo-thoracic shield (Fig. 116), which does not yet cover the thoracic segments dorsally. The further metamorphosis principally concerns the transformation of the different limbs. In the newly-hatched larva, the first antenna (a') is short, three-jointed, with a large hook-like appendage on its basal segment. The second antenna (a'') is distinctly larger and biramose, an endopodite ending in a hook, and an exopodite provided with setae being distinguishable in it. In the mandible (*md*) are found a basal segment (masticatory blade), which becomes included

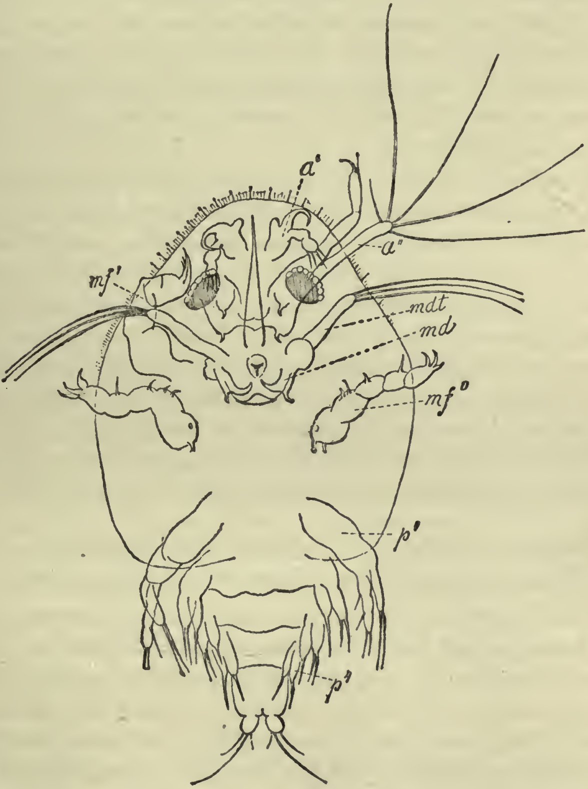

Fig. 116.—Newly-hatched larva of *Argulus foliaceus* (after Claus). a', first antenna; a'', second antenna; *md*, mandible; *mdt*, mandibular palp; mf', first, mf'', second maxillipede; p^1, p^4, first four swimming limbs.

in the proboscis, a middle portion forming the lateral wall of the proboscis, and a long, palp-like appendage provided with setae and projecting freely. This latter, the outer branch of the second antenna and the anterior pair of swimming appendages, are the most important locomotory organs of the larva. No trace could be found in the larva of the stylet-like maxillae which are contained within the adult proboscis. The two pairs of maxillipedes terminating in hooks (mf', mf'') serve for adhering organs. Of the four pairs of swimming limbs (p^1–p^4), only the anterior pair is free and movable, and somewhat resembles in shape a biramose Copepodan limb. The biramose rudiments of the three posterior swimming limbs are still unjointed and immovable.

During the course of metamorphosis, after several moults, the basal hook-like processes of the two pairs of antennae grow stronger; the exopodite of the second antenna and the palp of the mandible disappear, while the endopodite of the second antenna, losing its terminal hook, is transformed into a simple palp. The large sucking disc develops on the first maxillipede. The swimming limbs become biramose and are provided with setae, thus resembling the limbs of the Copepoda. In the two anterior pairs of these limbs the rudiments of the inner branches, known as the flagella, appear, while sexual differentiation is evident in the two posterior pairs, a characteristic transformation of the protopodite taking place in the male.

7. General Consideration regarding the Segmentation of the Body and the Metamorphoses of the Malacostraca.

In the Malacostraca the body consists of three primary regions, each of which, in all the divisions of this sub-class, contains a definite number of segments. In the anterior *cephalic region*, to which belong five pairs of limbs (the two pairs of antennae and the three pairs of jaws), there is, with few exceptions, no trace of a separation into distinct segments. In the *thoracic region*, which follows posteriorly and consists of eight limb-bearing segments, while the boundaries of the different segments are still more or less marked, only a slight power of movement between the individual segments is retained. But in the *abdominal region*, which consists of six limb-bearing segments and a terminal portion (telson), the full mobility of the separate segments is, as a rule, preserved, a fact connected with the development of the posterior end of the body into a swimming tail of great importance for the locomotion and the steering of the body.

The terga of the cephalic segments are thickened to form the carapace (dorsal shield); this, at its lateral and posterior margins, passes into an integumental fold which runs back over the thoracic region, and thus covers some or all of the thoracic segments dorsally. Only rarely do the terga of the thoracic segments covered by the dorsal shield retain any degree of independence (Stomatopoda, Fig. 141, p. 298, a few Schizopoda and *Nebalia*); in most cases the terga of the thoracic segments fuse closely with the integumental fold of the dorsal shield lying above them. A fusion of the cephalic and thoracic segments thus takes place, forming a common region of the body (*cephalo-thorax*). In one series of Malacostracan forms, however, the marginal fold of the dorsal shield has undergone degeneration (Arthrostraca); here, as a rule, only the anterior thoracic segment fuses with the cephalic region forming the small cephalo-thorax of this group, which is followed by seven free and movable thoracic segments.

The obliteration of the boundaries and consequent loss of movement between the segments of the cephalic and thoracic regions just mentioned has its effect on the condition of the limbs. Only in rare cases (*Nebalia*, *Euphausiidae*) do all the eight pairs of thoracic limbs agree more or less in structure. As a rule, one or more pairs belonging to the anterior part of the thorax enter into close relation with the mouth and become modified for the purpose of mastication. These are then distinguished as *maxillipedes*, while the succeeding thoracic limbs which serve for locomotion receive, in many groups, the name of ambulatory limbs. In the Arthrostraca, only the anterior pair of thoracic limbs is changed into a pair of maxillipedes, but in the Decapoda there are three pairs of maxillipedes, and in the Stomatopoda as many as five anterior pairs of thoracic limbs are thus transformed.

We must assume as the fundamental form of Malacostracan limb a biramose swimming limb with basal epipodial appendage, such as is retained as a thoracic limb in the Schizopoda. The shape of the thoracic limb in *Nebalia* (Fig. 91 *B*, p. 194) suggests to us that this form may perhaps have been developed from a more lamellate type of limb resembling that of the Phyllopoda. A two-jointed protopodite passes into a five-jointed endopodite, while the exopodite (flagellate branch), which often undergoes degeneration, frequently exhibits a large number of closely-crowded joints beset with setae.

If we compare the metamorphosis of most Entomostraca (especially that of the Phyllopoda) with that of the Malacostraca (p. 193), we find, in the first group, a more gradual transition through many moults from the *Nauplius* to the adult form, while in the Malacostraca the metamorphosis has attained a higher degree of specialisation, inasmuch as the separate stages appear more distinct from one another, and larval stages are intercalated which are not on the direct path of transition from the young to the adult form. These latter, by the development of secondary peculiarities, attain a certain independence and lead on to the adult condition only through further important changes in form. The metamorphosis of the lower Crustacea thus bears the same relationship to that of the Malacostraca as does incomplete to complete metamorphosis among the Insecta. As examples of these newly-introduced stages in the ontogenetic process, we must mention especially the *Zoaea* of the Decapoda and the *Zoaea*-like stage of the Schizopoda (*Calyptopis*) and the Stomatopoda, which are distinguished by the fact that although they possess the full number of body-segments, those of the middle region of the body are in a rudimentary condition. In this larva the posterior (five to seven) thoracic segments seem to be unusually backward in developing, and to have either no limbs or only very rudimentary ones, while the segments of the abdomen are already highly developed. The *Zoaea* is evidently a larval form secondarily changed by marked adaptation to a pelagic manner of life. From this standpoint it seems appropriate enough that the body retains a compressed form, that the most important locomotory organs (the maxillipedes and in some cases the antennae) are developed in the anterior region of the body, and that a posterior movable region (abdomen) develops early for swimming and steering purposes. The rudimentary condition of the middle region of the body thus appears to some extent explicable.

In regarding the *Zoaea* as a larval form secondarily intercalated in the course of development, which has attained a certain independent value and significance, special interest attaches to the development of the heart. Bearing in mind the condition of the heart in *Nebalia* and the Schizopoda, we should expect to find, in the larval forms of the Decapoda, a long tubular heart. We should also presuppose that the three pairs of ostia occurring in the Decapodan heart would already be found in the heart of the *Zoaea*. This, however, is not the case. The heart of the *Zoaea* is a short sac, recalling to some extent that of the Copepoda. It has only two pairs of lateral ostia (in individual cases, such as *Penaeus*, *Euphausia*, only one). The missing pairs of ostia only appear later. This proves clearly that the heart has undergone secondary modification corresponding to the requirements of the *Zoaea*. The phylogenetic stages in the development of the heart have been modified to suit the altered conditions of organisation of the *Zoaea* stage.

In the complete series of developmental stages of the Decapoda, which however is only retained in full in a very few cases, the following stages can usually be distinguished passing one into the other by a series of moults.

1. *The Nauplius stage* (Fig. 122 *A*, p. 267). This stage shows great agreement with the *Nauplius* of the Entomostraca in form and in the possession of the three typical pairs of limbs, the anterior limb (first antenna) being uniramose, but the two posterior limbs (second antenna and mandible) biramose. A free *Nauplius* stage is found in *Penaeus* and in *Euphausia*, among the Schizopoda.

2. *The Metanauplius stage* (Fig 117, p. 254, and Fig. 118, p. 258), in the form of the body, closely resembles the last stage, but shows, behind the Nauplius limbs which have shifted somewhat forward, the rudiments of four more pairs (in *Euphausia* only three). An integumental fold, which arises laterally and posteriorly, is the first rudiment of the dorsal shield. The posterior end of the body is marked by two short prominences bearing setae (furcal processes). The *Metanauplius* stage is the starting-point in the metamorphosis of *Lucifer.*

3. *The Protozoaea stage* (Fig. 119 *A*, *D*, p. 260, and Fig. 121 *A*, p. 264). The pairs of limbs which appeared as rudiments in the *Metanauplius* (first and second maxillae and second maxillipede) have now developed fully. The anterior region of the body is covered by the dorsal shield; posteriorly, the body passes into a narrower region combining the rudiments of the thorax and the abdomen, and already showing segmentation anteriorly, while the posterior (abdominal) region is not yet fully segmented. The antennae still possess the Nauplius character and function as oars, as also do the biramose maxillipedes. The mandibles have greatly altered; the basal joint is retained as a masticatory blade, while the distal part (palp) has disappeared. The *Protozoaea* stage occurs in the metamorphoses of the *Penaeidae* and *Sergestidae.* It is distinguished by the presence of distinct furcal processes. In individual cases (*Sergestes*) the third pair of maxillipedes may also be developed at this stage.

4. *The Zoaea stage* (Fig. 119 *E*, p. 260; Fig. 123 *C*, p. 269; Fig. 124, p. 272, and Fig. 136, p. 291). This stage agrees in all important characters with the preceding stage, from which it is distinguished by the distinct segmentation of the posterior or abdominal region. The sixth abdominal segment, it is true, often remains united with the telson for some time. The limbs of the *Zoaea* stage are the same as those of the preceding stage. In the more primitive Decapoda,

the antennae also serve as oars, while, in the *Zoaea* of the Brachyura, these limbs are kept in the background, and locomotion is carried on exclusively by the two pairs of biramose maxillipedes in conjunction with the movable abdomen. In many cases, the third pair of maxillipedes has already begun to function. The limbs which follow these may be present as sac-like, unjointed rudiments in close contact with the body, but they never function in the *Zoaea*. The pleopoda are still altogether wanting, except the sixth pair (uropoda), which may, in individual cases, develop as early as this stage. The spine-like process, which rises from the cephalo-thorax and occurs typically in the Brachyuran *Zoaea*, was formerly considered as a characteristic of this stage, and too great stress was laid upon this point. A really important characteristic of this stage, however, is the fact that the six posterior thoracic segments (commencing with that carrying the third pair of maxillipedes) are generally rudimentary and often difficult to recognise, while the abdominal segments are very apparent on account of their large size and distinct boundaries. The *Zoaea* stage indicates, in many Decapoda, the beginning of metamorphosis, many leaving the egg in this condition. The *Protozoaea* and *Zoaea*, in contrast to the *Metanauplius*, are distinguished by the gradual development of the paired stalked eye which, as in *Branchipus*, first arises as a lateral outgrowth of the cephalic region (*cf.* the *Zoaea* of *Lucifer*, Fig. 119 *E*, p. 260), the eye-stalk developing very gradually.

5. *The Mysis stage* (Fig. 120 *A*, p. 262, and Fig. 123 *D*, p. 269) and *Metazoaea stage* (Fig. 133 *B*, p. 287). By the development of the posterior thoracic limbs, the *Zoaea* passes into the *Mysis- or Schizopoda-like stage.* These limbs, which now begin to function, resemble the maxillipedes in being biramose swimming appendages provided with setae; they assist the maxillipedes in propelling the body, and recall the limbs of the Schizopoda. At this stage the pleopoda develop.

In the Brachyura and Anomura, the process of development seems to be simplified so far as the rudiments of the ambulatory limbs are concerned; these limbs, which are present in the late *Zoaea* stage, never resemble the Schizopodan limbs, but from the first are uniramose and pass direct into the adult form. An exopodite never develops on the rudiments of these limbs. Consequently, the *Zoaea* stage in these animals is followed by a stage in which the general form of the body resembles that of the *Zoaea*, but, in addition, the rudiments of the five pairs of ambulatory limbs are more or less developed, though still closely pressed against the body. This stage, which replaces the *Mysis* stage in the Anomura and Brachyura, has been called by CLAUS (No. 7) the *Metazoaea.*

6. *Last stages of metamorphosis.* These stages are now only distinguished from the adult form to which they lead by unimportant characteristics. In the *Sergestidae,* the loss of the exopodite on the thoracic limbs and the enlargement of the abdomen leads from the *Mysis* stage to the *Mastigopus stage* (Fig. 120 *C*, p. 262). In the *Penaeidae* and Caridea the corresponding stage is called the *first shrimp stage.* The last stages of metamorphosis in the Anomura and Brachyura are known as the *Megalopa* (Fig. 133 *A* and *B*, p. 287), the transition from this stage to the adult form involving considerably greater changes in the Brachyura than in the Anomura, because the latter remain throughout life at a stage of development nearer that of the *Megalopa.*

If we review the series of larval stages here described, we see that the order of development of the segments and limbs from before backward is as a rule retained. Only in details are there certain characteristic deviations from this order. For instance, the development of the thoracic segments in the *Zoaea* stage is usually retarded as compared with the development of the abdominal segments, and, among the limbs, an exception occurs in the early appearance of the sixth pair of pleopoda. These exceptions to the rule can be shown to result from the adaptation of the larva to a pelagic existence.

The whole series of ontogenetic stages described above is only passed through in very few cases in the Decapoda. *Penaeus* and *Lucifer* may serve as examples of such complete metamorphosis. As a rule, metamorphosis is more or less abbreviated, the early stages being obscured or hurried through within the egg. The *Sergestidae,* for instance, hatch at the *Protozoaea* stage, most of the Caridea at the *Zoaea* stage, the marine Astacidea at the *Mysis* stage. The most extreme case of abbreviated metamorphosis is found in many forms living in fresh water and on land (*Astacus*, *Telphusa*, and *Gecarcinus*).

The abbreviation of metamorphosis is also attained in another way, viz., by the tendency towards the obliteration of the characteristics of the special ontogenetic stages. Thus we shall see that, in the Caridea, the *Zoaea* stage appears altered by anticipating certain of the peculiarities of the *Mysis* stage. The complete disappearance of the *Mysis* stage in the metamorphosis of the Brachyura and Anomura can be explained in a similar way.

The series of ontogenetic stages described above refers to the Decapoda, but the Schizopoda (*Euphausiidae*) and the Stomatopoda are in this respect closely related to this order. The *Calyptopis* stage of the *Euphausiidae* might be assumed to be a *Protozoaea* or a *Zoaea* stage if it did not differ from the latter in the absence of the second pair of maxillipedes. In the metamorphosis of the Stomatopoda, on the other hand, we see that a suppression of the thoracic segments and the limbs belonging to them, similar to that in the Decapodan *Zoaea*, leads to larval forms which have been called the *Pseudozoaeae* of the Stomatopoda.

A second series of forms among the Malacostraca, however, including the Cumacea and the Arthrostraca, shows, in connection with the care of the brood which there prevails, an entire disappearance of metamorphosis. In these groups we have conditions related to those found in the *Mysidae* and Leptostraca. We do, indeed, find in the belated appearance of the last pairs of thoracic limbs in the Isopoda a last remains of that ontogenetic tendency which, in the Decapoda, led to the development of the *Zoaea* stage.

8. Leptostraca.

The Leptostraca (*Nebalia*), like the *Mysidae*, have no free-swimming larval stage. When the young animals leave the shell-cavity of the mother, which is used as a brood-chamber, they have in all essential points (Metschnikoff, No. 82) attained the final shape. Metamorphosis is therefore here, as in the *Mysidae*, confined to those stages which were passed through in the brood-cavity after the shedding of the egg-integument. With regard to the appearance of the different limbs, the order from before backward is retained. In this respect, and in the absence of a distinctly marked *Zoaea* stage, the Leptostraca nearly approach the Phyllopoda. The three pairs of Nauplius limbs appear first. There then follows a stage in which these three pairs of limbs have advanced in development, while behind them can be recognised four other pairs (two pairs of maxillae and the two anterior pairs of thoracic limbs). This stage thus shows, in the number of limb-rudiments, a certain agreement with the *Zoaea* form. At a later stage, the rudiment of a third pair of thoracic limbs can be made out. The embryo lies in the egg, curved in such a way that the ventral surface of the caudal region is in contact with the ventral surface of the anterior part of the body. The egg-integument then splits, and the larva, which is thus freed, but is still enveloped in the larval cuticle, and which shows the rudiments of all the thoracic limbs, not merely straightens out, but becomes even somewhat dorsally curved. We thus have, in *Nebalia*, a repetition of the changes with regard to the relative position of the body regions which we saw (p. 154) commencing in *Mysis*, but with the difference that, in the latter, the rupture of the egg-integument and the straightening of the body take place as early as the *Nauplius* stage, whereas here they occur at a later stage. The pleopoda now gradually appear in regular order from before backward, the body approaches the adult form, and the young leave the brood-cavity (Metschnikoff, No. 82).

9. Schizopoda.

A very primitive form of metamorphosis through many moults is retained among the Schizopoda by the *Euphausiidae.* The *Mysidae*, on the other hand, emerge from the Nauplius cuticle in a condition closely resembling the adult in form, and at this stage they leave the brood-pouch of the mother and swim about freely (p. 153).

The different larval stages of the *Euphausiidae*, none of which can be exactly identified with the *Protozoaea* and *Zoaea* of the Decapoda, were described by Dana as separate genera under the names of *Calyptopis*, *Furcilia*, and *Cyrtopia*, Claus (No. 97) being the first to prove that these forms belonged to the ontogeny of the *Euphausiidae.* The youngest stages were made known by Metschnikoff (Nos. 93 and 94), who established the important fact that the larva of *Euphausia* leaves the egg as a true *Nauplius.* The most important points in the later ontogenetic stages were made known to us chiefly by Claus (Nos. 91 and 8) for *Euphausia*, and more recently the process of development in various forms has been traced in greater detail by G. O. Sars (No. 95), Brook and Hoyle (No. 90).

The *Nauplius* of *Euphausia*, on leaving the egg, has an oval unsegmented body still without a shell-fold, and carrying on its anterior half the three pairs of typical Nauplius limbs. The anterior pair of these is uniramose, the two others biramose; their distal ends are beset with setae. A segmentation of the limbs is not yet distinctly evident. Only a very small oral aperture can be seen.

Later stages (Fig. 117 *A*) are distinguished by the development of three more limb-rudiments (two pairs of maxillae (*4* and *5*) and the first maxillipedes), and must therefore be regarded as *Metanauplius* stages. The three anterior pairs of limbs (*1*, *2*, *3*) have still the Nauplius character. We can recognise the rudiments of the Nauplius eye, the upper lip (*o*), the paired paragnatha (*u*), and a shield-like fold covering the lateral parts of the posterior limb-rudiments. The posterior end of the body, below the anal aperture which is now becoming more distinct, is lengthened into two rounded furcal processes fringed with setae. Later *Metanauplius* stages show a change in the third limb, which has entirely lost the form of a swimming appendage and has developed into a masticatory blade (mandible) with a greatly reduced palp. The shield-like fold has now developed in the anterior region of the body, and thus surrounds the cephalic portion of the larva (*cf.* the later stages, Fig. 117 *B* and *C*). In the posterior limbs, the first indication of

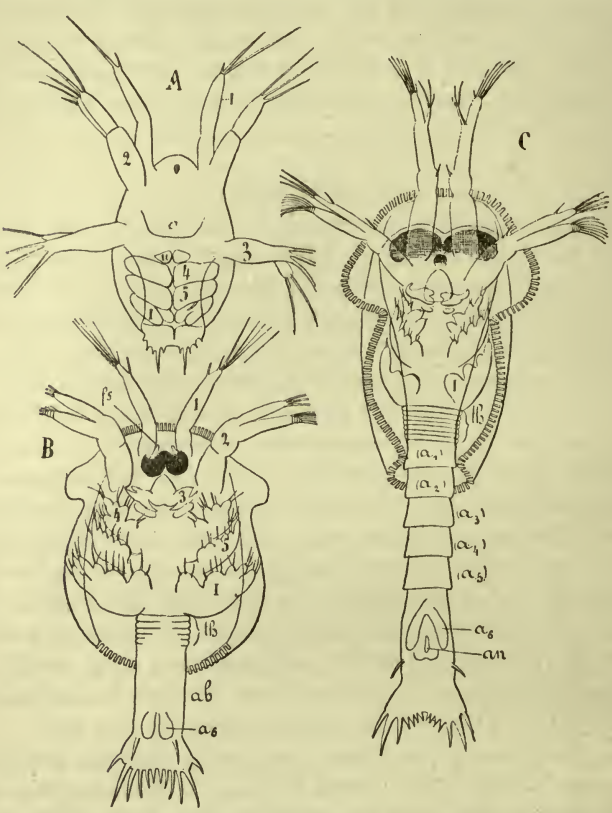

FIG. 117.—Three stages of development of *Euphausia* (from Lang's *Text-book*). *A*, *Metanauplius* (after Metschnikoff). *B*, *Calyptopis* (after Claus). *C*, older *Calyptopis* (after Claus). *1* and *2*, first and second antennae; *3*, mandible; *4*, *5*, first and second maxillae; *I*, first pair of maxillipedes; *ab*, abdomen; $(a_1–a_5)$ first five abdominal segments; a_6, sixth pair of pleopoda; *an*, anus; *fs*, frontal sensory organ; *o*, upper lip; *u*, paragnatha; *th*, thoracic segments.

the formation of lobes is evident, while, near the Nauplius eye, a paired frontal organ (*fs*) has developed, similar to that already described in the Phyllopod larva.

The *Metanauplius* gives rise through further moults to the series of *Calyptopis stages* (Fig. 117 *B* and *C*), which are characterised by the development of the six most anterior pairs of limbs, and of the long posterior (thoraco-abdominal) region of the body. The two pairs of antennae still retain essentially the Nauplius character, although they are now jointed. The first antenna now exhibits a three-jointed shaft, at the end of which two short processes (the rudiments of the future flagella) are inserted. In the second antenna, at the end of the exopodite which is covered with setae, a distinct segmentation into closely-crowded rings is evident. The two maxillae (*4*, *5*) and the first maxillipede (*I*) appear as richly-lobed appendages, showing in their form considerable agreement with the Phyllopodan limbs. The first maxilla (*4*), besides its two masticatory blades and its endopodite, shows a short truncated portion bearing setae (exopodite), the rudiment of the future fan-like plate. In the second maxilla (*5*) the exopodite is in quite a rudimentary condition, while, on the inner side of the protopodite, four masticatory processes have developed. The first maxillipede (*I*) has the character of a biramose swimming limb (especially in *Nyctiphanes*). At the beginning of the thoraco-abdomen, which lies behind these appendages, the closely-crowded rudiments of the other thoracic segments can already be distinctly seen (Fig. 117 *B*, *th*), while the abdomen (*ab*) still appears unsegmented. The posterior end of the abdomen has already been transformed into the middle plate of the caudal fin, and is beset with strong spines along its posterior edge. In front of the anal aperture the first rudiments of the lateral parts of the caudal fin (sixth pair of pleopoda, a_6) can be recognised. The cephalo-thoracic shield, which covers the anterior part of the body, has undergone great development. In *Euphausia* it is distinguished by the presence of an unpaired dorsal spine directed backwards, by the delicate dentation of its edges, and by a notch in its ventral margin which recalls the excavation in the edges of the shell in *Cypridina* and *Halocypris*. In other genera (*Nyctiphanes*) the shell has no dorsal spine and the margins are not toothed; there are also only very indistinct lateral notches in the margin of the shell. The internal organs, which should be noticed at this stage, are the gradually developing paired rudiments of the eye, the hepatic outgrowths of the alimentary canal, and the short sac-like heart which is continuous with a well-developed arterial system, and is provided with one pair of venous ostia.

Later Calyptopis stages (Fig. 117 *C*) are distinguished from those just described by the more distinct development of the rudiments of the eyes which are still hidden under the dorsal carapace, and by the full segmentation of the body. Not only is the thorax (*th*) divided into seven (short) segments, but the abdomen also (a_1–a_6) appears fully segmented In the last of these stages, the sixth pair of pleopoda (a_6) are developed as freely projecting lateral wings of the caudal fin.

If we compare the series of *Calyptopis* stages with the other stages of Malacostracan larvae, we must class the younger *Calyptopis* stage with the *Protozoaea*, the older with the *Zoaea*. The *Calyptopis* stages, however, differ from these in the absence of the second pair of maxillipedes which have not yet developed.

The later stages, known as the *Furcilia stages*, are characterised above all by the complete development of the stalked eye which is now movable, and which from this time onwards is not covered by the forward extension of the dorsal shield, but projects freely through an indentation at its edge. A corresponding change is found in the part of the cephalic shield lying between the eyes, which is gradually transformed into a frontal plate running out into a point to form a rostrum. While the six anterior pairs of limbs still retain for the time the shape seen in the *Calyptopis* stage, the missing posterior limbs are developed, the first *Furcilia* stage showing the rudiments of the second pair of maxillipedes and of the first pair of abdominal limbs. The other abdominal limbs develop very soon, while the third maxillipede and the ambulatory thoracic limbs, as well as the branchial rudiments belonging to them, appear more gradually in order from before backward. At the same time, in *Euphausia*, the rudiments of the eye-like luminous organs at the bases of the limbs develop.

The most characteristic feature of the *Cyrtopia stage* is the change in the shape of the antennae, which from this time are no longer used as oars, but approach the adult form. The two flagellate branches of the first antenna have lengthened considerably and have become segmented into many rings. In the second antenna, the transformation of the endopodite into the flagellum, and of the exopodite into a scale, are noticeable. Through the completion of the number of limb-rudiments and the development of the last thoracic limbs, the *Cyrtopia* larva passes gradually into the adult form.

The *Mysidae*, ike *Nebalia*, only undergo metamorphosis within the brood-cavity of the mother, the young which leave that cavity already showing the form of the adult. We have mentioned above (p. 154) that the egg-integument in *Mysis* is shed at the *Nauplius* stage. The larva, which is then enveloped in the Nauplius cuticle alone, is essentially embryonic in character. It is maggot-shaped and can move but little, the limbs are soft and have no fringe of setae. The larval cuticle, beneath which the remaining limbs develop, is distinguished, in *Mysis vulgaris* and *M. flexuosa*, by the fact that, at its posterior end, it runs out into two setose furcal processes. The next ten pairs of limbs (two pairs of maxillae and eight pairs of thoracic limbs) appear simultaneously. The first of the pleopoda to appear is the sixth pair which enters into the formation of the caudal fin (Fig. 77 *E*, p. 153); the five anterior pairs grow out only after the shedding of the Nauplius cuticle (P. J. and E. Van Beneden, Nusbaum).

The course of development in the *Lophogastridae* seems to be in complete agreement with that in the *Mysidae*. Sars, at least, has figured an ontogenetic stage of *Lophogaster*, which completely resembles a late larval stage of *Mysis*, the only distinction being that, in the former, all the pairs of pleopoda are already present; these limbs perhaps appearing somewhat earlier in *Lophogaster* than in *Mysis*.

The development of the *Mysidae* and the *Lophogastridae* may in a general way be described as essentially abbreviated in comparison with that of the *Euphausiidae*. In this respect, as well as in the inner ontogenetic processes, the *Mysidae* and *Lophogastridae* approach the Cumacea and the Arthrostraca.

10. Decapoda.

A. Sergestidae.*

Among the Decapoda, the *Sergestidae* and the *Penaeidae* are distinguished by the primitive conditions recalled by their metamorphoses, which begin with a very simple stage (*Nauplius* or *Metanauplius*), and also by the regular order of appearance (from before backward) retained by the body-segments.

In the family of the *Sergestidae*, the metamorphosis of the genus *Lucifer* has been specially accurately observed. The *Protozoaea* of this ontogenetic series was called by Dana *Ericthina demissa*; Claus (No. 8) afterwards found the *Zoaea* stage belonging to it, but Willemoes-Suhm (No. 157) first established its connection with the development of *Lucifer*, while Brooks (No. 109) observed the complete course of metamorphosis, from the hatching of the egg to the attainment of the adult form. His observations have been found to agree with those made on the Challenger material by Spence Bate (No. 100) and Willemoes-Suhm.

The actual *Nauplius* stage is passed through in the egg; the young *Lucifer* larva hatches at a stage which we must describe as a *Metanauplius* (Fig. 118 *A*). On the short oval body we can recognise the

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* [The *Sergestidae* and *Penaeidae* form the tribe Penaeidea comparable to the Caridea, etc.—Ed.]

Nauplius eye, the projecting upper lip (*ol*), and a few furcal setae, indicating its posterior end. There is as yet no trace of a shield-like fold. In the anterior region of the body, the three pairs of Nauplius limbs (*a'*, *a''*, *md*) are inserted. Of these, the first (*a'*) is uniramose; it consists of five joints and carries swimming setae at its end. The second antenna (*a''*) has a two-jointed protopodite and two swimming rami; when this appendage is compared with that of other forms, we are inclined, in opposition to BROOKS, to regard the ramus, which has several joints and is provided with setae, as the exopodite and the simpler, unjointed branch as the endopodite. The third pair of limbs (mandibles) resembles the second in structure, but is smaller and less jointed. It has an unsegmented protopodite, a single-jointed endopodite, and an exopodite consisting of three joints, both rami carry a few swimming setae. Following these posteriorly are four pairs of swellings, which represent the rudiments of the two pairs of maxillae (*mx'*, *mx''*) and the first and second pairs of maxillipedes. Later *Metanauplius* stages (Fig. 118 *B*), in which the Nauplius limbs show a slight degeneration, have at the sides of the body the rudiment of a shield-like fold (*d*), and besides this, on the basal joint of the mandible, a stiff masticatory process.

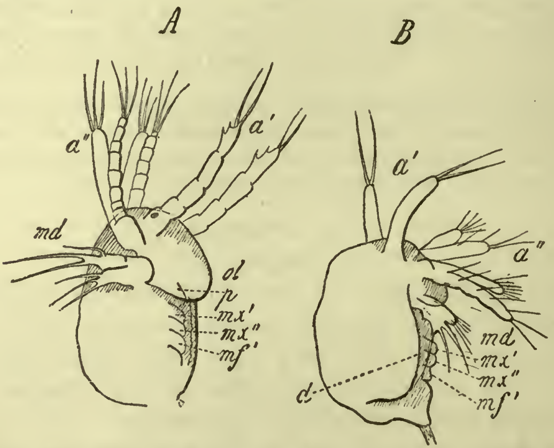

FIG. 118.—Two *Metanauplius* stages of *Lucifer* (after BROOKS). *A*, larva just hatched. *B*, somewhat older stage. *a'*, first antenna; *a''*, second antenna; *d*, shell-fold; *md*, mandible; *mx*, first maxilla; *mx'*, second maxilla; *mf'*, first maxillipede: *ol*, upper lip; *p*, paragnatha.

The *Protozoaea* stages which now follow show the seven anterior pairs of limbs characteristic of the Zoaea stage completely developed and functional. The anterior part of the body is covered by a dorsal shield which is continued anteriorly above the Nauplius eye into a long rostrum (*r*); this carries on its posterior margin one unpaired dorsal and two somewhat longer lateral spines. The posterior region of the body has developed into a large thoraco-abdomen, the most posterior end of which is transformed into the middle plate (telson) of the caudal fin, and is provided with strong spines. Behind the second maxillipede, four more segments have become distinct—that carrying the third pair of maxillipedes (Fig. 119 *A*, mp''') and those carrying the three anterior pairs of ambulatory limbs (t^1–t^3). The heart (*h*) and the hepatic outgrowths of the intestinal canal (*l*) have developed. The first antenna (a') now consists of two joints only, a long basal and a short terminal joint beset with setae; the second antenna (a'') has essentially the same shape as in the preceding stage; it has an exopodite of several joints beset with many setae and a simpler endopodite; it still functions as the chief locomotory organ of the larva. The mandible (Fig. 119 *D*, *md*) now consists exclusively of a masticatory blade toothed along its inner edge. All trace of the palp found on the mandible at earlier stages is now lost. The two pairs of maxillae already foreshadow their adult form. The first maxilla (Fig. 119 *B*) shows, on the inner side of the protopodite, two projecting masticatory blades, a short, two-jointed endopodite, and a truncated exopodite beset with feathered setae. The second maxilla (Fig. 119 *C*) is principally distinguished by the large number of masticatory processes borne on its inner border. The two pairs of maxillipedes (Fig. 119 *D*, mf', mf'') are shaped like biramose swimming limbs with long endopodites composed of several joints and short, unjointed exopodites. In the maxillary region a shell-gland is seen developing.

Later Protozoaea stages (Fig. 119 *D*), which correspond to Dana's *Erichthina demissa*, are distinguished by the commencing development of the paired eyes (*o*), as well as by the further advance of segmentation in the thoraco-abdomen. At the antero-lateral margin of the dorsal shield a swelling becomes apparent, within which an accumulation of pigment denotes the rudiment of the paired eye. Among the new segments that have appeared in the posterior region of the body are those carrying the fourth ambulatory limbs (t^4) and the four anterior abdominal segments (*1–4*). The last thoracic segment (that carrying the fifth pair of ambulatory limbs) never attains distinct development in *Lucifer*. The abdomen is not yet segmented.

The next stage (Fig. 119 *E*) is marked by the complete segmentation of the abdomen, and must therefore be called a *Zoaea* stage.

The completely developed limbs are the same as those of the *Protozoaea* stage, but behind these we find that the third maxillipede (mf''') and the four anterior ambulatory limbs (th^1-th^4) have appeared as small biramose rudiments. Besides these, rudiments of

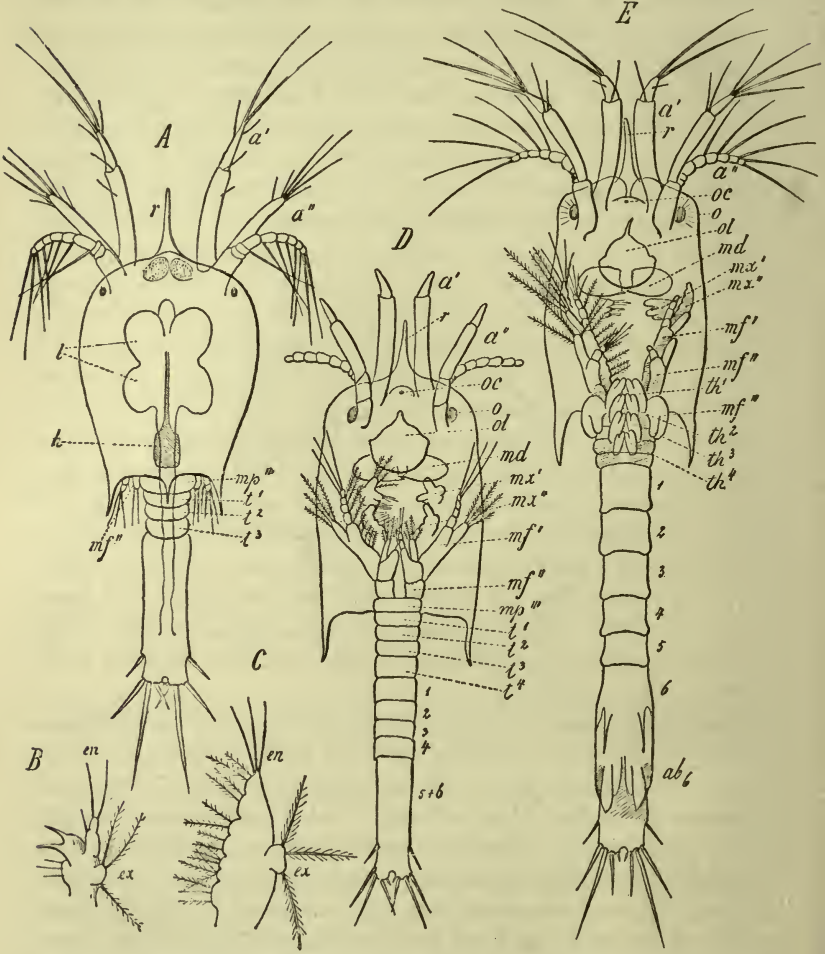

FIG. 119.—*Protozoaeae* and *Zoaea* of *Lucifer* (after BROOKS). *A*, first *Protozoaea* stage. *B*, first maxilla of the same. *C*, second maxilla of the same. *D*, later *Protozoaea* stage (*Erichthina*). *E*, *Zoaea* stage. a', first antenna; a'', second antenna; ab_6, sixth pair of pleopoda (lateral portions of the caudal fin); *en*, endopodite; *ex*, exopodite; *h*, heart; *l*, hepatic outgrowths; *md*, mandible; mf', first maxillipede; mf'', second maxillipede; mf''', third maxillipede; *mp*, protopodite of the third pair of maxillipedes; mx', first maxilla; mx'', second maxilla; *o*, paired compound eye; *oc*, Nauplius eye; *ol*, upper lip; *r*, rostrum; th^1-th^4, rudiments of the first four pairs of ambulatory limbs; t^1-t^4, the four segments carrying ambulatory limbs; *1-6*, the six abdominal segments.

the lateral portions of the caudal fin (sixth pair of pleopoda) have now appeared.

The next moult of the larva produces a very decided change in the external shape of the body. The larva now passes into the so-called *Mysis* or *Schizopod*-like stage (Fig. 120 *A*), which was described by DANA under the name of *Sceletina armata.* The antennae have lost their locomotory functions and tend to assume their adult form; the paired eyes (*o*) have become movable and stalked, and the Nauplius eye (*oc*) is still retained. The seven pairs of biramose swimming limbs (viz., the three pairs of maxillipedes and the four anterior pairs of ambulatory limbs) function as locomotory organs. The larva, from this time onward, ceases to progress in a jerking manner, as in the preceding stage, and swims evenly and swiftly. The dorsal shield has still the same general shape, but, in its anterior part, the stalked eyes have become cut off from it. The indentation of the shield which contains these latter is marked by a pair of antero-lateral spines, while the spines at the posterior margin of the shield have disappeared. The cephalo-thoracic shield remains short in comparison with the abdomen which, in the next stages, increases still more in length. In the abdomen, we can recognise six perfectly distinct segments and the caudal fin, consisting of the telson and the greatly enlarged sixth pair of pleopoda (ab_6).

The first antenna (a') now consists of a two- (later three-) jointed protopodite and a short terminal joint which is to be considered as the representative of the flagellum and is richly provided with feathered setae. The second antenna (a'') is a reduced biramose limb almost without setae. In the later *Mysis* stages this appendage makes a fresh growth, its endopodite being transformed into the flagellum and its exopodite into the scale-like appendage. The mandibles (*md*) are simple masticatory blades without palps. The maxillae (mx', mx'') have essentially the same form as in the preceding stages. This is also the case with the first pair of maxillipedes (mf'), the segmentation of which is somewhat less distinct than in the preceding stages. The six pairs of swimming limbs which follow (second and third maxillipedes and first four pairs of ambulatory limbs) are biramose and very similar in form. Each limb consists of a two-jointed protopodite, a long, four-jointed endopodite, and a shorter exopodite which is, however, indistinctly divided into numerous joints. An ample provision of setae enables these limbs to act as powerful swimming organs.

Later Mysis stages (Fig. 120 *B*), which are principally distin-

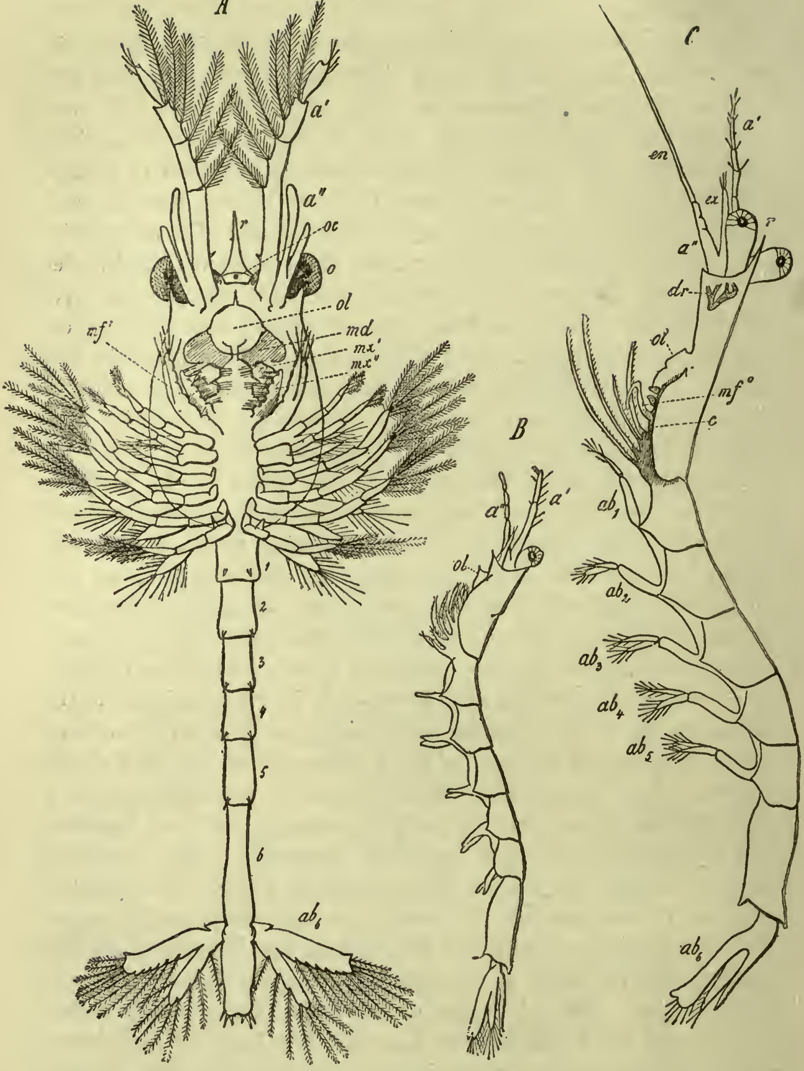

FIG. 120.—Three later larval stages of *Lucifer* (after BROOKS). *A*, younger *Mysis*- or *Schizopod*-like stage. *B*, older *Mysis*- or *Schizopod*-like stage less highly magnified. *C*, *Mastigopus* stage. *a'*, first antenna; *a''*, second antenna; ab_1–ab_6, the six pleopoda; *c*, cephalo-thoracic shield; *dr*, antennal gland; *en*, flagellum, and *ex*, scale of the second antenna; *md*, mandible; *mf'*, first maxillipede; *mf''*, second maxillipede; *mx'*, first maxilla; *mx''*, second maxilla; *o*, compound eye; *oc*, Nauplius eye; *ol*, upper lip; *r*, rostrum; *1–6*, six abdominal segments.

guished by the segmentation of the second antenna and the great development of the abdomen, show, on the five anterior abdominal segments, the bud-like rudiments of the pleopoda.

The transition from the *Mysis* stages to the adult form takes place through the *Mastigopus* stage (Fig. 120 *C*), which in length of body already approaches the adult *Lucifer*, but is distinguished from the latter by the absence of the neck-like prolongation of the cephalo-thorax. This stage is marked by the shortness of the flagellum of the first antenna (*a′*), while the flagellate appendage of the second antenna (*en*) has considerably lengthened. The mouth-parts and the thoracic limbs have attained their final condition. The mandible has no palp, the first maxilla has lost the exopodite, the latter portion of the second maxilla is transformed into a large, fan-like plate. The first maxillipede is changed into a short, two-jointed appendage; the second maxillipede (*mf″*) has, like all the other thoracic limbs, lost its exopodite and has lengthened out and become geniculate. The third maxillipede and the three anterior pairs of ambulatory limbs form a row of short, simple appendages covered with setae. The fourth pair of ambulatory limbs has entirely disappeared. The first pleopod (ab_1) is uniramose, while the four following pleopoda (*2–5*) have the usual biramose form. The Nauplius eye and the shell-gland have now disappeared; on the other hand, the antennal gland (*dr*), which opens on the base of the second antenna, can be recognised as a coiled canal.

The adult form, as contrasted with the *Mastigopus* stage, is characterised by the lengthening of the flagellum of the first antenna, in the basal joint of which the auditory organ develops, as well as by the neck-like prolongation of the head. The flagellum on the second antenna has also undergone considerable elongation. The sexual differentiation now develops, the male being distinguished by accessory structures on the first and second pairs of pleopoda, by spines on the ventral side of the fifth abdominal segment, as well as by certain differences in the caudal fin, while the female has in these respects retained the characters of the larval form.

The development of *Lucifer* just described is, in all essential points, repeated in the metamorphosis of *Sergestes*, although the two larvae are somewhat unlike in outward appearance. The *Zoaea* of *Sergestes*, which is remarkable for the dorso-ventral flattening of its body and its extraordinarily large, branched, spinous processes, was described by DANA under the name of *Elaphocaris*, the later stages already being known as *Acanthosoma* (CLAUS, No. 91) and *Mastigopus* (LEUCKART, CLAUS, No. 91). CLAUS and WILLEMOES-SUHM simultaneously proved that these forms belonged to the ontogeny of *Sergestes*, and discovered the *Protozoaea* stage of this genus. More recently, many larval forms belonging to this series have been described from the Challenger material (SPENCE BATE, No. 100).

The youngest Protozoaea of *Sergestes* is only known from a drawing by WILLEMOES-SUHM (No. 100, p. 354). It possesses the seven anterior pairs of limbs, but the third pair of maxillipedes has not yet developed. Only the first rudiments of the paired eyes can be made out. Within the alimentary canal a large amount of yolk remains, and this no doubt allows the larva to leave the egg at this stage. In all other respects the larva drawn by WILLEMOES-SUHM agrees with the youngest stage described by CLAUS (Fig. 121 *A*).

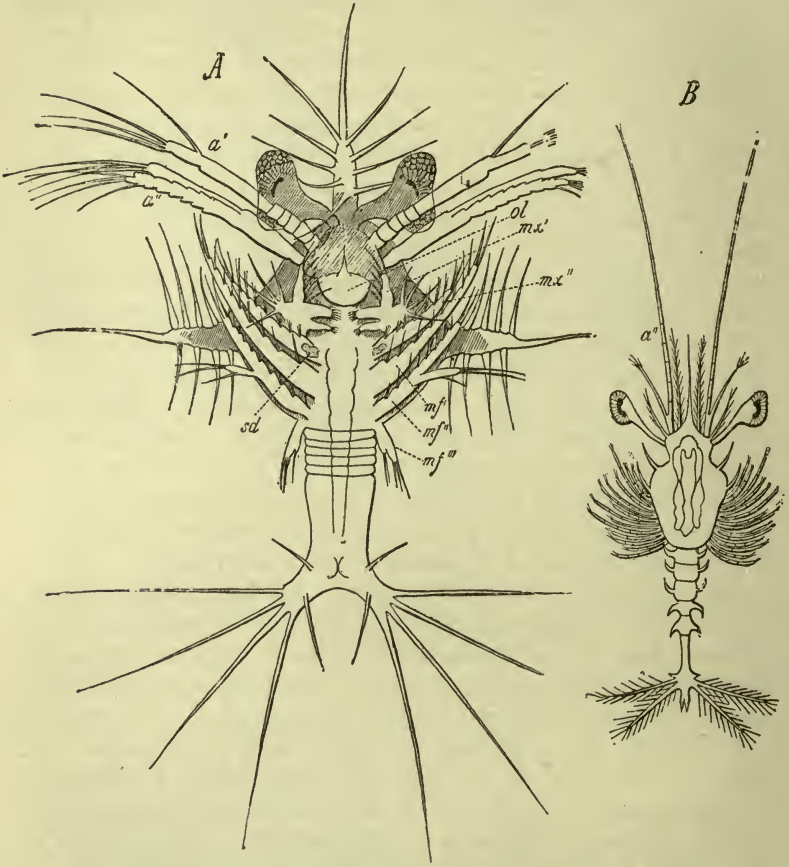

FIG. 121.—Two larval stages of *Sergestes* (after CLAUS). *A*, *Protozoaea* stage. *B*, *Acanthosoma* stage, seen from the dorsal side. *a'*, first antenna; *a''*, second antenna; *mf'*, first maxillipede; *mf''*, second maxillipede; *mf'''*, third maxillipede; *mx'*, first maxilla; *mx''*, second maxilla; *ol*, upper lip; *sd*, shell-gland.

This latter (Fig. 121 *A*) can be compared in all its essentials with the later

Protozoaea stage of *Lucifer*, from which, however, it is distinguished by the compact form of its body, the early development of the stalked eyes, and the appearance of the third pair of maxillipedes (mf'''). The seven anterior pairs of limbs agree very closely in structure with those of the *Protozoaea* stage of both *Lucifer* and *Penaeus*. The first antenna (a') especially shows a segmentation of the base into five joints which recurs in *Penaeus*. The mandibles have no palps, the first maxilla (mx') has its exopodite developed as a fan-like plate, such an exopodite again being found on the long leg-like second maxilla (mx''). At the base of the latter, CLAUS found the coiled shell-gland (sd). The three pairs of maxillipedes (mf'–mf'') are biramose limbs, the third pair, however, being somewhat small. Behind these are found the five narrow segments which later carry the ambulatory limbs, while the abdomen still appears altogether unsegmented. The latter terminates in a plate which runs out into prongs, and is here much more marked than in *Lucifer*. This terminal part seems to find its homologue in the anal segment of the Phyllopoda with its two furcal processes. A marked feature of this stage is the great development of the movable stalked eyes and the development of protective processes on the broadened dorsal shield. There are here one anterior rostral spine starting from a broad base, one dorsal and two lateral spines, each of which appears branched through the formation of secondary processes. These spines no doubt correspond to the much shorter ones of the *Lucifer* larva, with which they agree in position.

The *Zoaea* which emerges from the stage just described (*Elaphocaris*) is still more abundantly armed with spines. The frontal, dorsal, and lateral spines have greatly increased in size. The frontal spine has become comparatively slender, and a pair of branched antero-lateral spines have developed on its base. The separate segments of the abdomen also, which are now distinct (except that the sixth segment is still indistinguishable from the forked telson), are also well armed with lateral spines. While the anterior limbs, including the three pairs of maxillipedes, have the same character as in the former stage, only the rudiments of the biramose limbs are to be recognised on the five following thoracic segments. The sixth pair of pleopoda has also appeared.

In the transition to the *Mysis stage* (*Acanthosoma*, Fig. 121 *B*) the complicated armature of the dorsal shield is lost, only the basal portions of the branched processes found in the *Elaphocaris* being retained as short spines, but the spines on the abdomen are still retained. The furcal processes of the telson are also reduced to two short spines projecting backwards. Significant changes are found in the development of the limbs. The first antenna in younger *Acanthosoma* has a long, still unjointed protopodite (provided with a basal toothed process) and two short terminal processes which appear to be the rudiments of the principal and accessory flagella of later stages. In the second antenna (a'') the formerly many-jointed exopodite is transformed into a rod-like appendage, while the endopodite has developed into a long flagellum. The two pairs of maxillae still show the character described for the earlier stage. The anterior maxillipede is remarkable for the reduction of its exopodite; but the seven following pairs of limbs (the two remaining maxillipedes and the limbs which have developed from the five rudiments on the thoracic segments) are changed into conspicuous biramose limbs in which the exopodite, richly clothed with setae, is specially apparent. The limbs of the abdomen are short rudiments, except those of the sixth segment which, on the contrary, are well developed as the long lateral divisions of the caudal fin, and are provided with setae. Later

Acanthosoma stages are noteworthy on account of the development of the auditory vesicle at the base of the first antenna and the further growth of the rudiments of the pleopoda.

The *Mastigopus* form which develops from the *Acanthosoma* is very like that of *Lucifer.* Here also we find great development of the abdomen as opposed to relatively small size of the cephalo-thorax. The armature of spines, with the exception of the persistent rostrum, is reduced to small vestiges. The exopodites are lost on the thoracic limbs (maxillipedes and ambulatory limbs), and the last pair of these limbs have altogether disappeared. The pleopoda are now greatly developed, but still have no exopodites; these, however, are evident as buds on the two posterior pairs, but only attain functional development at a later stage.

The changes by which the *Mastigopus* passes into the adult form chiefly affect the limbs (above all the mouth-parts), which now approach the adult form; the mandibular palp, for instance, grows out, the two last pairs of thoracic limbs reappear, and the gills develop. The developing mandibular palp remains two-jointed in *Sergestes;* the anterior maxilla in the later *Mastigopus* stages still shows a short rudiment of the palp. In the posterior maxilla, on the contrary, the exopodite is transformed into a large, fan-like plate. In the anterior maxillipede, the exopodite and endopodite are short appendages, while a large, plate-like, masticatory blade has developed on the protopodite. The second maxillipede is short and geniculate, while the third has retained the form of a long limb. Even in early stages, the rudiments of the pincers are recognisable on the second and third ambulatory limbs. The loss of the Nauplius eye and the shell-gland, and the development, on the other hand, of the antennal gland are noticeable features in the internal anatomy.

In the absence of gills and of the two posterior pairs of thoracic limbs, *Lucifer* shows features which are present in *Sergestes* at the *Mastigopus* stage. *Lucifer* has thus retained certain larval characteristics.

The many larval stages of *Sergestes* found among the Challenger material agree in the most essential points with the stages above described, but show great variability in the armature of the cephalo-thorax and abdomen. The Sergestid *Zoaea* called *Platysaccus crenatus* is interesting; its dorsal shield, which is rounded and provided with marginal spinous lobes, leaves the four posterior thoracic segments (already provided with limbs) completely uncovered, a feature in which this form agrees with the *Penaeus* and *Lucifer* larvae. Some larvae of the *Mysis* and *Mastigopus* stage called *Sciocaris telsonis* are remarkable for the shape of the telson, which has segmented furcal processes.

The contrasts in outward appearance presented by the short, broad, and spiniferous larva of *Sergestes* and the slender larval form of *Lucifer* are brought about by a series of ontogenetic stages, which Brooks (No. 109) has traced back to a meeting point in the genus *Acetes.* These larvae are more compact than the *Lucifer* larva, and are also somewhat better supplied with spines. Brooks is inclined to refer to this series a *Protozoaea* larva described by Dohrn (No. 121, "Larva of an unknown Crustacean," Plates 29 and 30, Figs. 62–67) and Claus (No. 8, "Phyllopoda-like *Protozoaea* of unknown ancestry," Plate 4, Figs. 2–7). The latter larva is principally characterised by the great development of the still unstalked lateral eyes, which, as in *Lucifer*, cause a buckle-shaped projection of the dorsal carapace. With respect to the condition of the stalked eye, which is already very highly developed in the *Protozoaea* of *Sergestes*, this larva holds a position intermediate between the latter and *Lucifer.*

B. Penaeidae.

Our knowledge of the metamorphosis of *Penaeus* is due mainly to the researches of F. Müller (Nos. 141 and 142). It is of great significance in forming an estimate of the Decapodan metamorphosis, on account of the presence of the *Nauplius* stage, as well as the primitive order retained in the development of the segments and limbs. Claus (No. 8) has since added further details, especially with regard to the *Protozoaea* stage. More recent investigations have been made by Brooks (No. 110), who was able to observe the origin of all the stages following the first *Protozoaea* in specimens cultivated by him. A series of larval forms chiefly belonging to later stages are described by Spence Bate, who utilised the observations of Willemoes-Suhm (No. 100).

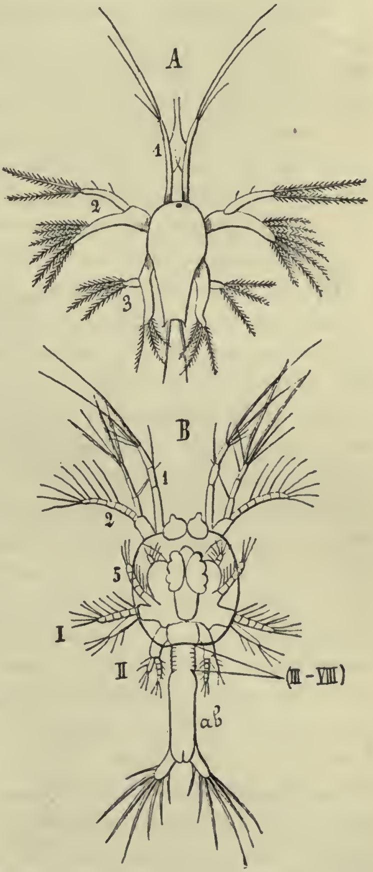

Fig. 122.—Two stages of development of *Penaeus* (after F. Müller, from Lang's *Text-book*). *A*, *Nauplius*. *B*, *Protozoaea*. *1*, first, *2*, second antenna; *3*, mandible; *5*, second maxilla; *I*, first, *II*, second maxillipede; (*III–VIII*), rudiments of the third to eighth thoracic segment; *ab*, abdomen.

Penaeus, like the *Euphausidae*, leaves the egg as a true *Nauplius* (Fig. 122 *A*). The long, pear-shaped body is still without a shell-fold, and terminates posteriorly in two long, furcal setae. At the anterior end of the body, the Nauplius eye is visible. The three typical pairs of Nauplius limbs are still unjointed, and are provided with swimming setae.

The succeeding *Metanauplius* stage, in outward appearance, still greatly resembles the *Nauplius*, but is distinguished from the latter by the appearance of a transverse dorsal integumental fold (rudiment of the dorsal shield) and two truncated processes provided with setae at the posterior end of the body (furcal processes). This stage greatly resembles the *Metanauplius* of *Lucifer* (Fig. 118 *B*, p. 258). Like the latter, it possesses a massive, helmet-shaped upper lip. The three pairs of Nauplius limbs appear shifted somewhat forward, and four pairs of bud-like limb-rudiments have arisen. The third Nauplius limb shows an important alteration, a thickening of its basal portion being evident as the rudiment of the masticatory blade of the future mandible, while, from the two swimming rami, the living contents have been withdrawn, an indication that these parts will be cast off in the next moult. Near the eye, the paired frontal organ (Fig. 122 *B*), which also occurs in the Zoaean series, can be recognised as a small, conical projection.

The next stage observed is the *Protozoaea* (Fig. 122 *B*), with well-developed, more or less rounded, cephalo-thoracic shield, seven pairs of limbs and an unsegmented abdomen (*ab*) terminating in distinct furcal processes. The antennae are still locomotory organs. The first antenna (*1*) is divided up into four joints. On the posterior antenna (*2*) a three-jointed endopodite and a four-jointed exopodite can be recognised. The upper lip is helmet-shaped and marked by a spine which points forward, this is also found in the larvae of the *Sergestidae*. The mandibles are now palpless, toothed, masticatory blades. The maxillae agree to a great extent in shape with those figured for *Lucifer* (Fig. 119 *B* and *C*, p. 260). In the first maxilla, two inwardly projecting cutting blades can be recognised on the protopodite, there is a jointed endopodite and a leaf-like exopodite provided with setae. The second maxilla resembles the first in shape, but has four blades on the protopodite and a somewhat longer endopodite. The two anterior pairs of maxillipedes (*I*, *II*) are developed as biramose swimming limbs. At the base of the succeeding (thoraco-abdominal) region of the body, transverse rings mark a division into six segments (those bearing the third maxillipede and the five ambulatory limbs, *III–VIII*). The position of the anal aperture is worthy of mention; it is, at this stage, exactly terminal, lying between the two furcal processes, and only later shifts to the ventral side of the telson. The presence of three pairs of hepatic outgrowths from the intestine is already evident. The heart, which is situated at the anterior extremity of the thoraco-abdomen, has only one pair of ostia (?). At the anterior margin of the cephalo-thorax, the rudiments of the paired eyes are visible as swellings in close contact with the frontal organ.

Later Protozoaea forms (Fig. 123 *A*) which Claus (No. 8) observed are chiefly characterised by the development of five abdominal segments (a_1–a_5) still hidden under the larval cuticle, they also show a greater development of the paired eyes and the division of the protopodite of the first antenna (*1*) into five joints (a feature which recurs in the *Protozoaea* of *Sergestes*). The sixth abdominal segment is still fused with the telson. Besides the rudiments of limbs already mentioned, the truncated rudiment of the third maxillipede (*III*) can now be seen.

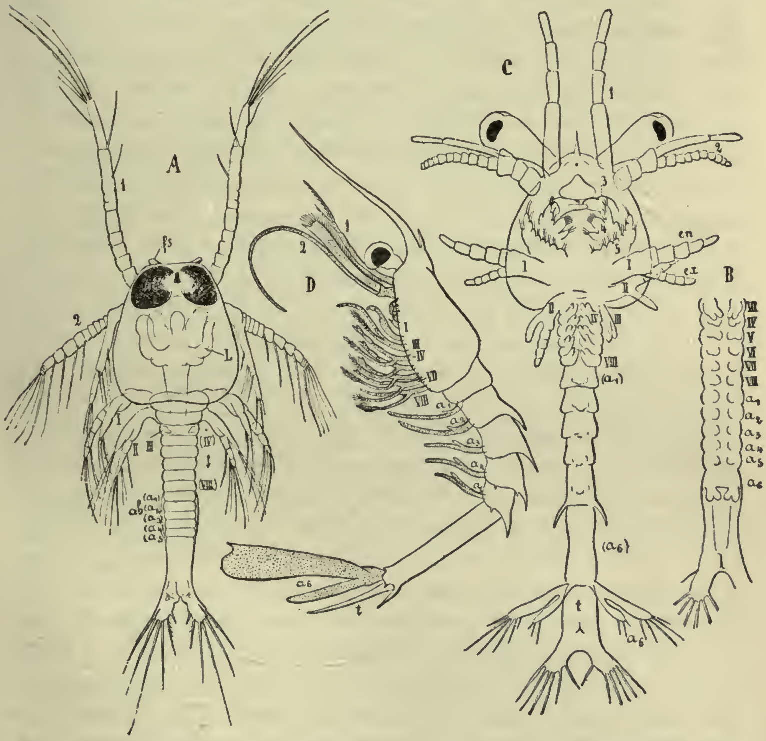

Fig. 123.—Later larval stages of *Penaeus* (after Claus, from Lang's *Text-book*). *A*, older *Protozoaea*, dorsal aspect. *B*, thoraco-abdominal region of a somewhat older larva with rudiments of limbs, ventral aspect. *C*, *Zoaea*, ventral aspect. *D*, *Mysis* stage, lateral aspect. *1*, *2*, first and second antennae; *3*, mandible; *4*, *5*, first and second maxillae; *I*, *II*, *III*, first three maxillipedes; *IV–VIII*, first five ambulatory limbs; (*IV–VIII*), five posterior thoracic segments; (a_1–a_6), the six abdominal segments; a_1–a_6, the six pleopoda; *ab*, abdomen; *en*, endopodite; *ex*, exopodite; *fr*, frontal sensory organ; *L*, liver; *t*, telson.

The *Zoaea* which proceeds from the above (Fig. 123 *B* and *C*) is marked by the development of the movable stalked eyes, and of a frontal spine found between these organs, as well as by that of the thoracic limbs. The abdominal segments now increase greatly in size, so that they are soon longer than those of the thorax. The third pair of maxillipedes can now be recognised as a short biramose limb (Fig. 123 *B*, *III*). Behind this, the rudiments of the ambulatory limbs (*IV–VIII*) are just visible, and still slighter prominences indicate the limb-rudiments on the five anterior abdominal segments. It is thus evident that, in *Penaeus*, the limbs have retained the order of development from before backwards. An exception to this order, however, is afforded by the sixth pair of pleopoda, which can at this stage already be recognised as bilobed rudiments (a_6), thus preceding the other abdominal appendages in development. This pair of pleopoda develops as the lateral portions of the caudal fin (Fig. 123 *C*, *a*), while the small limb-rudiments on the five anterior segments of the abdomen appear to be temporarily suppressed during the later *Zoaea* stage (Fig. 123 *C*, a_1–a_5). In such a later *Zoaea* stage, the five joints in the protopodite of the first antenna seem also to have disappeared; the rudiments of the five pairs of ambulatory limbs can now be recognised as small biramose appendages (*IV–VIII*).

In the *Mysis stage* which follows (Fig. 123 *D*), the antennae have ceased to function as locomotory organs, the locomotory function being now performed by the biramose thoracic limbs. The cephalothorax is now small as compared with the abdomen, which develops greatly, and in which the pleopoda have now reappeared. Dorsal spines appear on the abdominal segments from the second to the fifth. The anterior antenna (*1*) now exhibits a three-jointed protopodite and two still unjointed flagella; the latter become jointed at a future period; olfactory hairs develop, and an auditory organ forms at the base of this limb. In the second antenna (*2*), the exopodite has changed into a scale (squame) fringed with setae, while the endopodite becomes transformed into the adult flagellum. The upper lip has lost its spinous process. On the mandible, the two-jointed palp of the adult develops. In the anterior maxilla, the endopodite degenerates into a short truncated limb, while the exopodite is completely lost. The exopodite of the second maxilla changes into the large respiratory plate. The first maxillipede resembles that of *Sergestes*, the protopodite growing out into a large cutting plate, while the endopodite and exopodite are retained as small appendages, and a branchial pouch sprouts from the basal joint (Fig. 91 *C*, p. 194). The second and third maxillipedes (*II, III*), as well as the five following thoracic limbs (*IV–VIII*) are still large biramose limbs with well-developed exopodites.

In the transition from the *Mysis* stage to the *shrimp form*, the exopodites of the thoracic limbs are reduced, while the flagella of the antennae become jointed, and the pleopoda which appear in the *Mysis* stage attain their full development. The second and third maxillipedes retain the character of biramose limbs. The second maxillipede has a geniculate endopodite, a smaller exopodite (flagellate appendage), and gills; the third maxillipede has its endopodite developed as a long ambulatory limb, while, in it also, the exopodite persists as a flagellate appendage. The three following limbs (first, second, and third ambulatory limbs) are provided with rudimentary pincers as early as the *Mysis* stage.

The various ontogenetic stages of *Penaeus*, which have become known through the examination of the Challenger material, can easily be brought into agreement with the process of development just described. They, however, show many variations which may be regarded as generic and specific differences; these chiefly affect the armature of spines (especially in the abdomen) and the relative development of the limbs (the thoracic limbs and the pleopoda).

The remarkable *Peteinura gubernata*, which SPENCE BATE (No. 100), on account of certain points of agreement with *Aristeus*, regarded as possibly belonging to the *Penaeidae*, must no doubt also be considered as a larval form. This form agrees closely with that described by DOHRN (No. 121) as *Ceratapsis longiremis*, in the armature of the cephalo-thorax, the shape of the limbs, and the excessive development of the exopodite of the sixth pleopod. *Ceratapsis* is regarded by BOAS and CLAUS as a larva of some form which must be related to the *Penaeidae* on account of the structure of its gills, made known by the latter author.

The metamorphosis of *Stenopus*, which is allied to *Penaeus* and shows some relation to that of the *Sergestidae*, has been described by BROOKS and HERRICK (No. 111). The larva which hatches from the egg is a *Protozoaea* with sessile eyes, antennae serving as swimming limbs, a deeply-cleft telson, and a long rostrum, and with all the pairs of limbs as far back as the first thoracic appendage (inclusive) already developed. The posterior region of the body is only indistinctly segmented, and has no appendages. From this form a true *Zoaea* develops, showing the characters of a Caridid *Zoaea* (p. 272). A later stage is characterised by the enormous lengthening of the fifth pair of ambulatory limbs, which function as the principal locomotory organ of the larva and equal the whole body in length. These limbs are reduced in the following *Mastigopus* stage to small vestiges, and the preceding pair (fourth ambulatory limbs) also degenerate for the time only. In this respect, *Stenopus* recalls the *Sergestidae* (p. 266).

C. Caridea.

The metamorphosis of the Caridea (*Palaemonidae*, *Alpheidae*, *Crangonidae*, etc.) is, as compared with that of *Penaeus*, essentially abbreviated. The *Nauplius* and *Protozoaea* are never free stages in the Caridea, but are merged in the general embryonic development which takes place in the egg. The embryo leaves the egg, as a rule, as a peculiarly-shaped *Zoaea* (Fig. 124), which in certain characters anticipates the *Mysis* stage, and thus in many respects is more advanced than the typical *Zoaea.* We may take as an example a larva described by Claus (No. 113), and referred to the ontogeny of *Hippolyte.* In this larva we can distinguish an anterior cephalo-thoracic and a posterior abdominal region. The latter is long and already shows its full number of segments (in forms related to this *Zoaea*, however, the separation of the sixth segment from the telson is often at first indistinct). The telson is, as a rule, no longer cleft (furcal structure), but has the form of a broad plate with a spinous posterior margin; in individual cases, however (*e.g.*, *Pontophilus*, G. O. Sars, No. 151), a furcate condition with two lateral wings is found. The dorsal shield carries a simple pointed rostrum and short supra-orbital and antennal spines, but there is no further development of spinous processes. In many larvae of this group, however, there is a very prominent dorsal spine on the second abdominal segment, as well as smaller ones on the three following segments. In other respects, the spinous armature of this region of the body undergoes great variation in the forms belonging to this group. Near the Nauplius eye, the paired eyes are distinct and already stalked.

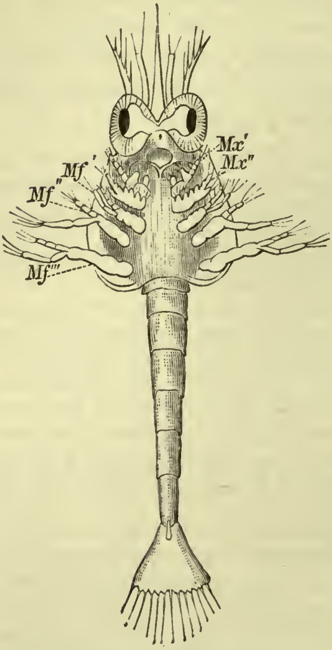

Fig. 124.—*Zoaea* of *Hippolyte* (after Claus, from Balfour's *Text-book*). Mx', first, Mx'', second maxilla; Mf', Mf'', Mf''', first, second, and third maxillipedes.

In the anterior region of the body, besides the seven pairs of limbs occurring in the *Zoaea*, the eighth pair (third maxillipedes, Fig. 124, Mf''') appear in the form of well developed swimming limbs. The region following this, which comprises the five segments carrying ambulatory limbs, is almost unrepresented, its segments and limbs only becoming apparent at a later period. The pleopoda are still altogether wanting. In the second antenna, the transformation of the exopodite into the scale and of the endopodite into the flagellum of the adult can be recognised, the mandibular palp is wanting as well as the leaf-like appendage (exopodite) of the first maxilla, which is found in *Penaeus*. The heart has two pairs of ostia, a normal condition in the *Zoaea*, the third pair developing during the *Mysis* stage.

While an apparent irregularity is produced in the order of development of the segments by the suppression of the fifth thoracic segment, the rudiments of the limbs appear in the regular order from before backwards. The only exception is afforded by the sixth pair of pleopoda, which frequently develop precociously. The ambulatory limbs develop gradually from before backwards, in contrast with those of the *Sergestidae* and of *Penaeus*, which appear simultaneously. The development of the thoracic limbs frequently shows variations in detail which are not all as yet accurately known.

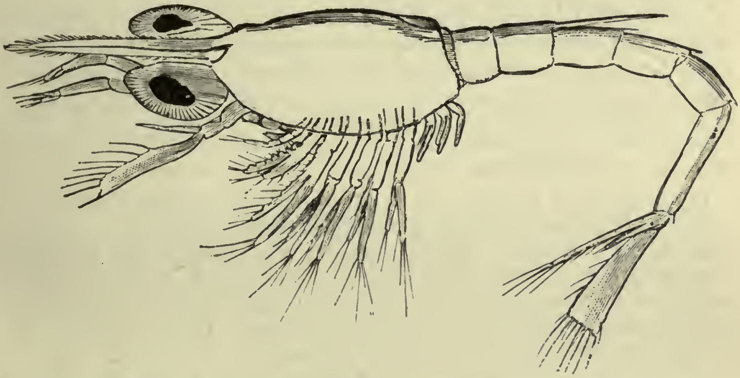
FIG. 125.—Older larva of *Hippolyte*, after the development of the thoracic appendages (after CLAUS, from BALFOUR'S *Text-book*).

In *Hippolyte*, the first two pairs of ambulatory limbs and the sixth pair of abdominal limbs (uropoda) appear simultaneously. In an older stage (Fig. 125) these become biramose, while the buds of the three posterior pairs of ambulatory limbs also appear. In *Palaemon*, the larva which hatches from the egg has the rudiments of the three following thoracic limbs developed behind the third pair of maxillipedes (BOBRETZKY). The larva of *Crangon*, when hatched, shows the bud-like rudiments of the two anterior pairs of ambulatory limbs (CLAUS, No. 113; EHRENBAUM, No. 123*), but the rudiments of the three following

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* G. O. SARS (No. 151), on the contrary, states that in *Crangon vulgaris* and in *Cheraphilus* and *Pontophilus* only the buds of the first pair of ambulatory limbs are present, while the four remaining pairs appear simultaneously in the next stage.

pairs develop very soon after. The earliest free larva of *Palaemonetes vulgaris* shows the rudiments of the two anterior pairs of thoracic limbs, while the posterior pairs arise independently in succeeding stages (W. FAXON).

Only after the thoracic limbs have developed do the pleopoda appear as buds. By the development of the thoracic limbs into biramose swimming appendages, the larva passes into the *Mysis* stage, which varies in its appendages in the different forms, inasmuch as the exopodite may be suppressed in individual thoracic limbs. In *Hippolyte*, *Caridina*, and *Palaemonetes vulgaris*, for instance, the last pair has no exopodite (this is perhaps the case in most Caridid larvae), while, in *Cheraphilus* and *Pontophilus* (G. O. SARS, No. 151), and in the fresh-water form *Palaemonetes varians*, the rudiment of the exopodite seems to be suppressed on the last three thoracic limbs, in *Crangon vulgaris* (EHRENBAUM and G. O. SARS) and in *Sabinea* (SARS) on the last four. In the latter forms there is thus an evident tendency to the elimination of the *Mysis* stage from the metamorphosis.

The tendency to simplification of the ontogenetic processes, which finds expression in the above conditions, has led, in individual cases, to a much more marked abbreviation of metamorphosis. The embryo of the arctic form *Hippolyte polaris*, as observed by KROYER (No. 136), showed the five pairs of ambulatory limbs as simple (uniramose), jointed appendages, the rudiments of pincers being already manifest on the anterior pair. The five anterior pairs of abdominal limbs could also be recognised as biramose rudiments, while the sixth pair was still wanting. The metamorphosis of *Sabinea* (G. O. SARS, No. 151) seems similarly abbreviated, the youngest larva (*Myto Gaimardii* of KROYER) hatched from the egg already showing the rudiments of all the five ambulatory limbs and of the five anterior (and already biramose) pairs of pleopoda. Only the first ambulatory limbs have exopodites, the second being uniramose and very small. In *Sclerocrangon boreas*, the eggs of which are distinguished by their large size, there appears to be entire suppression of metamorphosis (SPENCE BATE, No. 100, G. O. SARS, No. 151), and the same is the case with the deep sea forms *Cryptocheles* and *Bythocaris* (G. O. SARS, No. 151).

Many of the fresh-water Caridea (*e.g.*, *Caridina Desmarestii*) have, in contrast to their marine relations, no abbreviation of metamorphosis, but such abbreviation is distinctly evident in *Palaemon Potiuna* (F. MÜLLER, No. 143) and *Palaemonetes varians* (P. Mayer, No. 138). *Palaemon Potiuna* leaves the egg at a stage of development very similar to that of *Hippolyte polaris*, being only distinguished from the latter by the backward condition of the mouth-parts (for, owing to the larger amount of food-yolk present, the larva does not commence to feed until some time after hatching), and by the presence of gill-rudiments.

The variety of *Palaemonetes varians*, which occurs in fresh water in the South of Europe, hatches, according to P. MAYER, at an advanced *Zoaea* stage representing the transition to the *Mysis* stage, and possesses all the limbs except the last pair of pleopoda. The two anterior pairs of ambulatory limbs already show the rudiments of pincers, and are provided with exopodites, which are wanting on the three following ambulatory limbs. The gills (pleurobranchiae) are well developed on all the segments bearing the ambulatory limbs. The abdominal limbs are found as biramose buds. The telson, in shape and armature, resembles that of the Caridid *Zoaea*, and is not as yet sharply marked off from the sixth abdominal segment. In contrast to the above, it is an interesting fact that the variety of *Palaemonetes varians*, which occurs on the shores of Northern Europe (but also in brackish or fresh water), shows far less abbreviation of metamorphosis. According to Boas (No. 105), the *Zoaeae* which hatch from the eggs of this form have only truncated, unjointed ambulatory limbs, while the abdominal limbs are altogether wanting. In all forms with abbreviated development, the eggs are considerably larger and more richly provided with food-yolk, and the number produced by the female is consequently smaller. The young, when hatched, still retain a considerable amount of food-yolk, which is only gradually absorbed, and consequently they do not take food from outside until very late. In keeping with this, the mouth-parts of the otherwise highly-developed larva are in a very rudimentary condition.

According to Herrick (No. 133) and Packard (No. 144) a similar abbreviation of metamorphosis is found in two species of *Alpheus*. In other species of this genus the metamorphosis does not deviate from that of other Caridea, but in *Alpheus heterochelis* it is abbreviated, and in *Alpheus praecox*, which lives in Sponges, it is almost altogether lost.

In connection with the Caridea we should mention the genus *Amphion*, a form whose systematic position is still very doubtful. It agrees in the form of its *Zoaea* larva and in the possession of branchial rudiments which show the character of phyllobranchiae (Spence Bate, No. 100) with the Caridea. The oldest known stages of *Amphion* appear (in the deficient segmentation of the antennae) not to have attained full development, and must probably be considered as larvae, although Dohrn (No. 120) and Willemoes-Suhm, on account of the statement that genital rudiments appear in them, were inclined to regard them as adult forms. The long body moves by means of six pairs of biramose limbs, which correspond to the second and third maxillipedes and the four following thoracic limbs, while the last pair of thoracic limbs is present in an undeveloped condition. In the shape of its biramose limbs, as well as in the presence of branched hepatic tubes in the anterior part of the cephalo-thorax, *Amphion* shows striking agreement with the *Phyllosoma*, and Boas (No. 103) actually conjectured that it might be the larva of the genus *Polycheles*, which is related to the Loricata. The youngest known stages of *Amphion* are *Zoaeae* resembling in appearance the Caridid *Zoaeae*. The second and third pairs of maxillipedes, developed as biramose swimming limbs, are the principal locomotory organs, while the first pair of maxillipedes already appear drawn towards the mouth. The abdomen ends in an oval telson; the pleopoda are wanting, but the sixth pair very soon develops. Other forms nearly related to *Amphion* have been described by Willemoes-Suhm, their similarity in shape of body to *Sergestes* being pointed out. These forms are known as *Amphiones*.

D. Astacidea.

In the tribe of the Astacidea there is still greater abbreviation of metamorphosis than in most Caridea. There is no longer any free *Zoaea* stage. In *Homarus*, whose metamorphosis has become known by the works of Kroyer (No. 136), G. O. Sars (No. 148), S. J. Smith (No. 153), and Ryder (No. 147), the stage at which the young leaves the egg (Fig. 126) is the *Mysis* stage, which moves about by means of the exopodites of the third pair of maxillipedes and of the five pairs of ambulatory limbs (mf'''–p^V) developed as strong swimming organs. The dorsal shield passes anteriorly into a simple rostrum. The abdomen is distinguished by the presence on its segments of dorsal and lateral spines, but is still devoid of limb-rudiments. The telson is a triangular toothed plate, indented posteriorly. The first antenna (a') is still unjointed, the second (a'') is biramose, with an exopodite changed into a scale and a slender endopodite (rudiment of the flagellum). The mandible carries a three-jointed palp, there is no exopodite on the first maxilla. The second maxilla and the maxillipedes resemble in essentials those of the adult, but are still in many respects rudimentary. The endopodites of the three anterior pairs of ambulatory limbs already terminate in rudimentary pincers.

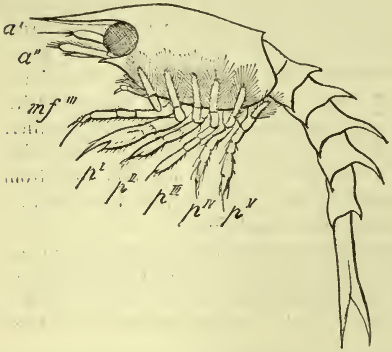

Fig. 126.—Larva of the American lobster, just hatched (after Smith). a', first, a'', second antenna; mf''', third maxillipede; p^I–p^V, first five ambulatory limbs.

In the next stage, the limb-buds appear on the second, third, fourth, and fifth abdominal segments. On the first antenna, the segmentation of the principal flagellum and the rudiment of the accessory flagellum can already be recognised. The three anterior pairs of ambulatory limbs have increased in size, and the pincer-rudiments are more clearly developed.

In the third larval stage, the Schizopodan features gradually disappear, while the adult characters begin to develop. The exopodite of the third maxillipede, as well as that of the fifth ambulatory limb, degenerate, while the limbs of the sixth abdominal segment attain development. The abdominal spines begin to degenerate.

In the next stage, the Schizopodan characters have been entirely lost. The exopodites of the ambulatory limbs are mere vestiges. The larva, in all essentials, resembles the adult, but still retains its pelagic manner of life, and swims by means of its abdominal limbs.

Only in a later young form, which has sunk to the bottom, does the asymmetry of the pincers become apparent; the first abdominal limbs which, to begin with, are similar in form in the two sexes, appear at this same time. At a still later stage sexual differentiation is attained.

The metamorphosis of *Nephrops norvegicus*, a single stage of which was made known long ago by Claus (No. 113), and which has more recently been completely described by G. O. Sars (No. 149), agrees in all its details with that of *Homarus*. Here, as in the latter, the four stages described above can be distinguished, being similarly characterised in both forms. The larva of *Nephrops*, however (Fig. 127), has a peculiar appearance, being distinguished by the spines on its abdomen. On the third abdominal segment there is a small dorsal spine, on the fourth and fifth a much larger one, while the sixth abdominal segment has a pair of long backwardly directed spines. The telson which, in the first and second stages, was not distinctly marked off from the sixth abdominal segment, runs out into two very large movable spinous processes which are retained even in the third stage, together with the lateral plates of the caudal fin (sixth pair of pleopoda), and only disappear in the fourth stage, in which the telson is transformed into the middle plate of that fin.

Fig. 127.—Later *Mysis* stage of *Nephrops norvegicus* (after Sars). *a'*, first antenna; *a''*, second antenna; *mf'''*, third maxillipede; p^1–p^5, first five ambulatory limbs; pl^2, pleopod of the second abdominal segment; pl^5, pleopod of the fifth abdominal segment; *r*, rostrum.

The young of *Astacus*, when hatched, are distinguished only in unessential points from the adult. The cephalo-thorax is swollen by the mass of nutritive yolk beneath it, and the rostrum is curved downwards between the eyes. The first pair of abdominal limbs is still undeveloped. The pleopoda of the sixth segment have also not attained free development. The telson has a peculiar oval shape. In other respects the young of *Astacus*, which still remain for some time hanging to the abdominal limbs of the mother and are protected by her, entirely resemble the adult. Metamorphosis here, as in so many fresh-water forms, has entirely disappeared.

The young of *Cambarus* (W. Faxon, No. 127) closely resemble in shape the above forms, and, like those of *Astacus*, recall in certain respects the *Parastacidae*. The first and sixth pairs of pleopoda are still wanting, and the transverse segmentation in the region of the telson-plate has not yet developed. The latter, unlike that of *Astacus*, has no fringe of setae. Development seems still more abbreviated than in *Astacus*, inasmuch as the caudal fin very soon attains completion.

E. Loricata.

The larvae of the Loricata hatch in a form long known as the *Phyllosoma*, which was formerly regarded as an independent genus and placed either among the Stomatopoda or among the Decapoda. That this form belonged to the ontogeny of the Loricata was first rendered probable by the experiments in cultivating specimens made by Couch (No. 116), who was able to hatch, from the eggs of *Palinurus*, larvae which Gerstäcker had already assumed to be *Phyllosoma*. Coste and Gerbe arrived at the same results almost simultaneously. The embryonic development of *Scyllarus* and *Palinurus*, as well as the transition into the young *Phyllosoma*, was made known by Dohrn (No. 119), while the metamorphosis of the *Phyllosoma* was established chiefly by Claus (Nos. 91 and 8) and Richters (No. 146). Various *Phyllosoma* have recently been described by Spence Bate (No. 100).

The *Phyllosoma* must be regarded as a peculiarly-shaped *Mysis* stage. The Loricata thus leave the egg at the stage at which many of the Astacidea hatch. The leaf-like, flatly compressed shape of the body and the slight development of the abdomen must be regarded as adaptations to a pelagic existence, while, on the other hand, apparently primitive characters are retained in the independence of the thorax and the presence of furcal processes on the telson. Other features, however, can only be explained as degeneration-phenomena, the correctness of this view being confirmed by comparison with the embryonic stages.

The embryos of *Scyllarus*, whose ontogeny was worked out by Dohrn, pass through a *Nauplius* stage which bears a general resemblance to that described above (p. 156) for *Astacus*, and is marked by the secretion of a larval integument (Nauplius cuticle). The later stage also resembles the corresponding stage of *Astacus*, in that the posterior region of the body which has now developed (thoraco-abdomen) appears flexed ventrally. The anterior region of the body, in which the food-yolk is deposited, bears the two pairs of antennae and the mouth-parts, including the first maxillipedes. The second and the third maxillipedes are found on the recurved thoraco-abdominal section, together with the rudiments of the three anterior ambulatory limbs. Behind the last pair of these rudiments there follows an unsegmented terminal region in the form of a square plate. Most of the limbs are still of a somewhat embryonic stamp, but it should be mentioned that the three anterior pairs of limbs of the thoraco-abdomen (second and third maxillipedes and first ambulatory limbs) consist of uniramose rudiments, while the two following pairs (second and third ambulatory limbs) are still simple bud-like outgrowths.

At a somewhat later stage, the second antennae, which are very little shorter than the first, show the rudiments of the antennal glands at their bases. The mandible, in which the palp is wanting, is slightly bilobate at the tip; the first maxilla is bilobate, and the second has incisions on its inner edge which break it up into three lobes. The first maxillipede also, which was simply truncated at an earlier stage, is now a short bilobed rudiment. On the other hand, the exopodites of the second and third maxillipedes have become reduced, while the second and third ambulatory limbs appear distinctly biramose. Further back are found the small truncated rudiments of the fourth and fifth ambulatory limbs.

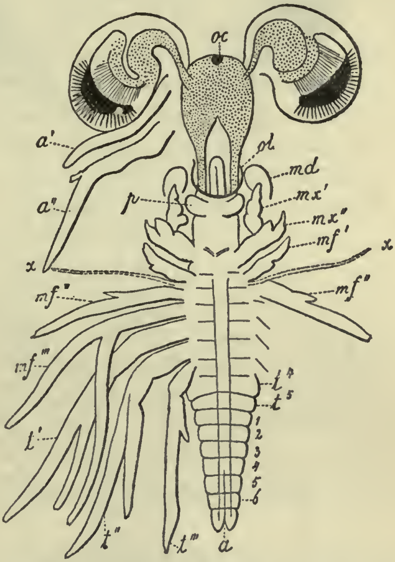

FIG. 128.—An embryo of *Palinurus quadricornis* with thoraco-abdomen turned back (after CLAUS). *a*, anus; a', first antenna; a'', second antenna; *md*, mandible; mf', mf'', mf''', first, second, and third maxillipedes; mx', mx'', first and second maxillae; *oc*, Nauplius eye; *ol*, upper lip; *p*, paragnatha; t', t'', t''', first three ambulatory limbs; t^4, t^5, segments carrying the fourth and fifth ambulatory limbs; *x–x*, boundary of the cephalo-thorax; *1–6*, first six abdominal segments.

A similar condition of the limbs is found in the *Palinurus* embryos at later stages (Fig. 128). The first antenna (a') is simple and unjointed, while the somewhat longer second antenna (a'') shows the rudiment of a lateral branch. The first maxilla (mx') is trilobate, the second bilobate. In the two anterior maxillipedes (mf', mf'') as well as in the third ambulatory limb (t'''), the exopodite is vestigial; the third maxillipede (mf'''), on the contrary, and the first and second ambulatory limbs (t', t'') are provided with large exopodites. The posterior region of the body contains the segments carrying the fourth and fifth pairs of ambulatory limbs (t^4, t^5), as well as the abdominal segments (*1–6*), and ends in a cleft telson.

The last stages of embryonic life already distinctly show the segmentation of the body characteristic of the *Phyllosoma* larva. The body falls into three sections, the anterior broadened section being still swollen by the food-yolk deposited in it, and carrying antennae, mandibles, and maxillae. This is followed by a moderately broad region, consisting of the segments which carry the maxillipedes and ambulatory limbs, and behind this comes a short narrow abdomen. Before the *Phyllosoma* leaves its embryonic envelope, certain processes of degeneration (Fig. 129) take place in the body. The second antennae (a'') are reduced to simple, unbranched processes, and the second maxillae (mx'') to short unjointed stumps. The first maxillipede in *Scyllarus* is altogether lost, while in *Palinurus* it is retained in the form of a much reduced vestige. The exopodites of the second and third maxillipedes

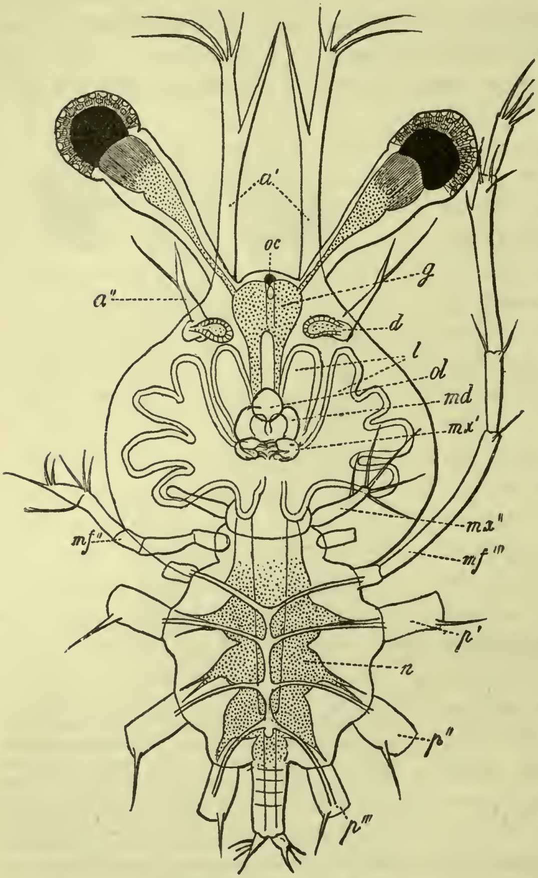

Fig. 129.—Young *Phyllosoma* of *Scyllarus* (after Claus). Only the basal joints of some of the limbs are drawn. a', first antenna; a'', second antenna; d, antennal gland; g, brain; l, liver; md, mandible; mx', first maxilla; mx'', second maxilla; mf'', second maxillipede; mf''', third maxillipede; n, ventral chain of ganglia; oc, Nauplius eye; ol, upper lip; p', p'', p''', first three ambulatory limbs.

(*mf*″, *mf*‴) were similarly reduced at a still earlier stage. The segments carrying the fourth and fifth ambulatory limbs and those of the abdomen become less distinct.

The youngest hatched *Phyllosoma* (Figs. 129 and 130) very closely resemble the oldest embryonic stages. The clear, transparent body is flattened out like a leaf, and divided into the three sections just described. The anterior (cephalic) section, which is usually ellipsoidal or oval in outline, carries at its anterior end the two pairs of antennae and the stalked eyes, while the Nauplius eye (*oc*) lies just above the brain. The mouth lies almost in the middle of the ventral surface, surrounded by the mandibles and first maxillae; the reduced second maxillae (*mx*″) have shifted further back. There is, in the *Phyllosoma* of *Scyllarus* (Fig. 129), no trace of the first maxillipedes, whereas, in *Palinurus*, these are present as vestigial prominences.

The thoracic region (Figs. 129 and 130) somewhat resembles a broadened disc, and carries the maxillipedes and ambulatory limbs. The two anterior pairs of these limbs (the second and third maxillipedes) in the youngest *Phyllosoma* of *Scyllarus* are uniramose and five-jointed, while the three anterior ambulatory limbs consist of six joints and carry exopodites. The rudiments of the fourth and fifth ambulatory limbs, together with the segments to which they belonged, have almost entirely disappeared. In the youngest *Phyllosoma* of *Palinurus* (Fig. 130), on the contrary, the third maxillipede has an exopodite, and the fourth and fifth pairs of ambulatory limbs are found as minute buds.

The thoracic region of the body is originally simply joined on posteriorly to the anterior cephalic section. Later, however, the dorsal surface of the cephalic region grows back over the thorax, thus forming the dorsal shield, while the thorax itself gives rise principally to the "sternal plastron."

The abdomen is a short, indistinctly-segmented, rudimentary appendage ending in two furcal processes. Between these, lying at the posterior end of the body, is the anal aperture, which only secondarily takes up a ventral position through the fusing of the basal parts of the furcal processes. This position of the anus recalls that described in *Penaeus* (p. 267) and *Astacus* (p. 157), and shows that the *Phyllosoma*, in the development of the posterior end of the body, has retained a peculiarity of an earlier larval stage (*Protozoaea* of *Penaeus*).

The metamorphosis of the *Phyllosoma* consists in the appearance (or rather reappearance) of the missing body-segments and pairs of limbs, and in a transformation of those already present. The first antenna becomes jointed and develops the rudiment of the accessory flagellum (Fig. 131), as well as the olfactory filaments of the principal flagellum and the auditory organ in the basal joint. The second antenna also (Fig. 131) becomes jointed, and, in the *Phyllosoma* of *Scyllarus*, already shows indications of the lamellate shape typical of the adult. In the mandible, a palp, at first simple and later three-jointed, develops. The maxillae approach the adult form. The first maxillipede and the fourth and fifth ambulatory limbs now develop, while the penultimate ambulatory limb, as well as the second maxillipede, develop still further. From the basal joints of the maxillipedes and ambulatory limbs, the branchial rudiments now grow out. The abdomen becomes distinctly segmented, and six pairs of rudiments of pleopoda appear on it, the last pair participating in the formation of the caudal fin. Internally, the formation of diverticula leads to the development of the hepatic tubes (*l*). This, in the *Phyllosoma* of *Scyllarus* (Fig. 129), is commenced by the development of three pairs of caeca, the middle pair soon showing secondary ramifications. The *Phyllosoma* of *Palinurus* (Fig. 129), on the other hand, shows, from the very beginning, richer ramification of the so-called hepatic tubes. The organs of the circulatory system are already, as Gegenbaur has proved, of the typical Decapodan character. There is a heart provided with three pairs of ostia, from which the arterial vessels proceed in a form characteristic of the Decapoda (Claus, No. 6).

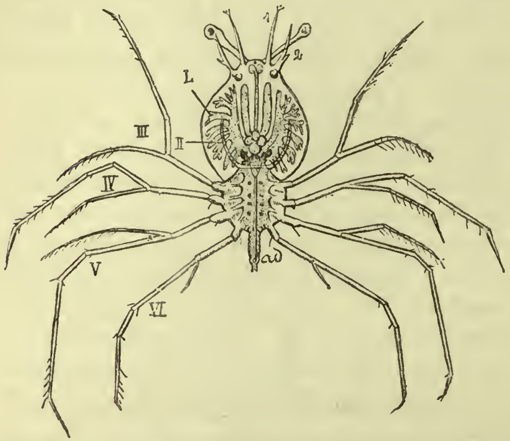

Fig. 130.—Young *Phyllosoma* of *Palinurus*, shortly before hatching (after Claus, from Lang's *Text-book*). *ab*, abdomen; *L*, liver; *II–III*, second and third maxillipedes; *IV–VI*, first three ambulatory limbs.

The change of the *Phyllosoma* larva into the young stages of the adult form, which are considerably smaller than the oldest *Phyllosoma*, has not yet been directly observed.

The *Phyllosoma* of *Palinurus* is to be distinguished from that of *Scyllarus* by certain features, some of which have already been pointed out. In the youngest *Phyllosoma* of *Palinurus*, the second antenna is shorter than the first (Fig. 130), but this condition is soon reversed (Fig. 131), and henceforth the second antenna remains longer. In *Scyllarus,* on the other hand (Fig. 129), the second antenna is always smaller than the first, and in later stages is transformed into the lamellate organ. Again, the presence of a rudiment of the first pair of maxillipedes is characteristic of the *Phyllosoma* of *Palinurus*, and so is the advanced development of the maxillipedes and ambulatory limbs in the youngest free stages. While it is in this way not difficult to identify the *Phyllosoma* of *Palinurus*, there yet remain many other *Phyllosoma* larvae, some of which are very remarkable forms, which can only conjecturally and with uncertainty be referred to the different genera of the lamellicorn Loricata (*Scyllarus*, *Thenus*, *Ibacus*, *Paribacus*, etc., Richters, No. 146). Among these last, Haswell (No. 131) has described a *Phyllosoma* probably belonging to *Ibacus*. This author considers it to be a further ontogenetic stage of *Phyllosoma Duperryi* Guerin, which belongs to Milne-Edwards' group of the "Phyllosomes

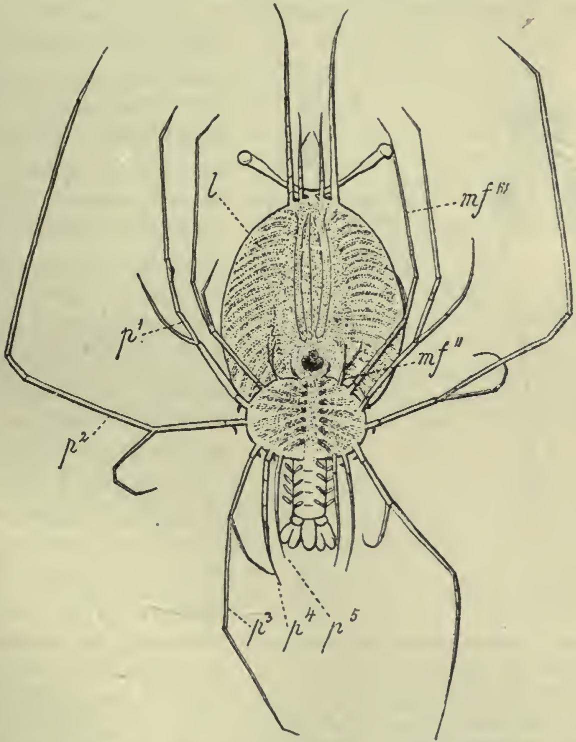

Fig. 131.—Older *Phyllosoma* of *Palinurus* (after Claus). *l*, liver; *mf''*, second maxillipede; *mf'''*, third maxillipede; p^1, p^2, p^3, p^4, p^5, the five ambulatory limbs.

laticaudes," in which the abdomen arises with a broad base as the direct prolongation of the thorax. Richters, on the other hand, has conjecturally referred the Brevicaudes to *Ibacus* and *Paribacus.* Fossil *Phyllosoma* have been recognised in the Solenhofen slates.

F. Thalassinidea.

The larvae of the Thalassinidea (*Gebia, Calocaris, Callianassa, Calliaxis*), known to us from the treatises of G. O. Sars (No. 149) and Claus (Nos. 6, 7, and 8), are allied to the Caridid larvae by the shape of the body, the possession of a long rostral spine, and the peculiar armature of the abdomen (wanting in *Gebia*); this latter consists of a long dorsal spine on the second and shorter spines on the three following abdominal segments. Their metamorphosis is, however, of special interest on account of the complete transition which they exhibit between the manner of development of the Caridids and that of the Anomura and Brachyura.

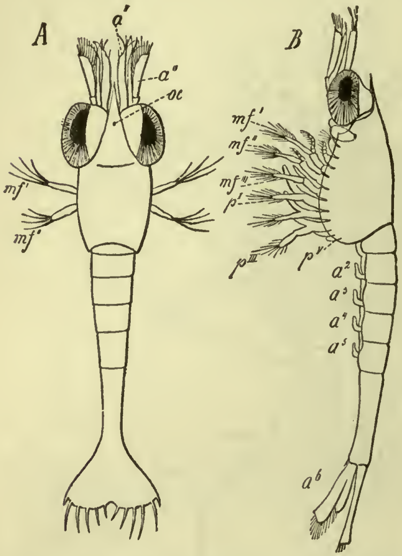

Fig. 132.—Two larval stages of *Gebia littoralis* (after G. O. Sars). *A*, *Zoaea* stage (dorsal view). *B*, *Mysis* stage (side view). a', first antenna; a'', second antenna; a^2–a^6, rudiments of the five posterior abdominal appendages; mf', mf'', mf''', the three maxillipedes; p^I–p^V, the five ambulatory limbs; *oc*, Nauplius eye.

The youngest larval stage of *Gebia* (Fig. 132 *A*) is a *Zoaea* which is distinguished from the *Zoaeae* of other Macrura chiefly by the fact that only the two anterior maxillipedes (mf', mf'') function as biramose swimming limbs, while the third maxillipedes, as well as the four following ambulatory limbs, are found as rudiments devoid of setae, the four anterior pairs being biramose, while the most posterior pair is still simple. The fifth pair of ambulatory limbs, as well as the pleopoda, are still altogether wanting. The telson, which is not yet marked off from the sixth abdominal segment, is a spade-shaped plate somewhat indented at its posterior edge and beset with setae. The paired eyes, which are still immovable, recall those of the Anomuran larva, in the great elongation of the posterior crystalline cones, causing the eye to project somewhat backwards.

The *Mysis* stage (Fig. 132 *B*), which results from the above through a transitionary stage, shows the fifth ambulatory limb as well as the rudiments of the pleopoda (except those of the first abdominal segment). The exopodites on the third maxillipede and on the three anterior ambulatory limbs (mf'''–p^{III}) are provided with setae and function as swimming limbs. The endopodites of these limbs, on the contrary, are still quite embryonic in appearance; they are unjointed and have no setae. The telson, which has now changed into a long rectangular plate, has, at its posterior margin, a small unpaired spine and seven longer spines on each side. The lateral limbs of the caudal fin (a^6) are already developed.

In later stages, the endopodites of the ambulatory limbs become more developed and the rudiments of pincers become evident on the first ambulatory limbs, while the exopodites gradually degenerate.

The agreement between the metamorphosis of *Gebia* and that of the Anomura consists in the form of the paired eyes and telson, in the biramose maxillipedes, and above all in the condition of the third maxillipede, which is first used as a swimming limb in the *Mysis* stage, while its endopodite is still rudimentary. While, in this respect, the larva of *Calliaxis* agrees with the *Zoaea* of *Gebia*, the *Zoaeae* of *Callianassa* and *Calocaris* agree with those of the Caridea, inasmuch as all the three maxillipedes here function as biramose swimming limbs.

As a contrast to the features which connect the metamorphosis of the Thalassinidea with that of the Anomura and Brachyura, the distinct development of the *Mysis* stage in the former group should be pointed out. This stage, which is characteristic of the Macruran metamorphosis, is, as we shall see, suppressed in that of the Anomura and Brachyura.

The *Zoaea* of the remarkable deep sea form *Calocaris Macandreae* is provided, like the other forms, with well developed paired eyes. The degeneration of these organs, which characterises the adult, takes place only after the *Mysis* stage (G. O. Sars, No. 149).

The *Calliaxis* larva (Claus, Nos. 6 and 7) is distinguished by a curious neck-like elongation of the cephalic region, which causes a certain resemblance to *Lucifer*. Another feature characteristic of this form, which was described by Brook (No. 107) as *Trachelifer*, is the lengthening of the telson into two wing-like lobes bearing spines posteriorly.

G. Anomura.

The Anomura in their metamorphosis show a somewhat primitive condition, in which, in many respects, they agree with the Brachyura. In most cases the young leaves the egg as a *Zoaea* (Fig. 133 *A*), in which, as in the Brachyura and a few Thalassinidea, the two anterior maxillipedes function as the chief locomotory organs.

The third pair of maxillipedes is only present in a rudimentary condition (Fig. 133 *C*). The next ontogenetic stage which develops from the *Zoaea* (Fig. 133 *B*), and which must be regarded as equivalent to the *Mysis* stage of the Macrura, already shows all the ambulatory limbs and the rudiments of most of the pleopoda. The ambulatory limbs have no exopodites, and already approach their final shape. We shall, in accordance with CLAUS (No. 7) and in agreement with the similarly-shaped stage of the Brachyura, define this stage as the *Metazoaea.* The characters of the *Mysis* stage here seem suppressed. The *Metazoaea* must be regarded as a transitionary form between the *Zoaea* and the youngest adult form (*Megalopa* of the Brachyura). In one important point the *Metazoaea* of the Anomura is distinguished from that of the Brachyura, viz., the condition of the third maxillipede which here, though possessing a rudimentary endopodite, has a well-developed exopodite functioning as a swimming limb, while, in the *Metazoaea* of the Brachyura, this limb still remains altogether rudimentary. This relation of the third maxillipede to the locomotory function is a link connecting the Anomura with the Caridea, in which the third maxillipede functions as a locomotory organ as early as the *Zoaea* stage (p. 272). We must consider this as a character of the *Mysis* stage precociously developed, in which the Caridid *Zoaea* departs from the typical *Zoaea*, while in the *Metazoaea* of the Anomura it must be regarded as a last vestige of a lost *Mysis* stage.

The development of the Anomura has recently been described in detail by G. O. SARS (No. 150), while fragmentary notices concerning it were published earlier by CLAUS (Nos. 6, 7, 8, and 113), SPENCE BATE (No. 98), DOHRN (No. 120), FAXON (No. 126), F. MÜLLER (No. 140), SMITH (No. 152), and others. The development of *Eupagurus Bernhardus* may serve as a type.

The *Zoäea* of *Eupagurus* (Fig. 133 *A*) has a somewhat compressed body, and is chiefly remarkable for the shape of its dorsal shield, which runs out anteriorly into a long rostral spine, but is deeply indented posteriorly, the indentation separating two points which are directed backwards. A similar form of dorsal shield is found in all Anomuran larvae. The short, stalked, and as yet immovable paired eyes are remarkable for the posterior projections already described in connection with *Gebia* (p. 284). Between them the Nauplius eye can be recognised. The two anterior abdominal segments are covered by the dorsal shield, the sixth abdominal segment is not yet marked off from the telson. The postero-dorsal margins of the intermediate segments of the abdomen are serrated. The telson is slightly cleft (a condition which reappears in the Brachyura) and is armed on each side with six setae. The first antennae (a') are simple and unjointed processes with setae at their tips. In the second antenna (a''), the unjointed endopodite is still continuous with the protopodite, while the small exopodite with setae on its inner side is already separated. The mandible has no palp. Behind the two pairs of maxillae there are two pairs of biramose swimming maxillipedes (mf', mf''), while the third pair (Fig. 133 *C*) is to be found only in the form of a very small two-jointed appendage pressed against the ventral surface. The five pairs of ambulatory limbs and the rudiments of the pleopoda are still altogether wanting.

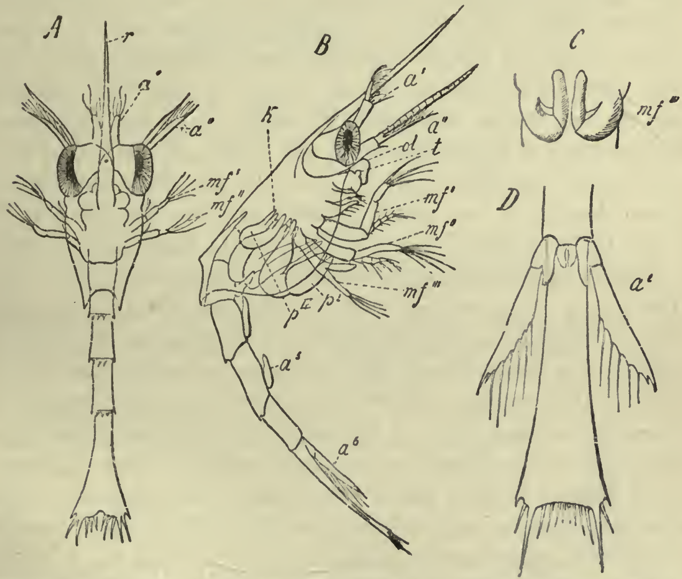

Fig. 133.—Larval stages of *Eupagurus Bernhardus* (after G. O. Sars). *A*, *Zoaea* (dorsal view). *B*, *Metazoaea* (side view). *C*, ventral view of the segment carrying the third maxillipedes in the *Zoaea*. *D*, caudal fin of the *Metazoaea*. a', first antenna; a'', second antenna; a^5, rudiment of the fifth pleopod; a^6, the sixth pleopod (uropod); mf', mf'', mf''', the three maxillipedes; p^{I}-p^{IV}, the first four ambulatory limbs; k, gill-rudiments; ol, upper lip; t, mandibular palp; r, rostrum.

In a later stage, known as the *Metazoaea* (Fig. 133 *B*), which still resembles the *Zoaea* in appearance, the rudiment of the third maxillipede (mf''') has developed further. It has a two-jointed exopodite beset with setae, which, like the exopodites of the preceding maxillipedes, functions for swimming, while the indistinctly segmented endopodite, still devoid of setae, appears rudimentary and functionless. The same character is shown by the rudiments of the four pairs of ambulatory limbs which follow (p^{I}–p^{IV}), the largest of which are those of the first pair, and show distinct rudiments of pincers. A similar very small rudiment is also carried by the fifth thoracic segment (not visible in the figure). In the abdomen, the separation of the sixth abdominal segment from the telson has taken place ; we still find no rudiments of pleopoda on the second abdominal segment to the fifth, but the rudiments of the sixth pleopod (a^6) appear highly developed. The exopodite is specially apparent as a setiparous plate (Fig. 133 *D*, *a*), while the endopodite is a small prominence and is not yet separated from the protopodite. The middle plate of the caudal fin, the telson, is long and truncated, while the indentation evident in the earlier stage has disappeared. The antennae and mouth-parts have also developed further. On the first antenna (Fig. 133 *B*, a') we now find the short rudiments of the two flagella, in the second antenna (a'') the endopodite is cut off from the protopodite, and is commencing to break up into joints the mandibular palp (*t*) has grown out as a short stump.

The young stage coming from the *Metazoaea* can be compared with the *Megalopa* of the Brachyura. It already, in all essentials, resembles the adult, except that the eyes are still comparatively large, that the abdomen and its limbs have not yet undergone the degeneration characteristic of the adult, and that the asymmetrical development of the body is not nearly so marked. The abdomen is not yet spirally twisted, but is symmetrical, consisting of six well-marked segments, on which (except on the first) pleopoda, provided with long swimming setae, are found. In the caudal fin, as well as in the pincers of the first ambulatory limbs, a certain degree of asymmetry is already evident. The scales of the second antennae have been cast off, the two flagella-rudiments on the anterior antenna have increased in size. The young forms following upon this stage, in which the asymmetry is still little marked, were classed together by M. Edwards under the name of *Glaucothoë*.

The metamorphoses of *Spiropagurus* and of *Galathea* agree in all essential points with that of *Eupagurus*. The *Zoaeae* of *Spiropagurus* are distinguished from those of *Eupagurus* by the form of the telson, which has no posterior incision. The larvae of *Galathea*, which so closely resemble those of *Eupagurus* as often to be confounded with them, can be recognised by the presence of small teeth on the two posteriorly directed points of the dorsal shield (*cf.* several larval forms belonging here and described by Spence Bate, No. 100, as *Zoontocaris*).

In individual cases, the metamorphosis is slightly abbreviated, the larvae first hatching as *Metazoaeae.* This is the case in *Galathodes* and in the genus *Lithodes,* which is closely related to the *Paguridae.* In both these forms, the eggs are comparatively large, and the escaping larvae take with them into larval life considerable masses of yolk, at the expense of which their further development is accomplished. In consequence of this, the mouth-parts of *Galathodes* (like those of *Palaemon Potuina,* mentioned above, p. 274) remain for some time in a remarkably undeveloped condition ; they are truncated and have no setae. In both these forms, the development of the sixth pair of pleopoda (uropoda) seem to be retarded as compared with that of the other abdominal limbs. A much greater reduction of the metamorphosis is found in *Birgus latro,* if the statement of WILLEMOES-SUHM, which rests on the report of a fisherman, is established, according to which the young of this species leaves the egg in a form very similar to that of the adult.

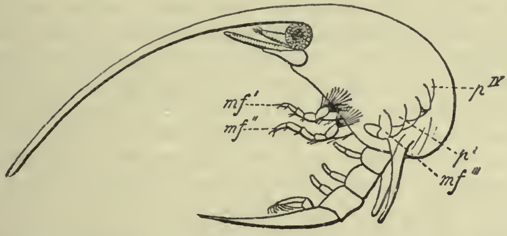

FIG. 134.—*Metazoaea* of *Hippa talpoidea* (after S. SMITH). *mf', mf'', mf'''*, the three maxillipedes ; p^I–p^{IV}, rudiments of the first four ambulatory limbs.

The larvae of *Munida*, whose metamorphosis in all important points agrees with that of the typical Anomuran described above, are distinguished by a greater development of the spines. The rostrum exceeds in length the rest of the dorsal shield, the two posterior tips of the latter are drawn out into long spines, and the deeply-cleft telson also runs out into two long spinous processes.

An excessive development of spines is found in the *Porcellana* larva (Fig. 135), which has long been known as *Lonchophorus* (ESCHSCHOLZ), whose development, excluding older accounts, has been made known by MÜLLER (No. 140), DOHRN (No. 121), CLAUS (No. 8), FAXON (No. 126), and G. O. SARS (No. 150). The frontal spine is here of quite unusual length. The two lateral spines also, which end like hooks and run out posteriorly, are of considerable length. The telson has here no posterior incision, but is a rhomboidal plate. In a few points, the metamorphosis of *Porcellana* approaches that of the crabs, viz., in the position of the abdomen, which is ventrally curved, and in the order in which the

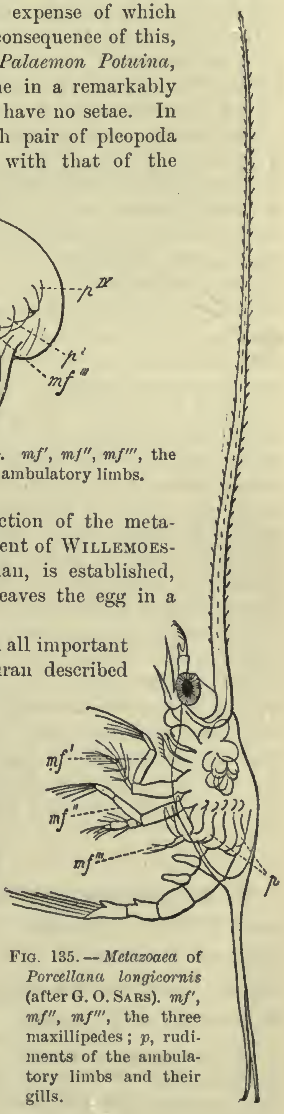

FIG. 135.—*Metazoaea* of *Porcellana longicornis* (after G. O. SARS). *mf', mf'', mf'''*, the three maxillipedes ; *p*, rudiments of the ambulatory limbs and their gills.

limbs bud out, which is distinguished by the fact that the third pair of maxillipedes develops simultaneously with the rudiments of the ambulatory limbs (Fig. 135, mf''' and p). The pleopoda of the second, third, and fourth abdominal segments are the first to appear, while those of the fifth segment and the lateral appendages of the caudal fin only develop at a later period.

The development of the sand crabs (*Hippidae*, Fig. 134) also, which was made known by the treatises of F. MÜLLER (No. 16), CLAUS (No. 8), SIDNEY SMITH (No. 152), and W. FAXON (No. 126), bears a general resemblance to that of the Anomura, although in this case, as in *Porcellana*, there are many suggestions of the Brachyuran affinities. The youngest stage, described by W. FAXON for *Hippa talpoida*, is a *Zoaea*, on whose dorsal shield only the rudiments of the later spinous processes can be recognised. The abdomen which is ventrally flexed has the first segment still indistinctly marked off from the thorax, and the sixth segment fused with the telson. The latter plate is toothed and rounded posteriorly. The rudiments of the two antennae, the maxillae, and the two anterior maxillipedes used, as swimming limbs, are present, while the third pair of maxillipedes, as well as all the following limbs, are still altogether wanting. From this stage proceeds the *Metazoaea* observed by SIDNEY SMITH (Fig. 134), which shows the rudiments of the third pair of maxillipedes (mf''') and the four anterior pairs of ambulatory limbs (p^{I}–p^{IV}). The fifth pair develops somewhat later. The third pair of maxillipedes is not used as a locomotory organ, although it functions in this way in the larva described by CLAUS and referred by him to *Albunea* (No. 8). In the *Hippa* larva, the dorsal spine of the cephalo-thorax, so characteristic of the Brachyuran *Zoaeae*, is wanting. On the other hand, a long, anteriorly-curved rostrum develops, as well as the lateral posteriorly-directed spines which occur in all Anomura. From the *Metazoaea*, after several moults, there comes a *Megalopa* very like the adult, being chiefly distinguished from it by the comparatively large size of the eyes and the presence of strong biramose swimmerets on the five posterior abdominal segments.

The larvae of the Apterura (*Dromia*, *Homola*) also, described by BOAS (No. 104) and GOURRET (No. 130), are nearly allied to those of the Anomura. Unlike the Brachyuran *Zoaea*, the third maxillipede in them has an exopodite which functions for swimming; in *Dromia*, indeed, there is a similar exopodite on the first ambulatory limb, this being a more distinct indication of a *Mysis* stage than is found in the Anomura. In the shape of the dorsal shield and of the abdomen, which is provided with two pairs of biramose pleopoda, the Apteruran larvae agree with the Anomura.*

H. Brachyura.

Most Brachyura leave the egg in the form of a *Zoaea* which varies very little in appearance throughout the group (Fig. 136). The compact and usually oval body is, as a rule, characterised by the regular development of spines.† There is a frontal spine sloping downwards and forwards, a dorsal spine rising from the centre of

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* [The Anomuran Decapoda were formerly divided up into the Pterygura and the Apterura. Of these the former (by far the larger group) are now classed by STEBBING with the Macrura as the Anomalous Macrura, and the latter, comprising the Drominea and Ranininea, as the Anomalous Brachyura.—ED.]

† WELDON has pointed out the significance of these spines in checking movement in certain directions. *Journ. Mar. Biol. Assoc.*, N. S., Vol. i.

the dorsal shield and sloping upwards and backwards, and a pair of lateral spines at the posterior lower angles of the shield which slope outwards. At the anterior part of the body, the large, short-stalked lateral eyes rise from broad bases; between them lies the Nauplius eye. The movable abdomen which is used as a rudder for steering, is ventrally flexed, and consists of five free segments, while the sixth still appears to be united in one piece with the telson. The posterior thoracic region, which later bears the ambulatory limbs, appears in the *Zoaea* very little developed. It is quite short and rudimentary, is hidden under the dorsal shield and shows either no indications at all of limbs (peraeopoda), or only short truncated rudiments. In the last case it would perhaps be more correct to call the stage at which the larva leaves the egg the *Metazoaea*.

The seven anterior pairs of limbs are present in the *Zoaea*, well developed and functional. The antennae are distinguished by great simplicity of shape. The first antennae are short, unjointed processes, at the ends of which only a few setae develop (in the youngest stage of *Carcinus maenas* only two (Spence Bate)). The second antenna consists of a protopodite which often grows out into a very long spinous process (Fig. 137 *B*, *ex*), which is seen less strongly developed in the Anomuran larvae (*e.g.*, *Eupagurus*). Another spinous process clothed at its end with setae must be regarded as the exopodite (squame, *st*). The endopodite (rudiment of the future flagellum) is at first altogether wanting, but soon appears in the form of a small prominence which grows out between these two spinous processes. The mandible still consists exclusively of the masticatory blade; the mandibular palp is altogether wanting. The maxillae already show the structure typical of the Decapoda (Fig. 137 *D* and *E*). The protopodite of the first maxilla has two masticatory blades turned inwards and provided with setae, and a two-jointed palp (endopodite). On the second maxilla there are four lobate masticatory processes on the protopodite, two occurring on each joint, an endopodite also divided up into lobes, and an

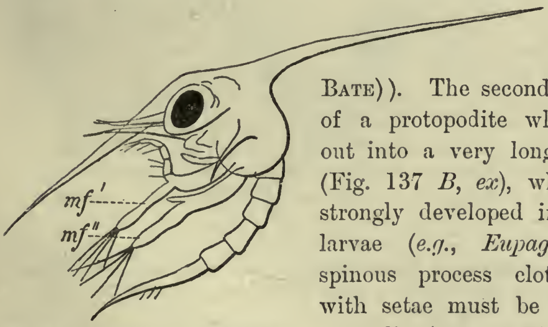

Fig. 136.—Zoaea of *Thia polita* (after Claus). *mf′*, first maxillipede; *mf″*, second maxillipede.

exopodite developed as a respiratory plate fringed with setae. The two anterior maxillipedes (Fig. 136, *mf′*, *mf″*) have developed as biramose swimming limbs. The endopodite of the first maxillipede has four joints, while that of the second maxillipede is more rudimentary and usually consists of three short joints. The exopodites (flagellate branches) have long swimming setae at their ends. The rudiments of the succeeding limbs (third maxillipedes and first five ambulatory limbs) seem entirely wanting in the youngest *Zoaea* of many Brachyura (*e.g.*, in *Pinnixa*, W. Faxon), in other cases some or all of them appear as short, truncated outgrowths (*Maja*, *Inachus*). The pleopoda are still altogether wanting. The abdomen is generally distinguished by a definite development of spines, the second segment having a pair directed anteriorly, and the three succeeding segments each having a pair directed posteriorly. The telson, as a rule, has a characteristic forked form, and is produced out laterally into a long spine. On the inner side of these two processes on the telson there are, in most cases, three strong setae.

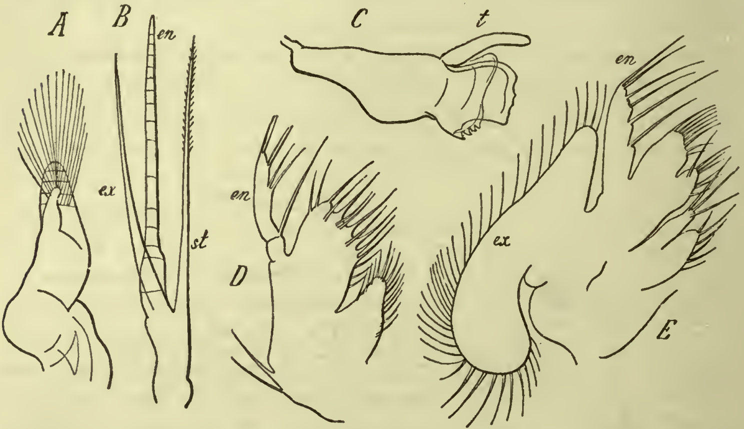

Fig. 137.—Limbs of an older *Zoaea* of *Portunus* (after Claus). *A*, first antenna. *B*, second antenna. *C*, mandible. *D*, first maxilla. *E*, second maxilla. *en*, endopodite; *st*, exopodite; *ex*, spinous process; *t*, mandibular palp.

The form of the Brachyuran *Zoaea* undergoes, in isolated cases, variations from the type here described, which are chiefly connected with the development of the spinous processes and the form of the telson. In *Gelasimus*, for instance, the spinous processes of the dorsal shield are unusually short. In *Achaeus*, there is no frontal spine, but a short dorsal spine is retained. In *Inachus* also the frontal spine is wanting (Claus, No. 8; Gourret, No. 130). In *Maja* (Couch) and in *Eurynome* (Kinahan) all the spinous processes are wanting. Claus, however, has described the presence of a long frontal spine on the *Zoaea* of *Maja*. In a larva described by Dohrn (No. 121) as *Fissocaris*, which has a long frontal spine and two pairs of large lateral spines, the dorsal spine is wanting. In other cases the dorsal and lateral spines may be exceedingly long, and may end in balloon-shaped swellings. Larvae thus provided with lateral spines projecting backwards were described as *Pluteocaridae* by Claus (No. 8). A *Zoaea* form distinguished as *Pterocaris* is remarkable for the wing-like elevations of the lateral parts of the carapace, and for the transversely-broadened form resulting from this.

Many of the *Zoaeae* of the Brachyura are distinguished by the great development of the spinous process on the second antenna; *e.g.*, those of *Xantho rivulosus* (Gourret, No. 130) and of *Panopeus Sayi* (W. Faxon, No. 125), in which this process equals in length the long frontal spine.

When the youngest *Zoaea* leaves the egg, it is not altogether free, but appears surrounded by a somewhat loose and detached larval integument (p. 119); this has been claimed by Conn as the cuticle of the *Protozoaea* stage passed through during embryonic life. Only after a moult, which usually takes place early, does the *Zoaea* become free. A similar condition is found in many other Decapoda (*e.g.*, in all Anomura and many Macrura). F. Müller (No. 16) has pointed out the morphological interest of a study of this larval integument, the form of the tail in this youngest integument in *Achaeus*, and perhaps also in *Maja*, recalling that of the shrimp larvae. This larval cuticle was utilised later by Paul Mayer (No. 137) in an attempt to derive the different forms of telson and for phylogenetic purposes. More recently, further investigations with regard to it have been made by W. Faxon (No. 125) and Conn (Nos. 114 and 115). The spinous processes of the dorsal shield are always wanting in the larval integument, but are often present as rudiments beneath the cuticle, withdrawn in a telescopic manner. While, in the group of the Grapsoidea (*Sesarma*), the larval integument, apart from the spinous processes, is a fairly true cast of the *Zoaea* which proceeds from it, in most other Brachyura it shows no inconsiderable deviations from that form. The antennae, especially, appear in the larval integument in a higher degree of development. The first antenna consists of a protopodite and two terminal branches provided with setae, one of which is of considerable length. The second antenna is specially remarkable for the presence of large processes provided with setae on the exopodite. In the posterior region of the body, the caudal fork is usually characterised by possessing seven feathered setae on each side. The number seven seems to be typical in the setae of the telson throughout the Decapoda, and renders the study of the hatched *Zoaea* before the casting of the larval integument a valuable aid in tracing back the shape of the telson, which often varies in a later stage, to the fundamental form already described (Paul Mayer).

The series of ontogenetic stages which follow after the *Zoaea* have usually received the same name, but have been more suitably called *Metazoaeae* by Claus (No. 7). They do not, in general shape (*cf.* the somewhat younger stage, Fig. 138), entirely resemble the *Zoaea*, but are distinguished by the greater development of the limb-rudiments. In the first antenna (Fig. 137 *A*) there is now an unjointed protopodite showing the rudiment of the auditory organ as a vesicular swelling, and two rudiments of flagella, the inner still being short and unjointed, while the outer flagellum, beset at its end with olfactory filaments, has broken up into short rings. The second antenna (Fig. 137 *B*) has the rudiment of the flagellum (endopodite) greatly developed; but the softer portions have withdrawn from the spinous process and the exopodite as a sign that these appendages will be lost in the next moult. On the mandible (*C*), a finger-shaped and still unjointed mandibular palp has developed. The two maxillae (*D* and *E*) have undergone changes which are comparatively slight, while in the two anterior maxillipedes the exopodites are divided up at their ends into short joints, and seem beset with numerous swimming setae. The rudiments of the third pair of maxillipedes and of the five ambulatory limbs (Fig. 138, *IV–VIII*) are already conspicuous. They, however, have no clothing of setae and are still functionless, being carried closely pressed against the sternal surface of the body. These rudiments develop gradually, but always in the direction of the form of the adult appendages. The third maxillipede thus soon shows all the parts of the future limb, a two-jointed exopodite and the branchial appendages, which also develop on the three following pairs of limbs. The most anterior pair of ambulatory limbs with their pincers develop greatly. On the abdomen, the pleopoda have now developed as indistinctly two-jointed appendages, while the sixth pair are still simple stumps. An exopodite does not develop on the ambulatory limbs. *The Mysis stage is thus suppressed in the metamorphosis of the Brachyura, and is replaced by the Metazoaea stage.* This is an interesting case of simplification of the course of development.

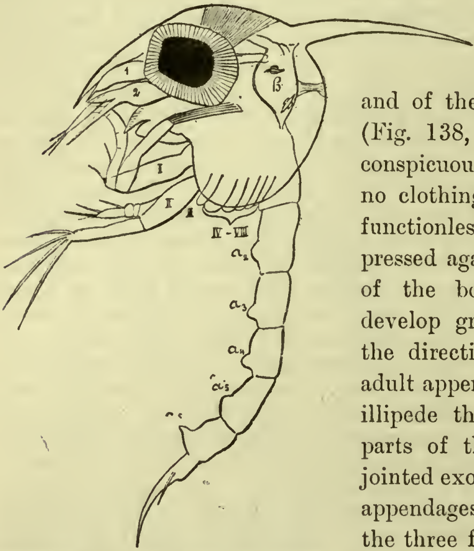

FIG. 138.—*Zoaea* of *Maja* after ecdysis (after CLAUS, from LANG'S *Text-book*). *1*, *2*, first and second antennae; *I*, *II*, *III*, first three maxillipedes; *IV–VIII*, first five ambulatory limbs; a_2–a_6, last five pleopoda; *h*, heart.

The *Metazoaea* passes into the young form of the Brachyuran known as the *Megalopa* (Fig. 139 *A* and *B*), which brings about the transition from the swimming to the creeping manner of life, and in the most important points of its segmentation already agrees with the adult. In the condition of the abdomen, the *Megalopa* is somewhat on a level with an adult Anomuran Decapod. The anterior part of the body with the limbs already shows the typical Brachyuran character. The youngest *Megalopa* stages, however, still in most cases carry on the dorsal shield traces of the former Zoaean spines (Fig. 139 *A*). The limbs have now attained their final shape; the maxillipedes have lost the locomotory function and are comparatively smaller. The ambulatory limbs, on the contrary, have developed greatly. The abdomen is still stretched out backwards, and shows the pleopoda as swimmerets provided with long setae; these consist of a basal joint and an oval terminal plate provided with setae (exopodite), while the quite short endopodites furnished with small hooks, as retinacula, serve to connect the right and left swimmeret, and consequently bring about a simultaneous movement of the two limbs. The forked telson of the *Zoaea* has changed into a rounded caudal plate.

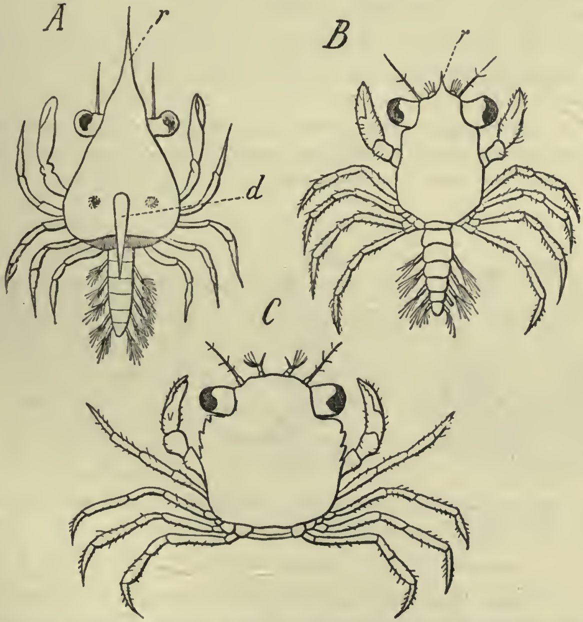

Fig. 139.—Three ontogenetic stages of *Carcinus maenas*. *A*, younger, and *B*, older *Megalopa* stage. *C*, young crab. (*A*, after Spence Bate; *B* and *C*, after Brook). *d*, dorsal spine; *r*, rostrum.

The different Brachyuran *Megalopae* also show variations in details, these leading to the formation of distinct genera by DANA (*Maresia*, *Monolepis*, *Cyllene*, *Triloba*). The youngest *Megalopa* stages of different forms vary with regard to the remains still to be found of the Zoaean spines. While these are still to a considerable extent retained in *Carcinus maenas* (SPENCE BATE, No. 97), they are, in other cases, more degenerate, and may even (*Portunus*) be altogether wanting in the youngest *Megalopa* which develops from the *Metazoaea*.

The *Megalopa* passes gradually through several moults into the final form (Fig. 139 *C*). The changes during this period, which were described for *Carcinus maenas* by BROOK (No. 106), are chiefly in the shape of the dorsal shield and the degeneration of the abdomen typical of the Brachyura, this part of the body being from this time curved ventrally and applied to the thoracic sterna.

While, in by far the greater number of Brachyura, metamorphosis takes the course described above, it undergoes considerable abbreviation in individual cases, by the suppression of certain stages. An interesting example of this is found in *Pinnixa*, where the *Metazoaea* stage, at the last moult, gives rise direct to a young crab, the *Megalopa* stage being entirely wanting in this form (W. FAXON, No. 126).

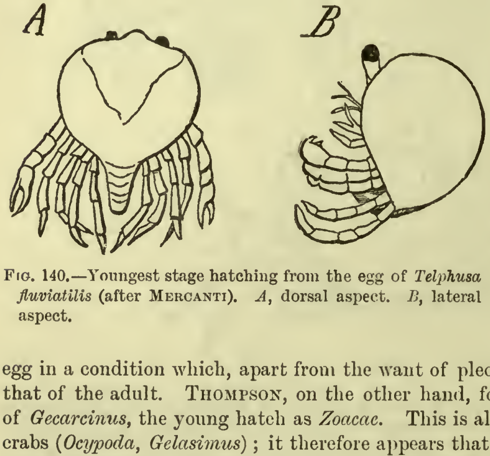

FIG. 140.—Youngest stage hatching from the egg of *Telphusa fluviatilis* (after MERCANTI). *A*, dorsal aspect. *B*, lateral aspect.

The metamorphosis of some land and fresh-water crabs appears abbreviated in another manner. WESTWOOD (No. 156) states that the young of a species of *Gecarcinus* leaves the egg in a condition which, apart from the want of pleopoda, altogether resembles that of the adult. THOMPSON, on the other hand, found that, in other species of *Gecarcinus*, the young hatch as *Zoaeae*. This is also the case with other land crabs (*Ocypoda*, *Gelasimus*); it therefore appears that, in most crabs that live on land, metamorphosis is not abbreviated, and that the young *Zoaeae* are hatched in the sea, a fact connected with the regular migration of the land crabs to the sea-shore (F. MÜLLER, No. 16).

The abbreviation of metamorphosis in fresh-water crabs (*Trichodactylus*, F. MÜLLER, No. 143; *Dilocarcinus*, GÖLDI, No. 129; *Telphusa*, MERCANTI, No. 139) is, on the other hand, in agreement with what is known of other fresh-water Decapods (*e.g.*, *Palaemonetes*, *Astacus*, &c.). The young (Fig. 140) here leave the egg in a form already greatly resembling the adult. The eyes still appear comparatively large, and the cephalo-thorax, on account of the presence of food-yolk, is much swollen. The abdomen has no pleopoda. In *Dilocarcinus*, the segments of the abdomen are still quite distinct, and do not yet show the fusion characteristic of the adult.

11. Stomatopoda.

The Stomatopoda are a branch of the higher Crustacea which very early separated from the common Malacostracan stock, and which retain in their organisation very primitive features, side by side with peculiar developmental forms. Among the former we may reckon the long dorsal heart provided with many pairs of ostia, and the condition of the dorsal shield which covers the segments carrying the maxillipedes, but does not fuse with them. Another primitive character is perhaps found in the presence of ten pairs of segmentally-arranged hepatic tubes, some of which belong to the abdomen. The position of the more important organs (hepatic tubes, genital organs, heart) in the large abdomen is a distinctive characteristic of the Stomatopoda, as opposed to other Malacostraca, in which this region of the body serves almost exclusively as a muscular locomotory organ.

On the other hand, the metamorphosis of the Stomatopoda shows peculiar characters, although it cannot be denied that it has a certain ontogenetic tendency in the same direction as that of other Malacostraca. In spite of the important treatises of Claus (No. 86) and Brooks (Nos. 83 and 84), our knowledge of the metamorphosis of the Stomatopoda is still somewhat incomplete, especially with regard to the first stages which hatch from the egg, and the connection between the larval forms, that often vary greatly, and the sexual animals to which they belong, these last differing less from one another than do the larvae. A general distinction may be made between two types of larvae which, however, are connected together by intermediate types; these two were formerly classed as separate genera under the names of *Erichthus* and *Alima*. Of these two forms the *Erichthus* shows the more primitive metamorphosis, so that we shall describe this larva first.

The youngest known stage of the *Erichthus* series, probably the one at which the young animal leaves the egg, is called the *Erichthoidina*. The youngest larva known (Fr. Müller and Claus, No. 87) is 2 mm. long, and is seen to be divided into three regions: (1) an anterior, unsegmented cephalic region which carries the eyes, antennae, and mouth-parts, and gives origin to the fold of the dorsal shield which projects backwards; (2) a middle thoracic region hidden under the dorsal shield and consisting of eight segments, the five anterior carrying Copepod-like biramose limbs, while the three posterior segments are limbless; (3) a posterior region in which the still unsegmented abdomen is developed in the form of a flat caudal plate. The spines of the dorsal shield recall the *Protozoaea* stage of *Lucifer*. There is a long, forwardly-directed rostrum, a short, unpaired median spine projecting backwards from the posterior edge of the dorsal shield, while, springing from the sides, are two long postero-lateral spines (Fig. 141 *A*). Besides the Nauplius eye, the paired stalked eyes are found on either side of the rostrum below the dorsal shield. The two pairs of antennae are still short and uniramose. The mandible has no palp, and the two pairs of maxillae are present in a very rudimentary condition as small lobes. The five

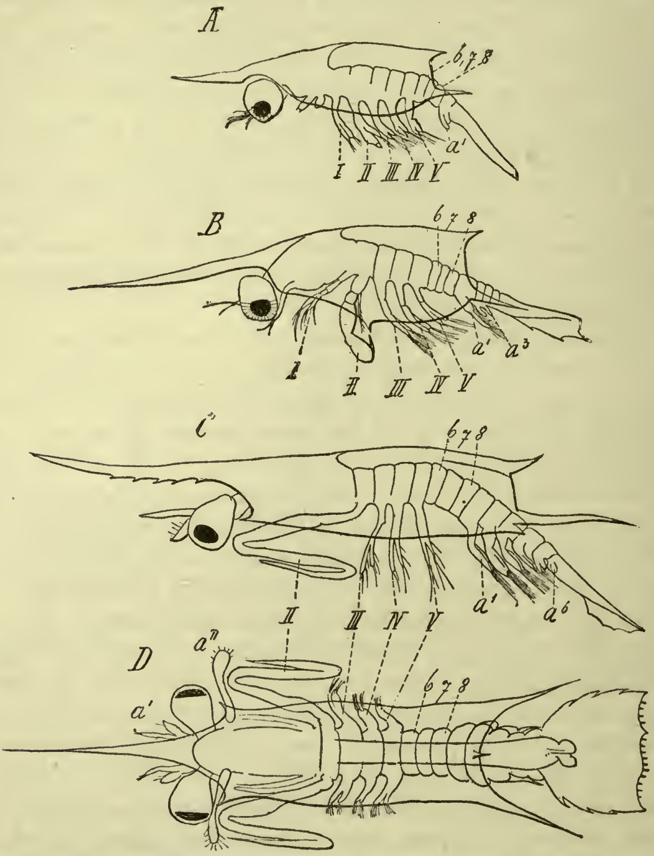

FIG. 141.—Several consecutive *Erichthoidina* stages (after CLAUS). *a'*, first antenna; *a''*, second antenna; a^1–a^6, the six pleopoda; *I–V*, the five maxillipedes; *6, 7, 8*, the three posterior thoracic segments which, in these stages, have no limbs.

pairs of swimming limbs which follow (Fig. 141, *I–V*) are biramose, and provided at their ends with setae; these appendages correspond to the five pairs of maxillipedes found later, while the next three limbless segments (*6*, *7*, *8*) carry at a later stage the biramose ambulatory limbs. In the stage now under consideration, all the thoracic segments are quite distinct, the five anterior ones being provided with limbs, while the abdomen is still unsegmented. In the following stages, the abdominal segments appear in regular order, as also do the pleopoda belonging to them, while still no trace of limb-rudiments can be seen on the last three thoracic segments. It results from this, that, in the Stomatopodan metamorphosis, the primitive order of development of the segments (from before backward) is retained, whereas this order is broken through in the formation of the limbs by the belated appearance of limb-rudiments on the three posterior thoracic segments.

In the next stage (3 mm. long, Fig. 141 *A*), the first abdominal segment is marked off, and the rudiment of the first pair of pleopoda, still devoid of setae, are already to be seen on it (a^1). In the first antenna, the rudiment of an accessory flagellum can be recognised as a short conical process. The five pairs of swimming limbs are also modified. In the second swimming limb particularly, the endopodite has enlarged as the rudiment of the future raptorial claw.

In the next stages (Fig. 141 *B* and *C*), the different abdominal segments and their limbs continue to appear in regular order. The anterior pair of pleopoda are already developed as biramose lamellate appendages furnished with setae, while those of the posterior segments are more rudimentary in shape (a^1–a^6). Even the sixth pair of pleopoda (a^6), which later attains great development as lateral limbs of the caudal fin, is no exception in this respect, but develops last and in a shape exactly resembling the other pleopoda.

Meantime, the limbs of the anterior portion of the body, especially those of the maxillary region, undergo important alteration. In the anterior antenna (Fig. 141 *D*, a'), we can distinguish a three-jointed protopodite, a short exopodite beset with olfactory setae, and a longer inner branch (the rudiment of the accessory flagellum appearing at a later stage). The second antenna, besides a fan-like plate which has developed on its extremity, shows the bud-like rudiment of a flagellum. Whereas the mandible is still for a long time without a palp, short rudiments of palps have already appeared on the two maxillae. The two anterior maxillipedes (Fig. 141 *B*, *C*, *D*, *I*, *II*) change in the direction of their final shape; the exopodite which serves as a swimming organ degenerates and finally altogether disappears. The endopodite of the first maxillipede remains comparatively small, and gradually develops the rudiment of a small prehensile claw at its end. The endopodite of the second maxillipede, on the contrary, early develops into a powerful, clawed raptorial limb. On the basal joints of both these limbs the rounded epipodial plates, which are still without setae, appear simultaneously. *The three following pairs of biramose limbs meantime undergo an unusually interesting process of degeneration*, by which their transformation into the adult form is introduced. Here also the exopodite gradually vanishes, but, in addition, the endopodite becomes an unjointed rudiment without setae, out of which, only in later stages, is produced the adult limb ending in a short prehensile claw. Indeed, the degeneration of these three limbs may go so far that they *disappear altogether*, only to reappear in later stages simultaneously with the rudiments of limbs of the three following thoracic segments (sixth, seventh, and eighth thoracic segments). In the latter case we have a larva which, in the possession of the seven anterior pairs of limbs and the absence of the six following thoracic limbs, shows a certain agreement with the *Zoaea* of other Malacostraca, and which has therefore been called the *Pseudozoaea* of the Stomatopoda (Fig. 143). This larval type, first described by FR. MÜLLER, chiefly occurs (CLAUS) in the larvae belonging to the genera *Pseudosquilla* and *Gonodactylus* which were described by BROOKS as *Pseuderichthus* and *Gonerichthus;* it is, however, also found (BROOKS) in the ontogenetic series (*Lysioerichthus*) of the genus *Lysiosquilla.*

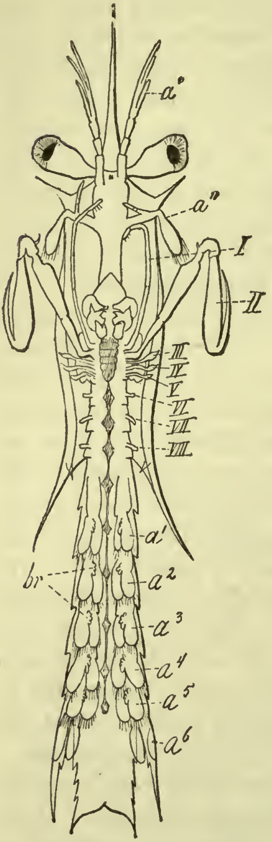

FIG. 142.—Older *Erichthus* (after CLAUS). a', first antenna; a'', second antenna; *I–V*, maxillipedes; *VI–VIII*, rudiments of the three ambulatory limbs; a^1–a^6, the six pleopoda; *br*, branchial rudiments.

Later stages, which are distinguished by the transformation of the sixth pair of pleopoda into the lateral appendages of the caudal fin, bring about the transition to the actual *Erichthus stage* (Fig. 142), the three posterior maxillipedes gradually reappearing and the hitherto missing pairs of limbs of the last three thoracic segments growing out as buds. When the rudiment of the rounded prehensile claw can be recognised on the last three maxillipedes, and the three posterior thoracic appendages are seen as rods which soon become biramose, the *Erichthus* stage appears to be reached. This stage thus possesses all the limbs of the adult form. The transition into the sexually mature form is accomplished very gradually, the abdomen continually increasing in size, and the branchial filaments (*br*) growing out on the exopodites of the abdominal limbs. The larval forms which bring about this transition to the sexually mature animal, when exhibiting broad and compact bodies and retaining the appearance of the *Erichthus*, are known as *Squillerichthus*, while certain ontogenetic forms which, even in the *Erichthoidina* and *Erichthus* stages, are remarkable for their slender bodies, pass from the latter into a *Squilloid* stage (Claus) which more nearly resembles the adult form.

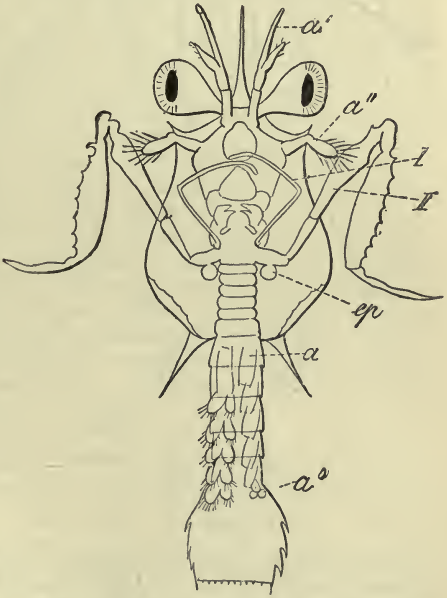

Fig. 143.—Squilloid larva (so-called *Pseudozoaea*), after Claus. *a'*, first antenna; *a''*, second antenna; *I*, *II*, first and second maxillipedes; *ep*, epipodial appendage; a^1–a^6, the six pleopoda.

A second Stomatopodan ontogenetic series consists of the *Alima* forms. These larvae (Fig. 144) are distinguished by their great size, the length of the body, and the broad, flat cephalo-thoracic shield, which usually does not cover the posterior thoracic segments; further, by the position of the mouth, which has shifted far back, and by the slight forward extension of the shield, owing to which the bases of the eye-stalks appear to be covered by the rostrum only. None of these features, taken alone, is to be relied upon in distinguishing between the *Alima* and the *Erichthus*, since forms are known which, by the anterior position of the mouth and the covering of all the thoracic segments by the dorsal shield, show affinities with the *Erichthus*, while, by the uncovered condition of the eye-stalks and the flattening of the cephalo-thorax, they show *Alima* characteristics. Such transitionary forms have been called *Alimerichthus.*

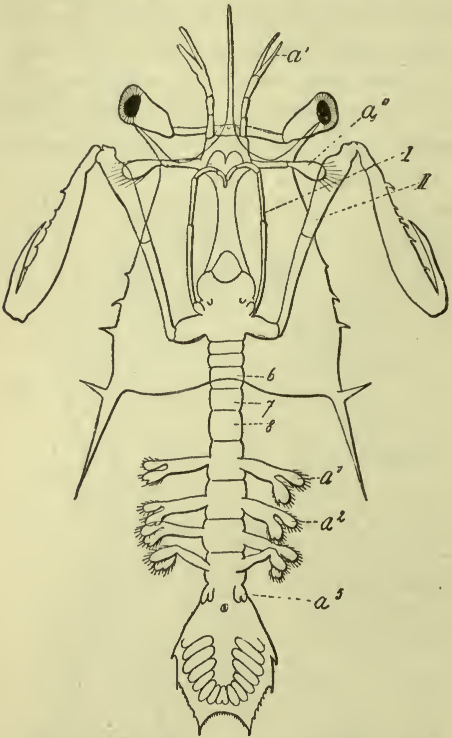

Fig. 144.—Young *Alima* larva (after **Brooks**). *a′*, first antenna; *a″*, second antenna; *I, II*, first and second maxillipedes; *6, 7, 8*, three posterior thoracic segments; a^1–a^5, first five pleopoda.

The youngest known *Alima* stages (Fig. 144) probably correspond to the *Pseudozoaea* described above in connection with the *Erichthus* series. The anterior antenna already shows the rudiment of the accessory flagellum, while in the second antenna, which ends in an oval plate, the rudiment of the flagellum is still wanting. The first pair of maxillipedes (*I*) are long and palp-like, while the second pair (*II*) have already assumed their final form as prehensile organs. The three following pairs of maxillipedes (*III–V*) as well as the three pairs of biramose ambulatory limbs are entirely wanting. The segments to which these latter belong may still be indistinctly marked off. The four anterior pairs of pleopoda are well developed, while the fifth and sixth abdominal segments are still but slightly developed as limbless rudiments. It appears that the *Alima* leaves the egg in the form just described (*cf.* P. Mayer, No. 138,

p. 219); the metamorphosis of the Alima series would thus appear abbreviated by the suppression of the *Erichthoidina* stages. The further course of development in the *Alima* form agrees with that in the *Erichthus* forms.

The connection of the various ontogenetic forms with definite genera and species of Stomatopoda can hardly be accomplished on account of the difficulty of obtaining continuous series of stages. It must, however, be considered probable (Brooks, No. 84) that the *Alima* and *Alimerichthus* forms represent the larvae of the genus *Squilla*. W. Faxon, at least, succeeded in producing from an advanced *Alima* the young stage of *Squilla empusa*. Brooks believes that he can recognise in *Alimerichthus* the larvae of species closely related to *Squilla microphthalma*. Still more difficult to decide is the question in what way the *Erichthus* forms which merge one into the other are to be distributed among the other Stomatopoda. Claus, however, has related certain *Erichthus* forms with high, laterally compressed frontal spine and short carapace (*Pseuderichthus*, Brooks) to the genus *Pseudosquilla*, while, on account of the slightly arched dorsal shield, the long rostrum and the closely approximated, posterior lateral spines, and, above all, the absence of teeth on the terminal joint of the large prehensile maxillipede, he has related other forms (*Gonerichthus*, Brooks) to *Gonodactylus*. Another series of larval forms (*Erichthus Duvaucellei* and *multispinosus*) characterised by a strongly arched dorsal shield, a flat abdomen, widely separated posterior lateral spines, as well as ventrally incurved lateral edges of the dorsal shield, may be referred, with Brooks, on account of the presence of numerous teeth on the terminal joint of the second maxillipede, to *Lysiosquilla*, and may therefore be called *Lysioerichthus*. Brooks was able to observe, in the case of a larva nearly related to *Lysioerichthus multispinosus*, the direct transition into *Lysiosquilla excavatrix*. With regard to the difficulty of classifying the other larval forms, it must be borne in mind that our knowledge of the adult forms is by no means complete, as has been proved by occasional discoveries (such as that of the remarkable *Pterygosquilla* found by Hilgendorf). Fossil Stomatopoda have also recently become known.

12. Cumacea.

The Cumacea, which occupy an intermediate position between the Schizopoda and the Arthrostraca (especially the Anisopoda), show an abbreviated and fairly direct form of development. As in the *Mysidae* (p. 257), metamorphosis is confined almost entirely to stages passed through within the brood-cavity of the mother. The embryos, by their dorsal curvature, as well as by the presence of the dorsal organ, recall the Isopoda. The compound eye, which in the adult is usually unpaired, arises by the fusion of paired rudiments. The young that emerge from the brood-cavity are still without the last pair of thoracic limbs, and, in this respect, resemble the Isopoda. Only the sixth pair of pleopoda is well developed. The five anterior pairs are wanting in the young (as is also the case in the Anisopoda), and are, as a rule, only partly developed in the adult males (Dohrn, No. 96).

13. Anisopoda.

Among the Arthrostraca, the Anisopoda (*Apseudes, Tanais*) show the most primitive condition, somewhat suggestive of that found in the Schizopoda. Embryonic development and the greater part of the metamorphosis here takes place within the brood-cavity of the mother (as in *Mysis* and the Cumacea). The young on emerging from the brood-cavity (Fig. 145), like those of the Isopoda, are distinguished from the adult by the absence of the last pair of thoracic limbs. As in the Cumacea, all the pleopoda, except the sixth pair, which are filamentous caudal appendages, are wanting. A point of great interest is the presence of a wing-like shell-fold (*ps*) standing out laterally from the cephalo-thorax. This renders possible the derivation of the Arthrostraca from a racial form provided with a dorsal shield, and also seems to establish the significance of the lobe-like appendages of the *Asellus* embryo (*cf.* above, p. 151).

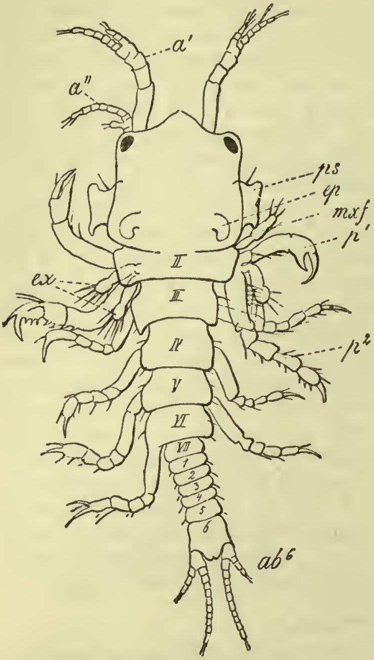

Fig. 145.—Young of *Apseudes Latreillii* from the brood-cavity (after Claus). *II–VII*, second to seventh thoracic segment; *1-6*, the six abdominal segments; *a'*, first antenna; *a''*, second antenna; ab^6, sixth pleopod; *ep*, epipodial appendage of the maxillipede; *ex*, exopodites of the first and second thoracic limbs; *mxf*, maxillipede; p^1, p^2, first and second thoracic limbs; *ps*, carapace.

14. Isopoda.

We have already had occasion to mention some features of the development of the Isopoda (p. 150), especially the dorsal curvature and the development of the dorsal organ in these animals. In the Isopoda also, after the full number of segments have appeared and the limb-rudiments have developed, the egg-envelope splits, and the larva, still incapable of motion, maggot-like, and surrounded by the Nauplius cuticle, undergoes its further development in the brood-cavity of the mother (*Asellus*). When it leaves that cavity, it already resembles the adult in the general segmentation of the body, being still distinguishable from the latter by the relatively large size of the head and the eyes, the incomplete segmentation and the non-existence of setae on the limbs, and above all by the *absence of the last pair of thoracic limbs.* This young form passes gradually through several moults into the adult stage. SCHIÖDTE and MEINERT (No. 175) distinguished in the *Aegidae* (and *Cymothoidae* generally) three consecutive larval stages, the youngest of which, found still in the brood-cavity of the mother, is marked by the absence of setae on the limbs and the telson. The second free-swimming stage has already developed setae, and during the third stage the limb-rudiments develop on the last thoracic segment. In the *Cymothoidae* we meet with indications of degeneration owing to the parasitic life adopted by these forms; these even appear during metamorphosis, finding expression in the shortening of the antennae and the changing of the thoracic limbs into adhesive organs.

In individual cases, these changes lead, through the reductions caused by parasitism, to a much more distinctly marked metamorphosis, the sexual heteromorphism also being more accentuated than in the free-living Isopoda. This is the case in the families of the *Anceidae*, *Bopyridae*, and *Entoniscidae*.

In the genus *Gnathia*, the female form (*Praniza*) is very different from the sexually mature male (*Anceus*). In the female, the head is small and triangular, and three of the posterior thoracic segments fuse to form a swollen region (brood-chamber); in the male, the head is broad and square, and the seizing pincers are branched like the horns of the stag-beetle. The young forms of this family show the elongate *Praniza* type, but from the very earliest stages there are indications of sexual dimorphism, the larvae which will become females already showing signs of the fusion of three thoracic segments, which, in the young males, are quite distinct from one another. These *Praniza*-like larvae lead a parasitic life (on fishes). Consequently, mouth-parts which are adapted for piercing and for suction project forward under a large upper lip. The mandibles and maxillae are adapted for piercing; they are palpless, and pointed like stylets, and the mandible and second maxilla are toothed at their ends. A pair of maxillipedes follows, the segment carrying them being fused with the head. This anterior maxillipede, which is somewhat long, forms a kind of lower lip, while the second gnathopod ends in an anchoring hook. The five following thoracic segments (the third to the seventh) carry five pairs of limbs changed into anchoring organs, the fifth to seventh being fused in the female.* The eighth thoracic segment is retained in a very rudimentary condition, and is followed by a well-segmented abdomen furnished with biramose pleopoda used for swimming. During the transformation into the adult form, the upper lip and the maxillae are lost, while the maxillipedes undergo important alteration. They become lamellate organs for promoting circulation of the surrounding water. In the

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* [According to STEBBING (*A History of Crustacea*, London, 1893) it is the fourth, fifth, and often the sixth thoracic segments which fuse and form the brood-chamber.—ED.]

female larva the head decreases in size, the eyes undergo degeneration, while in the male larva the head grows out into a large square region of the body, which is also provided with degenerate eyes, and from which project, anteriorly at the sides of the rudimentary upper lip, two strong seizing pincers. We should feel inclined to derive these latter from the mandibles of the young form, had not DOHRN observed that they have an independent origin (*cf.* the treatises of SPENCE BATE, No. 161; HESSE, No. 168, and DOHRN, No. 164).

In those much specialised parasites, the *Bopyridae*, which have sucking and very much reduced mouth-parts, striking sexual dimorphism develops in a manner similar to that found in many parasitic Copepoda (*Lernaeopodidae*), the less degenerate but smaller dwarf males (Fig. 147 *A*) appearing attached to the large and much deformed females. The males retain in general the Isopod appearance, the body remains symmetrical and distinctly segmented, the eyes are retained, although in a reduced condition. In the female, on the contrary, the eyes are almost entirely lost; the disc-like broadened body is asymmetrical, and its segments often indistinctly marked off one from the other. The segmentation of the abdomen may in both sexes be reduced.

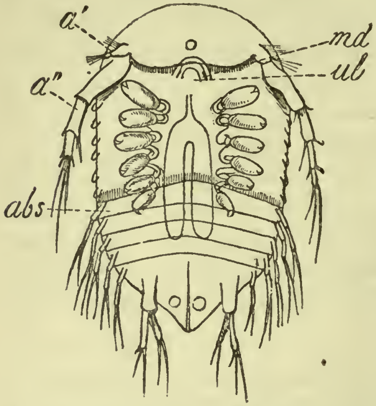

FIG. 146.—Larva of *Bopyrus* with six pairs of thoracic limbs (after WALZ). *a'*, first antenna; *a''*, second antenna; *md*, mandible; *ul*, lower lip; *abs*, first abdominal segment.

The larvae of the *Bopyridae*, when they leave the brood-cavity (Fig. 146), have well-developed jointed antennae, the second pair being principally used for locomotion. The mouth-parts already show the structure characteristic of the adult. The six pairs of thoracic limbs are developed as anchoring organs. The last thoracic segment is still, as in all Isopod larvae, without limb-rudiments. Most of the abdominal segments are distinct from one another, only the last two are fused with the telson. There are five biramose (in many forms uniramose) pairs of pleopoda used as swimming limbs, while the limbs of the sixth segment (uropoda) have developed as caudal hooks. There are no distinctions of sex at this stage between the larvae, which swim about freely and seek for their future host.

After attachment has taken place in the branchial cavity of the host (commonly a prawn), the larva develops further through the appearance of the last pair of thoracic limbs, and the great reduction of the antennae and the pleopoda, till, finally, the reduced adult form above described is reached. The abdomen of the adult, in many forms, carries unjointed tubes or lamellae corresponding in position to the pleopoda; these are, perhaps, of importance as respiratory organs, and were formerly repeatedly claimed as transformed pleopoda. Kossmann, however, has pointed out that they appear as new structures only after the entire disappearance of the latter. This, however, does not disprove the pleopodan character of these appendages, since individual appendages often completely degenerate in the metamorphosis of the Crustacea, and reappear again later.

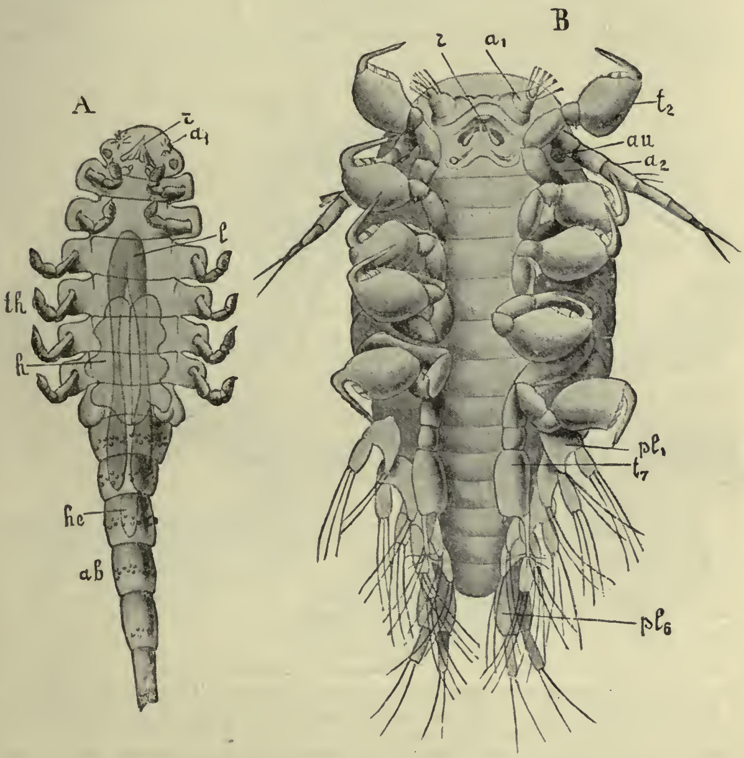

Fig. 147.—*A*, male of an Entoniscid (*Cuncrion miser*). *B*, young larva of an Entoniscid (*Portunion maenadis*), after Giard and Bonnier, from Lang's *Text-book*. *a′*, first antenna; *a″*, second antenna; *ab*, abdomen; *au*, eye; *h*, testis; *he*, heart; *l*, hepatic tubes; pl_1–pl_6, the six pleopoda; *r*, rostrum; t_2–t_7, the second to the seventh thoracic limb; *th*, thorax.

The most marked parasitic transformations of the female are found in the *Entoniscidae*, which, as has been confirmed by the recent researches of Giard and Bonnier (No. 167), are very closely related to the *Bopyridae*. These parasites are found within the body-cavity of the host (crabs, *Paguridae*), but must be described as ectoparasites, as they are enclosed in a chitinous sac derived from an invagination of the outer surface of the body (wall of the branchial cavity) of the host. The body of the female (Fig. 148 *B*) is very peculiar in shape and dorsally curved; it has a rounded cephalic region (*cg*) with piercing mouth-parts and vestigies of antennae (*ae*, *ai*), an unsegmented thorax (*th*) which carries the ventral brood-cavity formed by the lamellae of the limbs (Fig. 148 *A*), and a segmented abdomen (*ab*) with sabre-shaped or lamellate pleopoda (en_3). The small males (Fig. 147 *A*) become attached to the females and resemble in appearance the Bopyrid males, being, however, distinguished from these by the absence of the last pair of thoracic limbs (which have degenerated) and of the second antennae. The young larvae (Fig. 147 *B*) very closely resemble those of the *Bopyridae*, and always possess paired eyes (*au*), and sometimes also a Nauplius eye (*Grapsion*). They are distinguished from the Bopyrid larvae chiefly by the shape of the penultimate thoracic limbs (t_7), which varies in different genera, and also differs from that of the other

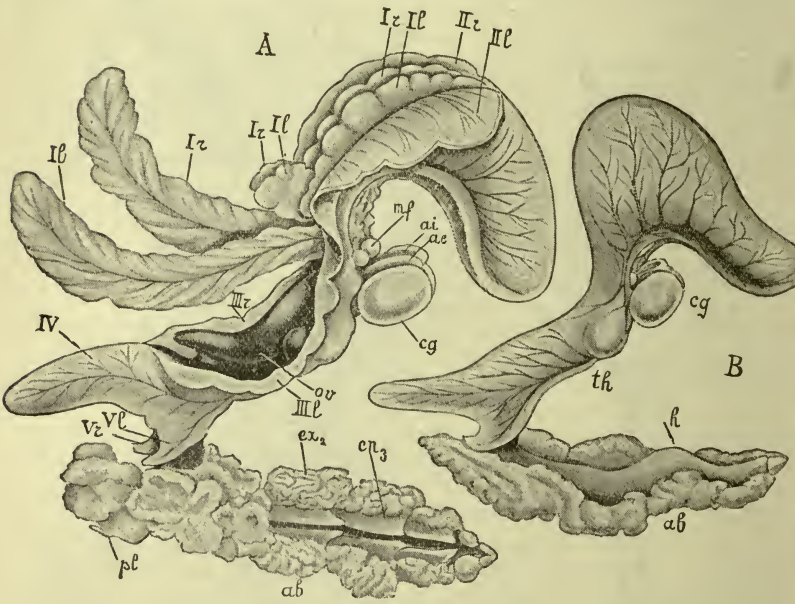

FIG. 148.—Adult female of an Entoniscid (*Portunion maenadis*), after GIARD and BONNIER, from LANG's *Text-book*). *A*, with the brood-cavity partly opened in the ventral median line and the brood-lamellae separated. The abdomen (*ab*) is so placed that the ventral side is seen. *B*, brood-cavity not opened, showing the dorsal surface of the abdomen (*ab*) *Ir*, the anterior, middle, and posterior lobes of the first brood-lamella on the right side; *Il*, the same of the first brood-lamella on the left; *IIr*, *IIl*, second brood lamellae (right and left); *IIIr*, *IIIl*, third brood-lamellae (right and left); *IV*, fourth brood-lamella; *Vr*, *Vl*, fifth brood-lamellae (right and left); *ab*, abdomen; *ae*, outer, *ai*, inner antennae; ex_2, exopodite of the second pleopod; en_3, endopodite of the third pleopod; *co*, cephalic region (so-called cephalogaster); *h*, cardial prominence; *mf*, maxillipede; *pl*, pleural lamella of the first abdominal segment; *ov*, ovary; *th*, thorax.

thoracic limbs. The last pair is, as in all Isopoda, wanting. In a later stage (*Cryptoniscus* stage) this missing pair of limbs develops. The larvae of this stage become sexually mature as complemental males, protandrous hermaphroditism occurring here as in all other Isopoda (BULLAR, P. MAYER). At a later stage they change into females or into the final degenerated male forms (GIARD and BONNIER, No. 167).

15. Amphipoda.

The embryos of the Amphipoda, which, as has been previously mentioned (p. 148), are distinguished from those of the Isopoda by the ventral curvature of the body within the egg, already have the full number of segments and limbs of the adult. Even the fusions which take place between special segments in some forms are already present in the embryo (F. MÜLLER, No. 16). Metamorphosis is consequently reduced to small alterations of shape, increase in number of the joints and olfactory filaments of the antennae, and additions of setae and teeth.

A somewhat more pronounced metamorphosis is found in the Hyperidea. In the newly hatched young of *Hyperia*, F. MÜLLER found no rudiments of pleopoda, whereas CLAUS, in a *Hyperia* parasitic on a Discomedusa, found, at a similar stage, the pleopoda and uropoda already developed. As a rule, the young of the Hyperidea, as compared with the adults, in which the eyes are often excessively developed, are remarkable for the smallness of the eyes, and consequently of the head. They are often further distinguished by the shape of the limbs. The young of *Phronima*, for example, have no powerful pincers on the antepenultimate pair of limbs (PAGENSTECHER). SPENCE BATE (No. 2) and more recently CLAUS (No. 177) have published accounts of remarkable differences between the young and the adults, some of which can be referred to the general manner of life. The larvae of *Rhabdosoma* thus appear remarkably compact; those of *Eutyphis*, on the contrary, are long. The *Rhabdosoma* larva recalls in its structure the genus *Vibilia*. The abdominal limbs first appear in the form of small rudiments. The *Eutyphis* larvae resemble in appearance the *Gammaridae*, so that the derivation of the Hyperidea from the Crevettina seems supported by the young stages (CLAUS, No. 177).

16. General Considerations Regarding the Development of the Crustacea.

The study of the metamorphosis of a group so varied and so rich in forms as the Crustacea is one of the most attractive and interesting pursuits for the morphologist. Great importance has repeatedly been attached to individual larval stages from a phylogenetic point of view. Although, in recent times, the *Nauplius* and *Zoaea* have been robbed of their glory as racial forms of the Crustacea, the study of Crustacean metamorphosis does not lose all phylogenetic significance, inasmuch as very distinct indications as to the relationships of the different groups are afforded by the manner of their development.

Great interest also attaches to the consideration of the causes which have brought about secondary modifications in the metamorphosis of the Crustacea.

The view that the *Nauplius* stage corresponds to the racial form of the Crustacea is associated above all with the name of Fr. Müller (No. 16), and received considerable support from his discovery that even among the Malacostraca there is a form (*Penaeus*) whose metamorphosis begins with a free-swimming *Nauplius*. After Haeckel, in his *Generelle Morphologie*, had adopted this view, it received the support of the most prominent investigators of the Crustacea (Dohrn, Claus). For a long time it remained the prevailing view. As to the way in which the *Nauplius* was to be deduced from lower forms of Invertebrata, only careful conjectures were hazarded. Worms devoid of segmentation, or with only a few segments, had to be investigated, and from this point of view the Rotatoria or simply-shaped Annelid larvae naturally came first under consideration.

In the same way as the *Nauplius* was said to be the racial form of all Crustacea, the *Zoaea* was regarded as the racial form of the higher Crustacea or Malacostraca. This view was due chiefly to the state of knowledge at that time concerning the structure of the Brachyuran *Zoaea*. Starting from the view that the segments of the central part of the body (the five posterior thoracic segments) are only rudimentary in the *Zoaea*, or, as was repeatedly asserted, are not present, F. Müller (No. 16) put forth the view that the Malacostraca were separated from the Entomostraca by the entirely different order of formation of the segments. He distinguished in the body of the Malacostraca four regions, each said to consist of five segments: the primitive body, the anterior body, the middle and the posterior body. The primitive body is a direct derivative of the Nauplius body, and yields the three anterior segments (those of the first and second antennae and mandibles) and the two posterior segments (those of the uropoda and of the telson). Later on the more newly-acquired regions of the body appear intercalated between the anterior and posterior portions of the primitive body, the segments of the anterior body (maxillae and maxillipedes) being formed first, next those of the posterior body (five anterior abdominal segments), and finally those of the middle body (segments of the five ambulatory limbs). This view was opposed as early as 1871 by Claus from the study of the ontogeny of the Stomatopoda, in which, as in the Phyllopoda, the different segments appear successively in regular order from before backward.

The idea that the *Zoaea* had significance as a hypothetical racial form was widened and modified by DOHRN (No. 9). Relying on certain features found among the Entomostraca, which were interpreted as Zoaean characteristics, and supported above all by the consideration of the *Nauplius* of *Lepas*, which was taken for the *Archizoaea* because of its spinous structures, DOHRN thought himself justified in claiming the *Zoaea* as the racial form of all the Crustacea, which, proceeding from the *Nauplius*, had brought about the transition to a Phyllopod-like ancestral form of the Crustacea. DOHRN was the principal founder of the view that the most primitive Crustacean forms are retained in the central groups of the Phyllopoda, and that all other Crustacean groups can be derived from the Phyllopoda, a view which still prevails and which we ourselves accept, although, with CLAUS, we do not regard the hypothetical racial form as possessing exclusively the characters of the living Phyllopoda, but would construct a hypothetical racial group of primitive Phyllopods, in many respects, especially in the structure of the mouth-parts, more primitively constituted than the existing forms.

DOHRN's assertion of the importance of the Phyllopoda as the central group from which all Crustacea can be derived was, in any case, a distinct advance, in so far as it removed the contrast made by F. MÜLLER between the Malacostraca and the Entomostraca by providing a possible common derivation for all classes of Crustacea. Indeed, DOHRN's view smoothed the way for further advance, since it led easily, by logical sequence, to the direct deduction of the Phyllopoda from ancestral forms resembling the Annelida.

Such a derivation of the Crustacea was, however, only very gradually accepted. The *Nauplius* at first remained unshaken in its position as racial form of all Crustacea, but the supposed phylogenetic significance of the *Zoaea* fell into the background. To CLAUS (No. 8) is due the credit of having, in consequence of his comprehensive investigations, recognised and established the nature of the *Zoaea* as a secondarily modified larval form. The ontogeny of the Stomatopoda and, above all, the metamorphosis of *Penaeus*, most distinctly show that there is no essential difference between the larval development of the Malacostraca and that of the Entomostraca, with regard to the order in which the new segments appear, that order, in both cases, being from before backwards. One of the most important peculiarities of the *Zoaeae* of the higher Macrura and Brachyura, viz., the retarded development of the segments in the middle region of the body, was thus recognised as being only a secondarily acquired character. But even for these last forms it has been distinctly shown by the more recent researches of Claus (No. 6), that these segments are not, as was formerly assumed, altogether wanting, but that they are present, although in a form difficult to recognise externally, and in a very compressed condition. Thus Claus has observed that, in the *Zoaea* stage, all the pairs of ganglia of the apparently undeveloped segments in the middle of the body were already present as the closely crowded thoracic ganglionic mass, already perforated by the sternal artery, a relationship which foreshadows the adult condition, as does the whole of the vascular system of the *Zoaea*.

Balfour, however,* believed that certain phenomena of Malacostracan ontogeny, especially the disappearance and reappearance of some of the appendages (the mandibular palp, the last two pairs of thoracic limbs in the *Mastigopus* stage of the *Sergestidae*, the three posterior pairs of maxillipedes in the Stomatopoda), could only be explained with the help of a racial form which, in many respects (above all, in the rudimentary condition of the middle region of the body), showed Zoaean characters. According to this view, there would have developed from the primitive Phyllopods, first *Nebalia*-like, so-called pre-zoaeal forms, from these *Zoaea*-like forms, and from the latter the post-zoaeal Malacostraca (Thoracostraca and Arthrostraca). Though it is a remarkable fact that in *Nebalia* the eight thoracic segments are closely crowded together and compose a comparatively short portion of the body, and that the limbs of this part are Phyllopoda-like in appearance, we are not bound to assume that this region underwent still greater reduction in the racial forms which led to the primitive Schizopoda (the ancestral forms of the other Malacostraca). With regard also to the disappearance and reappearance of individual appendages, it should be pointed out that this feature remains equally unexplained whether regarded as an ontogenetic or as a phylogenetic phenomenon. Indeed, many reasons may be given why this need not appear so altogether inexplicable, under the assumption that we have here a process of development which is modified caenogenetically. Lang† considers the limbs from their first appearance in the younger larval stages to be inherited from an ancestral form (Annelida), while the temporary disappearance of the same can be explained by the change in the condition of life of the pelagic larva. It must also be pointed out that these limbs in the adult condition are usually of quite a different shape from that in which they first appear in the larva. It is repeatedly found that limbs, while changing from one form to another, pass through a temporary intermediate stage (striking examples of this are afforded by the ontogeny of *Lucifer*, according to Brooks). This may represent an abbreviation of development, where, instead of a gradual change taking place in a limb, an ontogenetic stage has been introduced, in which, after complete loss of the larval limb, the differently shaped adult limb simply appeared as a new rudiment. Such a change in the process of development would take place especially in those

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* *Text-book of Comparative Embryology*, Vol. i., p. 508, 2nd. Ed.

† *Text-book of Comparative Anatomy*, English Ed., Vol. i., pp. 406–410.

cases in which, in consequence of the peculiar conditions of life, the limb in question was of little use to the larva at that stage. Parallel cases of this kind of change in the process of development, where there is considerable difference of shape between the larva and the adult forms, might be cited from other groups of animals. We need here only recall the loss of the larval nervous system and of the integument of the *Pilidium*, and the origin of these organs in the Nemertine from new rudiments. In other points, regarding BALFOUR's view, we can only refer our readers to its refutation by P. MAYER (No. 138), which is supported by important arguments (above all, by the reference to the systematic position and development of *Penaeus*).

We thus, with CLAUS, regard the *Zoaea* as a secondarily modified larval form related to peculiar conditions of larval life, which cannot be classed with the series of hypothetical ancestors of the Malacostraca.

In the same way the *Nauplius* also must be regarded as a secondarily modified Crustacean larval form.* In this case we have to do with a shifting back of specific Crustacean characters into earlier stages. HATSCHEK (No. 15) was the first to point out that, in a derivation of the Crustacea from Phyllopoda-like ancestors, a connection of the latter with the Annelida yields the most natural derivation for the whole group. HATSCHEK supported this view mainly on the agreement found to exist between the body-segmentation and the structure of the adult Crustacean and those of the Annelida, which had already caused CUVIER and VON BAER to establish the type of the *Articulata* (Annelida and Arthropoda). Above all, the agreement prevailing in the structure of the central nervous system (segmental chain of ventral ganglia) is so great that we can only refer it to true homology. If, on the other hand, we endeavour to derive the Crustacea through the *Nauplius* from an unsegmented form of worm, we should be compelled to assume that the points of structure in which the Crustacea and the Annelida agree had arisen independently in the two groups (convergence), and thus rested merely on analogy, an assumption which is hardly justified by the facts of comparative anatomy. Besides the agreement in structure of the central nervous system, the antennal gland should also be referred to, the homology of which with the segmental organs of the Annelida may be considered as proved. DOHRN (No. 11) arrived at a similar estimate of the value of the *Nauplius*.

If, accordingly, we derive the Crustacea (Phyllopoda) from Annelidan ancestors, we must assume for the latter a development through a *Trochophore* stage and through a further Polytrochan

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* [See foot-note, p. 319.]

larval stage consisting of few segments. In the accurate reproduction of the ancestral characters, we should expect the Crustacea also to develop through such larval stages; instead of which we find the *Nauplius* stage as the typical starting point of Crustacean metamorphosis. The larvae of the Crustacea are thus secondarily modified by the premature development of Crustacean characters. HATSCHEK was inclined, in accordance with the then prevailing conception of the *Nauplius*, to compare it, as an unsegmented form, with the Annelidan *Trochophore.* More recent observations have shown, however, that the *Nauplius* possesses several true body-segments. This is especially supported by the fact, proved by CLAUS and DOHRN, that the second pair of limbs of the *Nauplius* is innervated by a post-oral ganglion. The *Nauplius* consequently has to be considered as an already segmented larval form, and comparable at least with an already metamerically segmented young Annelidan larva (CLAUS, No. 7). Opinions as to how many trunk-segments can be attributed to the *Nauplius* will vary according to the view taken as to the segmentation of the cephalic section in the Crustacea. It appears to us best to agree with the facts of ontogeny and with the anatomy of the Crustacean brain to claim a true trunk-segment for each pair of the Nauplius limbs, and to assume, in addition, a primary cephalic section lying in front of these, and a posterior terminal region (anal segment) closely united with the budding zone (for the formation of new segments), this latter region giving rise to the telson (*cf.* on the primary segmentation of the head in the Crustacea, p. 164, and on the *Nauplius* stage, p. 191).

The transition from the Annelida to the ancestral forms of the Crustacea (*Protostraca*, CLAUS) was connected with certain modifications of structure and of method of locomotion. Even in pelagic Annelida (*e.g.*, *Tomopteris*), locomotion is effected by lateral serpentine movements of the body. The mobility of the segments *inter se* here comes to the fore, the parapodia having only a slighter degree of independent mobility. The greater cuticularisation of the surface of the body in the ancestors of the Crustacea, led to the limitation of the mobility of the metameres *inter se.* The trunk became firm and more rigid, while the limbs became articulated with the trunk and capable of independent movement. It is certain that a more perfect form of movement with less expenditure of force was thus attained. The transformation of the Annelidan parapodia into independently movable oars indicates the reason for the modifications in shape undergone by these appendages, which finally led to the development of the biramose Crustacean limb. In view of the fact that many of the parapodia of pelagic Annelida actually assume a lamellate form, we may suppose that the hypothetical ancestor of the Crustacea had similarly shaped limbs. We shall therefore be inclined to accept the view that the lamellate and as yet unlengthened form of Phyllopodan limb, which recurs in *Nebalia* and in the maxillae of the Copepoda and Malacostraca, approaches the primitive type, and that the elongate forms of limb have been secondarily developed from this. We shall then be able to derive the biramose character of the Crustacean limb direct from the correspondingly shaped Annelidan parapodium, and should perhaps be justified in deriving the epipodial appendages of the Crustacean limb from the dorsal gills of the Annelidan parapodia. On the other hand, the greater mobility of the segmental appendages led to the development of a new function, viz., the interaction of the two limbs of one and the same pair, this again leading to the development of corresponding lobate structures (endites, masticatory processes) on the mesial sides of the limbs. Such processes occur on all the trunk-limbs of the Branchiopoda, and are there used for the purpose of passing on particles of food. In most Crustacea, on the contrary, the accessory structures are limited to the limbs surrounding the mouth. It is a fact worthy of special attention that the second antenna in the *Nauplius* stage also participates in the work of mastication by means of the masticatory process on its basal joint, and attains its pre-oral position only at a later stage, when it loses its masticatory function.

If we imagine a *Protostracan* serving as a racial form of the Crustacea produced out of an Annelidan type by the modification above described in the method of locomotion, and the changes in the limbs (with which is connected a modification in the condition of the body-cavity), it becomes evident that we cannot attribute to it all those characters by which the group of the Crustacea is distinguished. The union of the five anterior limb-bearing segments to form a common region of the body (head), the transformation of the two anterior pairs of limbs into typical Crustacean antennae, the development through the *Nauplius*—these are characters which occur in all Crustacea, and which we shall also attribute to the *primitive Phyllopod*, but which need not necessarily be claimed for the Protostracan form. We may, on the contrary, claim a great latitude of variation for this latter. We shall have to assume that the hypothetical Protostracan group comprised forms of life far removed from the typical Crustacean structure. As such stocks produced independently from the Protostracan group, we may point to the Palaeostraca (Trilobita, Gigantostraca, Xiphosura), as also to the Pantopoda, of which we shall treat later.

It should here be pointed out that *Peripatus* also, in a few respects, shows wonderful agreement with the Crustacea. The researches of SEDGWICK have revealed a great similarity in the structure of the nephridia in the two groups. The relation of the maxillary ganglion to the brain in *Peripatus* recalls the corresponding relation of the antennal ganglion in the Crustacea. It has further become probable that a structure in *Peripatus*, until recently little observed, is the homologue of the Crustacean frontal organ. In consequence of these points of agreement, we may conjecture that the ancestral forms of the Arthropodan series leading to the Myriopoda and the Insecta also sprung from the Protostracan group.

If we try to give a sketch of those ancestral forms which led on from the more generally circumscribed Protostraca to the actual Crustacea, and which we are accustomed to call the primitive Phyllopoda, we shall have to presuppose in them a more homonomously segmented body, and a slighter differentiation of the various sections of the body, than are found in the Crustacea of to-day. Each of the similar trunk-segments which together constituted the greater part of the body had a pair of ventral ganglia, a pair of biramose, lamellate, Phyllopod-like limbs, and perhaps also (like *Peripatus*) a pair of nephridia. Then, as we have to regard the antennal glands and the shell-glands as well as the genital ducts as transformed nephridia, the very varying position of these latter ducts in the different groups of Crustacea seems to indicate that we must attribute to the ancestral form of the Crustacea a large number of pairs of nephridia. We may perhaps assume for the limbless posterior region of the body (terminal or anal segment) paired furcal processes as inherited from the common ancestral form of the Crustacea. The most typical Crustacean characters had, however, evidently already found expression in the primitive Phyllopoda in the structure of the anterior region of the body. We find here the fusion of the five anterior, limb-bearing segments (to which, as a sixth, should apparently be added an anterior primary cephalic segment with the eyes and the frontal organ) to form a common region of the body, the dorsal integument of which, enlarged by folding, formed the protective dorsal shield. Among the five pairs of limbs belonging to this region, the antennules, which were in all cases originally uniramose, assumed an exceptional position as bearers of the more important sensory organs. The second antennae, which followed them, were biramose and functioned chiefly as oars, perhaps also participating in the work of mastication. For this latter purpose, the mandibles lying behind the upper lip were specially suited through the modification of the basal joint, while the other part of the limb was retained in the Copepoda as a two-jointed palp. Next came two pairs of maxillae approaching in structure the subsequent trunk-limbs, and perhaps still retaining their original characters in the existing Crustacea. The presence behind the mandibles of a paired lower lip (paragnatha) in various groups of

Crustacea enables us to ascribe such a structure to the common racial form. The anterior cephalic region comprised the frontal organ (primary cephalic tentacle of the Annelida?), the unpaired (so-called Nauplius) eye, and the paired compound eyes, which we must evidently assume to be inherited from the common racial form. This development of the cephalic region and its limbs gave those characters by which the Crustacea proper (primitive Phyllopoda) were distinguished from the Palaeostraca and the other Arthropodan stocks. In the primitive Phyllopoda the sexes were probably separate; they possessed a long dorsal blood-vessel with segmental pairs of ostia, and perhaps also a pair of hepatic outgrowths in each segment. The presence of this last character is supported by the organisation of the Stomatopoda (*cf.* on the common racial form of the Crustacea, LANG'S *Text-book of Comparative Anatomy*, Vol. i., p. 406).

In conclusion we must briefly refer to the interrelationships of the different groups of Crustacea. Among the Entomostraca the Branchiopoda, among the Malacostraca *Nebalia*, and in many points of inner organisation the Stomatopoda, stand nearest to the primitive Phyllopoda. Among the Entomostraca, the Copepoda were probably the first to branch off independently; these while undergoing, in adaptation to pelagic life, a certain degeneration (that of the dorsal shield, the heart, and the respiratory organs, and the loss of the paired eyes), in other respects, especially in the structure of the mouth-parts, retained a very primitive condition. The other Entomostraca (Phyllopoda, Ostracoda, and Cirripedia) seem to stand somewhat nearer one another. Among the Phyllopoda, the small Cladocera, consisting of few segments are evidently a degenerate form of the *Estheridae*. For the Ostracoda we shall have to take as a starting point a very primitive Phyllopod completely enclosed in a bivalve shell, a form which thus must have resembled in appearance the *Estheridae*. In the most primitive form among the Ostracoda, *Cypridina*, the structure of the limbs clearly indicates a relationship with the Phyllopoda. Since we were obliged to presuppose for the primitive Phyllopoda a body of many segments, we shall have to assume for the Ostracoda a secondary diminution in number of the segments. The Cirripedia also must be deduced from a racial form similar to that of the Ostracoda, starting from the free-swimming *Cypris*-like larva. According to CLAUS, a nearer relationship to the Copepoda must often be assumed. This latter assumption rests upon the similarity of the thoracic limbs, and the similar number of segments in the thorax of the two groups. These features may, however, have been acquired independently in the two groups, since they actually recur in other Crustacea (the Cladocera, for example, having six thoracic segments), we cannot therefore consider the question as decided. For instance, we do not forget that the typical Copepodan characters (degeneration of the lateral eyes and of the dorsal shield, breaking up of the second maxillae into two pairs of maxillipedes) are not found in the *Cypris* larva of the Cirripedes. In judging of the systematic position of these latter, we shall have to lay special stress on the presence of a large bivalve shell from which the mantle of the adult develops. It therefore appears to us that there is only a distant relationship between this group and the Copepoda, and, taking into account the *Cypris* larva, we are justified in assuming a derivation from a primitive Phyllopod with a bivalve shell. In these points we agree with the view of BALFOUR (*Text-book of Comparative Embryology*, Vol. I., p. 509) and FOWLER (No. 43).

Among the Malacostraca, the Leptostraca which, besides the now living genus *Nebalia* and its relations, probably comprises a series of fossil forms such as *Ceratocaris*, *Dictyocaris*, and *Hymenocaris*, occupy the most primitive position and show morphological characters which connect this group directly with the Phyllopoda. *Nebalia*, for the accurate knowledge of whose structure and the definition of whose systematic position we are indebted to CLAUS, shows decidedly the Malacostracan type in the division of the body into regions, in the structure and number of the limbs, and in many points of internal anatomy (presence of a masticatory stomach as part of the stomodaeum, number and distribution of the hepatic tubes), so that there can be no doubt about its connection with the Malacostraca. Even the eight similarly shaped pairs of thoracic appendages, resembling the Phyllopodan limbs, are related to those of the Malacostraca by the number of joints in the endopodites. Contrasted with this, the presence at the posterior end of the abdomen of a supernumerary limbless segment is of smaller importance. Among the features which connect the *Nebalidae* with the Phyllopoda and thus constitute them direct descendants of the hypothetical group of primitive Phyllopoda must be enumerated: the presence of a long heart with a large number of venous ostia (four large and three small pairs), the very primitive structure of the ventral chain of ganglia, the maxillary ganglion having, as in *Branchipus*, remained separate, the flat, lamellate form of the eight pairs of thoracic limbs which recalls the Phyllopoda, and in which the separation of maxillipedes from the ambulatory or from the swimming limbs has not yet taken place, the presence of a large bivalve shell closing by means of a special adductor muscle, and finally the possession of two long, independently movable furcal processes strongly resembling those of *Branchipus*.

Among the other Malacostraca, the Stomatopoda occupy an unusually isolated position. We evidently have here to do with a stock which separated very early from the primitive Malacostraca. While the form of the heart, and perhaps also the arrangement of the hepatic tubes, indicate a primitive condition, there is a development in many other directions of new and evidently independently acquired characters.

The principal stock of the Malacostraca, on the other hand, is to be derived from the Leptostraca through the Schizopoda, among which, again, the *Euphausiidae* must be regarded as the most primitive group. Their primitive character can chiefly be recognised in the shape of the thoracic limbs, which are all developed as biramose swimming limbs, and more or less resemble one another. The view that the Decapoda are descended from Schizopoda is supported chiefly by the presence of a Schizopoda-like stage in the metamorphosis of many Decapods. Among these the Penaeidea, to which also the Astacidea are nearly related, approach the Schizopoda most closely. The other Decapoda seem to be derived forms of the ontogenetic series proceeding from the Schizopoda. The Brachyura, which are connected with the Macrura through many transitionary forms known as Anomura, must be regarded as the most highly developed but most specialised group of this series of forms.

A second series of forms proceeding from the Schizopoda leads through the

Mysidae and the Cumacea to the Arthrostraca, which we must regard as derived from the Schizopoda by the degeneration of the dorsal shield, the stalked eyes, and the exopodites of the thoracic limbs. This derivation has recently been strongly advocated by BOAS (No. 4). It is supported by the structure of the Anisopoda, in which rudimentary exopodites are retained on the two anterior thoracic limbs, and by the presence of a remnant of the dorsal shield. It receives further countenance from NUSBAUM'S observation in the embryo of *Ligia* (Lit., p. 189, No. 85a) of a biramose rudiment in the case of all the thoracic limbs. The Anisopoda are nearly related to the Isopoda, among which *Asellus* especially has retained a primitive condition, while the Amphipoda must be regarded as a more specialised group.*

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* [*Anaspides*, a most remarkable fresh-water Crustacean from Tasmania, combines in many respects the characters of the Schizopoda and Arthrostraca. In general form it resembles the Amphipoda, but it possesses stalk eyes, auditory organs in the two-jointed protopodite of the antennule, exopodites and epipodial plates on the thoracic limbs, and typical biramose swimmerets on the abdomen. It was placed by THOMSON (*Trans. Lin. Soc. Zool.* (2), vi. 3) among the Schizopoda. Great interest lies in the comparison made by CALMAN (*Trans. Roy. Soc. Edinb.*, xxxviii., p. 787) between *Anaspides* and the Palaeozoic forms *Palaeocaris*, *Gampsonyx*, and *Acanthotelson*.—ED.]

[Since the above was published in 1891, a new attempt has been made to deduce the Crustacea from the Phyllopoda, *Apus* being the form which, it is claimed, supplies all the requirements of the common ancestor. BERNARD'S arguments are too numerous to be detailed here, and should be studied in the originals (App. to Lit. on Crust. in Gen., I. and II.). We will confine ourselves to remarking that this derivation would account for the very general presence of the *Nauplius* larval form, the *Nauplius* being merely the young *Apus* stage in the development of its derived forms. BERNARD'S method of deducing *Apus* from an Annelid with its prostomium and mouth bent ventrally so as to use its parapodia as jaws seems, as he claims, to find support from the varying mouth-parts of the Trilobita and the Gigantostraca, and, in general, it must be admitted that the recent discoveries of the appendages of Trilobites have largely helped to confirm his argument. On the other hand, it has led him to conclusions about the origin of the shell- and antennal-glands, which most investigators of the ontogeny of these organs will not regard as justifiable.—ED.]

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CHAPTER XX.

PALAEOSTRACA.

UNDER the name Palaeostraca, STEINMANN and DÖDERLEIN have united the groups of the Trilobita, the Gigantostraca, and the Xiphosura. There can hardly be any doubt, as DOHRN (No. 11) and others have shown, that these three groups are closely connected. The Xiphosura (among which the genus *Limulus*, as sole living representative, is of special interest) show, in the shape of the cephalo-thorax, especially in *Belinurus*, a striking resemblance to the Trilobites, which are also recalled in the ontogenetic stages of *Limulus*. On the other hand, the Gigantostraca (*Eurypterus*, *Pterygotus*), in the division of the body into regions and in the structure of the limbs, are closely allied to *Limulus*. Like the latter, they possess an anterior cephalo-thoracic region, with six pairs of limbs, some, being chelate, taking part, by means of their broadened coxal portions, in the work of mastication. The masticatory region is bounded posteriorly by a lower lip known as the metastoma (in *Limulus* by paired *chilaria*, Fig. 158, *ch*, p. 345, and Fig. 159 *B*, p. 346). The region which follows the cephalo-thorax, the pre-abdomen, consists of six segments, the leaf-like limbs of which served for respiration, while there follows posteriorly a post-abdomen, consisting of six limbless segments and the telson. This latter region, in *Limulus*, is in a reduced condition. If we attempt to classify the Palaeostraca under the Crustacea, as has repeatedly been done, we shall be compelled to widen our conception of the latter group. The Crustacea, as a group, appear to be characterised by the possession of two pre-oral pairs of antennae, which, in the adult, take no part in the work of mastication, and besides their locomotory function serve chiefly as sensory organs.* The

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* The Crustacea are further distinguished from the Palaeostraca by the structure of the mouth-parts, which are developed typically in the form of mandibles and maxillae, and in the position of the paired lower lip (paragnatha), which appears in various groups behind the mandibles and in front of the maxillae. In the adult Crustacean, the maxillae can hardly be regarded as locomotory organs.

Nauplius stage, further, is typical of their development. The Palaeostraca, on the contrary, seem to lack both these characteristics. We shall therefore, perhaps, be more accurate in our determination of the systematic position of the Palaeostraca if we consider them, not as true Crustacea, but as a distinct group, nearly related to the Crustacea, which branched off independently from the ancestral form (Protostraca) before the first typical characters (the two pairs of antennae and the *Nauplius* stage) had developed (p. 315). A feature which is very common among the Palaeostraca, but does not occur to the same extent among true Crustacea, is the frequent fusing of the posterior segments of the body to form a distinct region (pygidium). This is evidently an adaptation to the habit of rolling up that part of the body. Among the Palaeostraca, the lowest grade of development is found in the Trilobites, as is evident from the more homonomous segmentation of the post-cephalic region, and, according to WALCOTT, the uniform character of the numerous limbs. The same author has shown (No. 5) that the limbs of the Trilobites exhibit in their structure remarkable agreement with the typical Crustacean limb. The former are biramose (Fig. 149), with a five- or many-jointed endopodite (*en*) ending in a claw, and a two- to three-jointed exopodite (*ex*). On the outer side of the coxal (basal) joint, spiral epipodial appendages (*ep*), thought to be gills, are attached.* It may be pointed out that, in *Limulus* also, the biramose character of the Crustacean limb finds expression in the presence of an

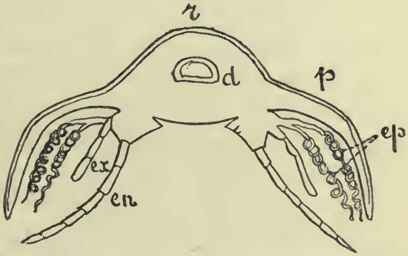

FIG. 149.—Diagrammatic cross-section through a trunk-limb of a Trilobite (after WALCOTT, from LANG'S *Text-book*). *en*, endopodite; *ep*, epipodial appendages; *ex*, exopodite; *d*, intestinal canal; *r*, tergum; *p*, pleura.

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* [The recent researches, more especially those of BEECHER (No. II.), on the limbs of Trilobites show that these appendages, with the exception of the highly specialised antennae, were but slightly modified in the different body-regions. Typically each appendage was biramous, consisting of a two-jointed protopodite, whose coxal joint in the more anterior limbs formed a masticatory blade, a five-jointed endopodite, and a strongly setiparous exopodite with an expanded basal joint, and a multiarticulate palp. On the pygidium, these appendages were more lamellate, and closely resemble those of the larval *Apus*, being typically phyllopodiform, and it is these limbs that BEECHER regards as indicative of the primitive type of limb-structure. Anteriorly, the endopodites assume a more cylindrical form.—ED.]

appendage which may be regarded as an exopodite, on the sixth pair of limbs (Fig. 158, *x*, p. 345), as well as in the form of the abdominal limbs (a_1, a_2).

While the Palaeostraca in one direction join on to the Crustacea and to their hypothetical ancestors, the Protostraca, they are further of great interest as probably the original group from which the air-breathing Arachnida developed. The view that the Arachnida, and above all the Scorpiones, are closely related to *Limulus*—first put forth by STRAUSS-DÜRKHEIM, and more recently established on a firmer basis by RAY LANKESTER (No. 16)—appears supported by so many points of agreement in the structure and the development of the two groups, that we cannot refuse to accept it; it will be more fully discussed below.

Only a few of the ontogenetic stages of the fossil Palaeostraca have been preserved through the favourable character of the stone enclosing them. The ontogenetic stages of many Trilobites are, however, known, and in some cases it has been possible to put together complete series, so that we are able to solve many important problems in the metamorphosis of the Trilobites. The ontogenetic stages of the Gigantostraca, on the contrary, have not as yet been observed.

I. Trilobita.

Notwithstanding the more recent researches of FORD (Nos. 2 and 3), WALCOTT (No. 6), MATTHEW (No. 4), the earlier investigations of BARRANDE (No. 1), which are here followed, still provide the foundation for our knowledge of the metamorphosis of the Trilobites.* BARRANDE distinguished four ontogenetic types which, however, he considered as merely provisional. Three of these methods of development may be regarded as modifications of one type, while the *Agnostus* type seems quite distinct from the others.

1. Type in which the adult pygidium develops late.

A very complete metamorphosis, consisting of many consecutive stages, was established by BARRANDE for *Sao hirsuta* (Fig. 150), a form belonging to his first ontogenetic type. The youngest known stages (*A*) still differ greatly in appearance from the adult. They are exceedingly small (two-thirds of a millimetre in diameter), rounded, and disc-shaped, and as yet show no distinct segmentation of the body. The latter consists chiefly of the rudiment of the future cephalic region, in which the glabella is already marked off from the cheeks by dorsal furrows. The posterior border of the

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* [See BEECHER, Append. Lit. Trilobita, No. I.—ED.]

glabella is not yet distinct. At its sides, close to the anterior margin of the body, two arched indentations can be recognised; these, it may be conjectured, are connected with the rudiments of the eyes (*a*). The rudiment of the cephalic shield forms the chief part of the body at this stage. The posterior section is small and shows the rudiments of a few indistinct segments. A few tooth-like projections of the posterior margin are to be regarded as the pleura of these segments. This region contains the rudiment of the whole of the future thorax and pygidium.

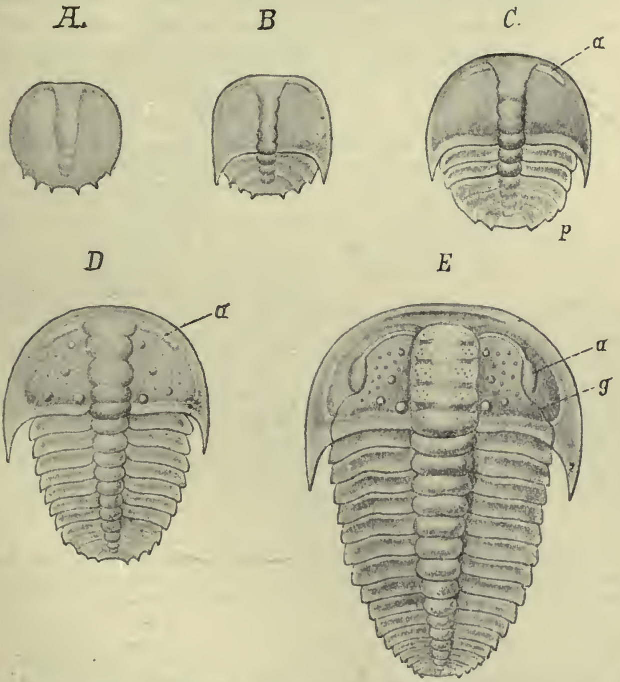

Fig. 150.—Five ontogenetic stages of *Sao hirsuta* (after Barrande). *A*, youngest stage. *B*, somewhat older stage with more distinct demarcation of the cephalic region. *C*, stage with two free thoracic segments. *D*, stage with seven free thoracic segments. *E*, stage with twelve free thoracic segments. *a*, rudiment of eye; *g*, facial suture; *p*, transitory pygidium.

In a later and somewhat larger stage (*B*) the cephalic region has become marked off by a distinct boundary from the posterior region. In this latter, the rudiments of the segments have become more distinct, and they have increased in number. In the succeeding stages (*C*, *D*, *E*) the thorax first makes its appearance as a distinct body-region, being formed from the anterior segment-rudiments of the posterior growing mass, the most anterior of these rudiments becoming segmented off as the free, movable thoracic somites. Fresh thoracic segments are successively set free from the anterior end of the posterior mass, which itself continues to grow and form new segment-rudiments. This posterior mass of incompletely separated segment-rudiments is nothing more than the budding zone of the still undeveloped thoracic segments, and must not be confounded with the pygidium of the adult. It was called by Barrande the "pygidium transitoire," and is distinguished externally from the adult pygidium by the fact that the latter, in *Sao* and *Dalmanites*, has an unbroken margin, while the posterior margin of the transitory pygidium shows freely-projecting teeth which are connected with the development of the pleura of the free thoracic segments. Only after the full number of free thoracic segments (in *Sao* 17) is attained does the adult pygidium develop; this, in *Sao*, is very short.

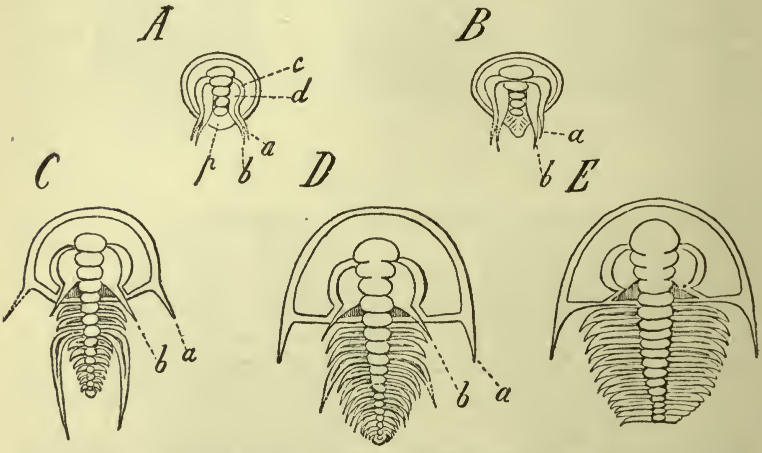

Fig. 151.—Five ontogenetic stages of *Olenellus asaphoides* (after Ford). *A* and *B*, younger stages. *C* and *D*, older stages. *E*, adult form. *a*, cheek-spine; *b*, inner spine; *c*, optic rudiment; *d*, swelling within that rudiment; *p*, transitory pygidium.

While the full segmentation of the adult is in this way gradually attained, the cephalic region, apparently through modifications brought about simply by growth, undergoes transformation which causes it to approach nearer to the shape of the adult head-shield. The limbs, the occipital furrow, and the cheek (genal) spines appear. The glabella becomes more distinct, and the transverse furrows appear on it, giving a suggestion of segmentation. Finally, the facial suture (*g*) can be distinctly recognised, and the granulated ornamentation of the surface characteristic of *Sao* develops. The changes in the position of the optic rudiments (*a*) in *Sao* is of great interest in connection with the position of the lateral eyes of *Limulus.* The optic rudiments originally lie quite near the anterior margin of the cephalic shield on each side of the glabella, and at this stage the transverse diameter of the eye is its greatest diameter. Their position in these early stages somewhat recalls the position retained throughout life by the eyes of *Cromus intercostatus.* Only in the later ontogenetic stages of *Sao* do the eyes shift laterally and posteriorly away from the glabella, in such a way that their greatest diameter runs parallel with the longitudinal axis of the body.

The development of *Dalmanites socialis* follows a precisely similar course. That of *Ptychoparia Linnarssoni* also, which was made known by MATTHEW (No. 4), does not differ essentially from that of *Sao.* A remarkable feature of the first stages of *Ptychoparia* is the approximation of the two dorsal furrows, causing the narrowing of the glabella which is not yet sharply defined. In the glabella itself, it is evident that the posterior segments, separated by transverse furrows, are at first shorter and more crowded than the long anterior segments, a contrast which disappears as the cephalic region develops further. Here also the position of the optic rudiments changes, in the way described above in connection with *Sao* and *Dalmanites.*

Special interest attaches to the statements of FORD (Nos. 2 and 3) concerning the ontogenetic stages of the American form *Olenellus asaphoides.* The youngest stages are here, as in *Sao*, disc-shaped (Fig. 151 *A*). The rudiment of the glabella, consisting of five consecutive segments, can be recognised, and behind this a small, still unsegmented region (*p*), in which lie the rudiments of the whole thorax and pygidium. In the next stage (*B*), this region shows the first traces of segmentation. On each side of the glabella lie the two **S**-shaped swellings (*c*, *d*), which are continued posteriorly into spines (*a*, *b*) that project beyond the margin of the body. The outer swelling (*c*) represents the rudiment of the eye, while the inner (*d*) takes part in the formation of the "fixed cheek." Of the two pairs of spines which run backwards, the outer (*a*) probably persists as the "cheek spines." The inner spines (*b*) are still recognisable in later stages, but then disappear, and in the adult (*E*) are represented merely by a ridge which runs diagonally from the eyes to the posterior margin of the cephalic shield. During development, a considerable portion of the posterior margin of the cephalic shield becomes intercalated between the two pairs of spines. The inner spine is of interest on account of its position. We are perhaps justified, as will be shown when we come to describe the development of the cephalic shield in *Limulus* (p. 352), in distinguishing three regions in the cephalic shield of the Trilobites (as also in that of *Limulus*), the boundaries of these regions being indicated by the facial suture. We should then have to regard only the "fixed cheeks" as the pleurae of the posterior segments of the glabella, while the "movable" or "free" cheeks, together with the eyes, belonged originally to the most anterior cephalic segment, these latter having shifted by lateral and backward growth round the posterior cephalic segments until they assumed the position in which we now see them. The position of the eyes of *Limulus* in a posterior, so-called thoracic segment would thus be explained. When we consider the ontogenetic stages of *Olenellus* (Fig. 151 *C* and *D*), we see that the pleurae of the free thoracic segments do not at first extend laterally beyond the middle of the cephalic region, as above described. We are therefore led to ask whether the inner spine (*b*), alluded to above, is not to be referred to the category of pleurae of one of those posterior segments (*i.e.*, trunk-segments) which have fused secondarily with the glabella.

The later ontogenetic stages of *Olenellus asaphoides* are marked by the fact that the pleurae of the third free thoracic segment appear greatly lengthened posteriorly (Fig. 151 *C* and *D*), a feature wanting in the adult, but recurring in the anterior segments of a few species of *Paradoxides*. Since the young stages of *Olenellus* further agree with these species of *Paradoxides* in the notching of the posterior margin of the cephalic shield, the metamorphosis of the former seems to suggest certain stages in the phylogeny of the latter genus.

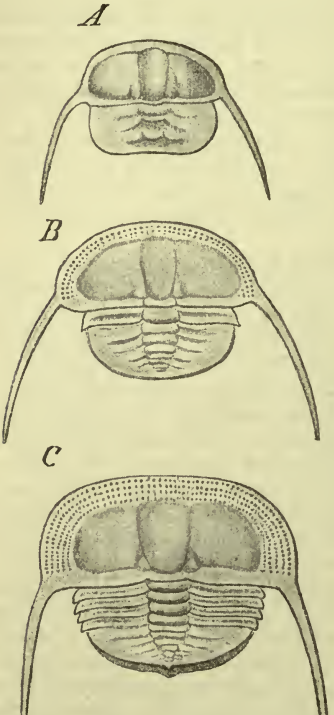

Fig. 152.—Three stages in the development of *Trinucleus ornatus* (after Barrande). *A*, youngest stage, consisting merely of the cephalic shield and the pygidium. *B*, stage with one free thoracic segment. *C*, stage with four free thoracic segments.

The third ontogenetic type of Barrande contains those forms whose stages of development exhibit the same characters as the later stages of *Sao hirsuta.* The cephalic region usually already shows the adult form; the number of the thoracic segments is, however, incomplete, while the posterior region of the body, functioning as transitory pygidium, has still to yield, by segmentation of its anterior portion, the free thoracic segments, which are at present wanting. Further development takes place as in the first type. We must assume that Barrande's third type contains forms whose youngest stages are not known, or those whose metamorphosis is actually abbreviated in such a way that they leave the egg at a later ontogenetic stage. Barrande classes under this type the following genera:—*Arethusina*, *Cyphaspis*, *Proetus*, *Arionellus*, *Conocephalites*, *Aeglina*, *Hydrocephalus*, *Illaenus*, *Acidaspis*, *Ampyx*, *Ogygia*, and *Triarthrus*.

A still more abbreviated metamorphosis seems to characterise

BARRANDE's fourth type. The cephalic region and the thorax are here already completely developed; the pygidium, on the contrary, is somewhat undeveloped, the number of segments composing it being still incomplete. We must class under this type *Paradoxides*, the species of *Dalmanites* which belong to the Hausmann group, a few species of *Phacops*, *Proetus*, *Asaphus*, etc.

2. Type with early development of the adult pygidium.

This division corresponds to the second of BARRANDE's ontogenetic types, to which belong *Agnostus* and *Trinucleus*. The youngest known stages consist merely of the rudiments of the cephalic shield and the pygidium. The latter, although still incomplete, has essentially the characters of the adult. Metamorphosis is thus limited to the development of the thoracic region, which takes place in such a way that, as in forms already described, successive free segments become cut off from the anterior part of the pygidium. The other modifications consist in the increase in the number of the rudiments of the segments in the pygidium, and in the more perfect shaping of the cephalic region. In *Trinucleus*, for example, the characteristic rows of pores of the "limb" of the head-shield are developed.

This form of development, as contrasted with the earlier type, must be regarded as more specialised. In view of the evident importance of the presence of the pygidium, we cannot greatly wonder that the modification of the posterior segments of the body to form this structure was shifted to quite an early stage. In the small number of segment-rudiments in the first stages, the abstriction of the thoracic segments and the development of new rudiments of segments at its anterior end, the pygidium, in the younger stages of this type, closely resembles the transitory pygidium of the types described above. It is, however, distinguished from these by the fact that, in form, it more nearly approaches that of the adult. It is evident that no sharp distinction can be made between these two types of development.

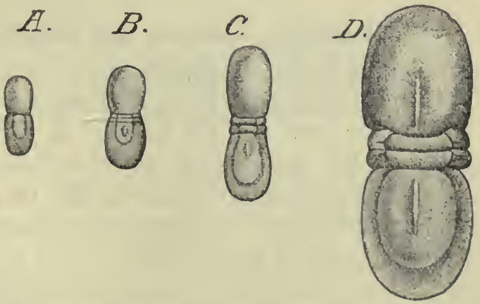

FIG. 153 —Four stages in the development of *Agnostus nudus* (after BARRANDE). *A*, youngest stage, consisting of the cephalic shield and the pygidium. *B*, stage with the rudiments of two thoracic segments. *C*, stage with two fully formed thoracic segments. *D*, adult form.

The ontogenetic stages of *Agnostus* and of *Trinucleus* strikingly recall certain early stages in the development of the germ-band in the Scorpiones, as described by METSCHNIKOFF and others (Vol. iii.). In the latter also are found at first an anterior and a posterior region of the body; a few small free segments, arising successively, being cut off from the posterior region and intercalated between the two regions. Similar stages are found in the Araneae. We must, however, bear in mind that the free segments of this germ-band are later drawn into the head, and are evidently represented in the Trilobites by the segments of the glabella. These cannot, therefore, be homologised with the free thoracic segments of the Trilobites. A certain similarity is, however, brought about by the presence of a large posterior section from which the trunk-segments arise later.

BARRANDE pointed out that most species of Trilobites in which metamorphosis occurs belong to the older strata of the Bohemian Silurian, while, in the more recent strata, young stages of Trilobites are much less frequently found, although, in these same strata, the number of species is richer, and the conditions for the preservation of these delicate forms are also to some extent favourable. BARRANDE therefore seems justified in conjecturing that metamorphosis was perhaps replaced by direct development in the later and perhaps more specialised Trilobites.

II. Xiphosura.

Limulus polyphemus is the only Xiphosurid whose ontogeny has as yet been investigated.* The metamorphosis of *L. mollucanus* is still unknown, but it should be mentioned that WILLEMOES-SUHM (No. 31) believed that a pelagic Crustacean larva obtained off the Philippines by the Challenger, which resembled the Cirripede larvae (p. 209), could be referred to *L. mollucanus*. He, however, changed his opinion later, and classed the larva among the Cirripedes.

1. Oviposition, Cleavage, and Formation of Germ-layers.

The eggs of *L. polyphemus* are laid on the seashore in holes dug in the sand half-way between high and low water mark (KINGSLEY, No. 14), or even near the former. *L. rotundicauda* and *L. mollucanus*, on the contrary, do not deposit their eggs, but carry them about attached to the swimmerets. The eggs, when laid, are enclosed in a very thick leathery membrane composed of several layers, which has been described as the chorion, and is perhaps not formed in the ovary itself (DOHRN, No. 11), but in a special portion of the genital ducts. As the embryo increases in size, this membrane bursts, so that, in the later stages, the embryo is covered solely by the later formed blastodermic cuticle.

For information as to the first ontogenetic processes in the egg of *Limulus* we are entirely dependent on the short accounts of OSBORN

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* *L. longispinus* has also recently been investigated by KISHINOUYE (*Zool. Anz.*, 14, No. 369), but we are not here able to give his statements in detail [see App. Lit. on Xiphosura, No. II. See note, p. 343.]

(No. 22), BROOKS and BRUCE (No. 10), and KINGSLEY (No. 15). Judging from these, considerable agreement with the ontogeny of the Arachnida, especially the Scorpiones, appears to prevail. In tracing the first stages of development we shall chiefly follow the more recent observations of KINGSLEY.

The first cleavage-nucleus lies, surrounded by formative yolk, near the centre of the egg.* Repeated division gives rise to a large number of cleavage-nuclei which become distributed within the egg before cleavage of the egg-contents (formation of definite cell-areas) takes place. This distribution is not regular, for the cell-nuclei wander to the surface most abundantly at the point where, in later stages, the first rudiment of the embryo will appear. Since a demarcation of the cleavage-cells takes place first at this point, the cleavage is apparently meroblastic (discoidal) in character, and thus recalls the processes observed in the Scorpiones (Vol. iii., Figs. 1 and 2). Finally, however, the whole egg breaks up into segmentation-spheres which are chiefly composed of food-yolk elements; each, however, contains a cleavage-nucleus surrounded by protoplasm.

The wandering to the surface of the cleavage-nuclei mentioned above leads, by the demarcation of cells in that region, to the formation of the blastoderm. The latter is thus first completely formed at the special point referred to, and in these stages presents the appearance of an accumulation of closely packed cells at this pole, while the rest of the surface of the egg is still covered with large cells filled with food-yolk. It appears that, in later stages also, a blastodermic thickening is retained at this spot after the blastoderm-formation has advanced over the rest of the surface; this thickening may be compared with the primitive cumulus (CLAPARÈDE) of the spider's egg.

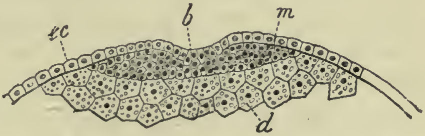

FIG. 154.—Cross section through the germ-disc of *Limulus* showing the formation of the germ-layers (after KINGSLEY). *b*, blastopore (primitive groove); *d*, yolk-cells; *ec*, ectoderm; *m*, mesoderm.

While the formation of the blastoderm is still going on, a cuticular secretion takes place at the surface of the blastoderm-cells, this leading, as in many Crustacea (p. 118), to the development of the

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* [KINGSLEY surmises this, but was unable to find the first cleavage-nucleus. —ED.]

blastodermic cuticle. This cuticle, which attains a considerable thickness and, at later stages, when the chorion has been shed, is the only covering of the embryo, is marked out into polygonal areas which correspond to the limits of the individual blastoderm-cells concerned in its secretion.

Not all the cleavage-cells enter into the formation of the blastoderm. Many remain, filled with food-yolk, near the centre of the egg. The sum total of these so-called yolk-cells represents the entoderm. The blastoderm, on the other hand, contains the elements of the future ectoderm and mesoderm.*

The next processes, which must be described as gastrulation, and which lead to the formation of the germ-band, now start from the primitive cumulus. At the middle of this latter there first appears a round depression, the blastopore, which soon becomes triangular and then lengthens. A primitive groove thus forms (Fig. 155 *A*). Simultaneously, behind the primitive cumulus, a second blastodermic thickening arises, connected with the former; this, in superficial figures, appears as a white patch. The primitive groove, which lengthens posteriorly, soon stretches into this second prominence. During this process the proliferation of mesoderm-cells takes place from the primitive groove, these cells spreading out below the ectoderm (Fig. 154). The groove here yields only mesoderm and no entoderm.

The extension of the mesoderm-elements below the ectoderm, which proceeds from the primitive groove, appears in superficial figures as a clear area surrounding the latter (Fig. 155 *A*). This area soon extends, and the whole of the clear region under which the mesoderm lies must be regarded as the commencing embryonic rudiment, and may now be called the germ-disc. At its centre, the primitive streak can be recognised, although this is much less distinct in the stages which now follow than when it first appears.

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* [According to the latest researches of KINGSLEY (No. I.), each surface-cell divides tangentially into a smaller external and a larger internal cell; the latter cells are rich in yolk and yield the entoderm, while the smaller cells yield the mesoderm. In surface view the primitive cumulus appears like a pit, but this is merely an optical effect produced by the greatly thickened centre. From this point and from the primitive streak which extends backwards from it, we find a proliferation of mesoderm-cells.

KISHINOUYE (No. II.) regards the ectoderm as having a double origin, that of the ventral surface arising from the blastoderm, while that of the dorsal surface arises from the yolk. The mesoderm, he states, arises in three ways: that of the cephalo-thorax from the deeper cells of the blastoderm, and that of the abdomen from the primitive streak; a third portion arises from the yolk-cells and possibly gives rise to the blood-corpuscles.—ED.]

2. Development of the external form of the body.

The germ-disc, whose form is now that of an elongated oval, and the bilateral symmetry of which is marked by the remains of the indistinct primitive groove, next becomes divided by a transverse furrow into an anterior cephalic area and a posterior post-oral thoraco-abdominal region. A second transverse furrow very soon occurs behind the first, cutting off from the thoraco-abdominal region the most anterior thoracic segment. This stage, in which the body consists of a rounded cephalic portion, a still unsegmented posterior region, and a trunk-segment intercalated between these two, strikingly recalls a similar stage observed in *Scorpio*. The median furrow extends anteriorly into the cephalic segment, while posteriorly it is lost in the unsegmented region of the body. New thoracic segments now successively separate from the posterior region, until the number of free thoracic segments amounts to six. A similar stage has been observed in the Araneae (Vol. iii., Fig. 25 *A*).

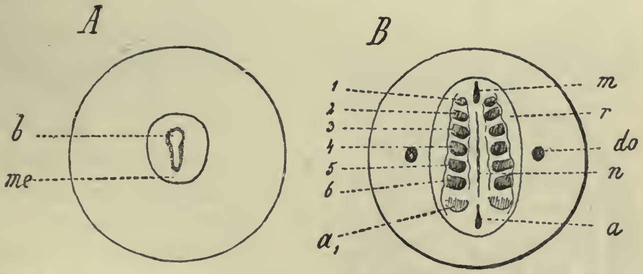

Fig. 155.—Two embryonic stages of *Limulus* (after Kingsley). *A*, stage with primitive groove. *B*, stage with rudiments of limbs. *1–6*, the six thoracic limbs; *a*, anus; *b*, primitive groove (blastopore); *do*, dorsal organ; *me*, germ-disc with subjacent mesoderm-layer; *m*, mouth; *n*, neural groove; a_1, rudiment of the operculum (first abdominal limb).

We now distinguish (Figs. 155 *B* and 162) a semicircular, anterior cephalic region, six thoracic segments, and a posterior abdominal region, also semicircular in outline. The rudiments of the limbs (the chelicerae, *1*, and the five following pairs, *2–6*) very soon appear on the thoracic segments, at first as button-like prominences. The smallest of these are the rudiments of the chelicerae, and each subsequent pair is larger than the one in front of it. The oral and anal apertures (*m* and *a*) are marked by ectodermal depressions. The first of these lies in the cephalic region, and consequently in front of the first pair of limbs (chelicerae), which belong to the first thoracic segment (Packard, Kingsley). In later stages, the mouth changes its position, shifting further back, so that it comes to lie behind the chelicerae, between the second pair of limbs (Fig. 156). Between the oral and anal apertures, which, according to KINGSLEY (No. 14) are peculiarly elongate, runs the neural groove (Fig. 155, *n*), which occupies the place of the primitive groove, that has now disappeared. The whole of the long germ-disc is bordered laterally by a thickened wall (Fig. 156, *r*), in which we recognise the first rudiment of the cephalo-thoracic shield. The first rudiments of the most anterior pair of limbs of the abdomen (a_1, operculum) very soon appear. Even at this stage, on either side and beyond the limits of the germ-disc, on the level of the fourth thoracic segment, two rounded thickenings (Fig. 155 *B*, *do*), can be recognised; these probably correspond to the so-called *dorsal organ* (WATASE).

The following stage (Fig. 156) shows the thoracic limbs more strongly developed and each bent on itself inwards and downwards. There are now the rudiments of two pairs of leaf-like abdominal limbs (a_1, a_2) which are distinguished from the thoracic limbs by their form, by their position near the median line, and by the manner of their appearance. They become separated from the germ-disc by an infolding of the body-surface taking place below and behind them (KINGSLEY). At this stage, PACKARD thought that he could recognise an indication of the boundaries of the segments on the lateral parts of the yolk near the germ-disc; this, however, KINGSLEY was unable to confirm.

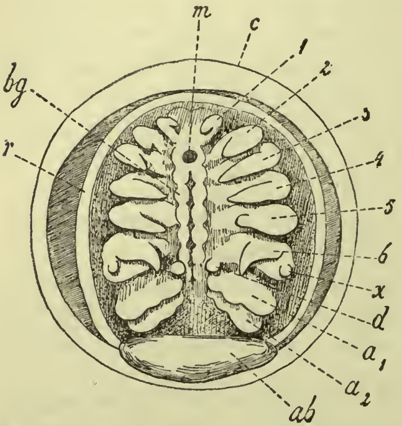

FIG. 156.—Embryo of *Limulus* (after DOHRN). *1–6*, the six pairs of thoracic limbs; a_1, first abdominal limb (operculum); a_2, second abdominal limb; *ab*, abdomen flexed ventrally; *bg*, ventral chain of ganglia; *c*, blastodermic cuticle; *d*, chilaria; *m*, mouth; *r*, margin of the future cephalo-thoracic shield; *x*, exopodite of the sixth thoracic limb.

The embryonic rudiment lies, up to this time, as a gradually extending flat disc on the sphere of yolk. The latter now begins to change into the dorsal half of the embryo by the absorption of the nutritive material (Fig. 157). The abdominal region (*ab*) is still very short, its posterior end being flexed downwards (Dohrn, *cf.* Fig. 156, *ab*). The embryo now becomes covered with a delicate cuticular integument, which is cast off by ecdysis in the next stage and then comes to lie within the space which is enclosed by the blastodermic cuticle.

The next stage (Fig. 158) is characterised by the transverse splitting of the chorion, the two halves of which remain for a long time attached to the egg as a hemispherical shell. The embryo moves within the space enclosed by the blastodermic cuticle, which is now increased by the sea-water taken into it. The cuticle is thus stretched, and the cell-like mosaic on its surface disappears. The limbs now gradually develop more in the direction of their final shape, their segmentation and the rudiments of the pincers becoming apparent. The outer appendage of the coxa (x) of the sixth pair of limbs, usually regarded as the exopodite, appears. Behind these limbs the rudiments of the paired lower lip, known as the chilaria (*ch*, *metastoma*), become apparent close to the middle line of the body; since this appendage has no ventral ganglion of its own, and does not correspond to any mesoderm-segment (Kingsley, No. 14), it should not be regarded as a limb.* An indication of segmentation now appears in the abdominal region (Figs. 157, 158, *ab*).

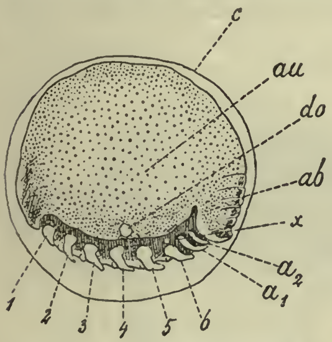

Fig. 157.—Embryo of *Limulus* (after Watase). *1–6*, the six thoracic limbs; a_1, first abdominal limb (operculum); a_2, second abdominal limb; *ab*, abdomen; *do*, dorsal organ; *au*, position of the rudiment of the lateral eye (Watase); *c*, blastodermic cuticle; *x*, exopodite of the sixth thoracic limb.

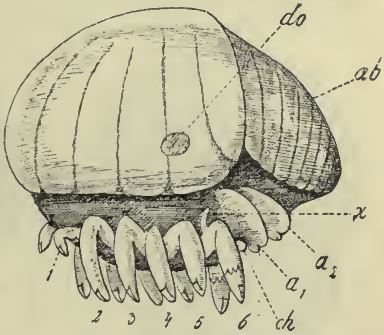

Fig. 158.—*Limulus* embryo, lateral view (after Kingsley). *1–6*, the six thoracic limbs; a_1, first abdominal limb (operculum); a_2, second abdominal limb; *ab*, abdomen; *ch*, chilaria; *do*, dorsal organ; *x*, exopodite of the sixth thoracic limb.

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* [According to Kishinouye, this pair of appendages has a ventral ganglion of its own, and is therefore to be considered as a pair of limbs. Kingsley (No. III.) believes that Kishinouye mistook the operculum for the metastoma.—Ed.]

With the gradual diminution of the food-yolk and the development of the dorsal region, the adult form becomes evident in the embryo at the next stage. The anterior region of the body, which consists of the cephalic segment and the six thoracic segments added to it, has now the form of a shield, although its dorsal side is still swollen and hemispherical. The dorsal side of this region of the body now exhibits a segmentation corresponding to the six thoracic segments; this is brought about by the re-distribution of the food-yolk (rudiment of the enteron) and by the formation of the mesodermal septa which grow inwards. On each side of the body, six outgrowths of the yolk-laden entoderm (hepatic rudiments), separated by mesodermal septa, can be recognised, the distal end of the lobes being again secondarily branched (Fig. 158). The anterior lobes now no longer lie transversely, but radially. The rudiments of the eyes have also become distinct. Those of the middle eyes are originally situated ventrally (PACKARD, No. 23), but soon shift over the anterior margin of the cephalo-thorax on to its dorsal surface. The rudiments of the lateral eyes correspond in position (WATASE) to the fourth hepatic lobe, and lie on the inner side of the dorsal organ described by this author (Fig. 157). The abdominal region now shows distinct segmentation, which, however, according to KINGSLEY, only affects the internal organs, while the ectoderm appears untouched by it (?). Nine abdominal segments in all can be distinguished (Fig. 160), the last representing the rudiment of the caudal spine, which is surrounded laterally by

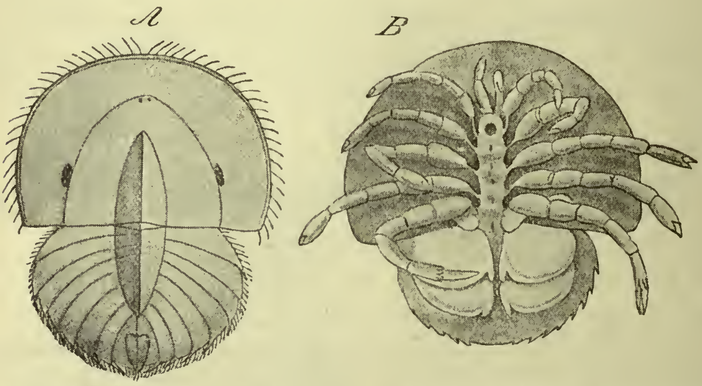

FIG. 159.—Two stages in the development of *Limulus* (after KINGSLEY, from LANG'S *Text-book*). *A*, young embryo, just hatched in the Trilobite stage, seen from the dorsal side. *B*, embryo a short time before hatching, seen from the ventral side.

the incurved segments in front of it (Fig. 159 *A*). At the base of this segment lies the anal aperture. The limbs now grow more and more like those of the adult, but the teeth are still wanting on the coxal joints, which are modified into masticatory ridges. The two anterior pairs of abdominal appendages, behind which a third pair has become recognisable, have attained the typical biramose form by the development of a small inner lobe (endopodite—Fig. 158, a_1, a_2, Fig. 159 *B*).

The stage at which the embryo emerges from the blastodermic cuticle is known as the Trilobite stage (Figs. 158 *A*, 159). The cephalo-thoracic shield is now flatter and wider, and has lost all traces of segmentation. It is distinctly divided by two longitudinal furrows into a central region with a well-marked keel and two lateral regions. The large eyes are situated in the furrows separating the median from the lateral lobes, and a semicircular ridge connects the median with the lateral eyes. The abdominal region still appears divided up into segments. Six movable thorns can be recognised on its lateral margins (Fig. 160) from the second segment to the seventh. The rudiment of a fourth pair of abdominal limbs now appears. The first pair is changed into the operculum and a fusion of the inner margins of the two exopodites takes place, accompanied by a degeneration of the endopodite. In the second and following abdominal limbs the rudiments of the branchial lamellae now appear, only four being at first apparent on each limb. Their number is increased later by the budding of new lamellae at the bases of the limbs. The endopodites of these limbs become divided up into three segments.

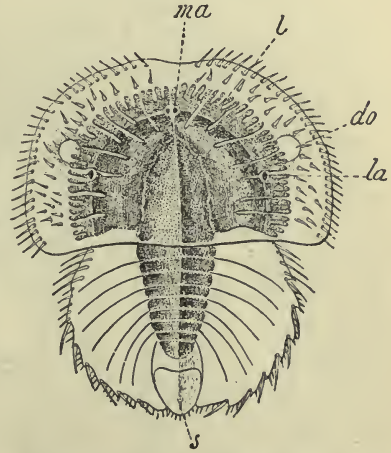

Fig. 160.—Larva of *Limulus*, at the Trilobite stage (after Watase). *do*, dorsal organ; *l*, hepatic diverticula; *la*, lateral eye; *ma*, median eyes; *s*, rudiment of the caudal spine.

The young which hatch at the Trilobite stage are endowed with great activity, and already burrow in the sand like the adults. By means of their abdominal limbs they can swim about freely, and are consequently occasionally taken in tow-nets, A. Agassiz having found a specimen three miles from the coast. After the first moult, they pass into a stage which is distinguished from the preceding by the richer ramification of the hepatic tubes, by the closer fusion of the abdominal segments, and by the lengthening of the caudal spine. This stage (Fig. 161) is worthy of notice on account of its resemblance to the Hemiaspid genus *Prestwichia*. The later stages already show the characters of the adult in all respects except sexual differentiation. The latter seems to develop very late (according to Lockwood, in the third or fourth year). Until this occurs, the males resemble the females, they then develop strong terminal claws on the second pair of limbs instead of pincers.

3. Formation of the Organs.

A. Nervous System and Sensory Organs.

The *ventral chain of ganglia* develops in the form of two ectodermal thickenings (Fig. 156, *bg*) on either side of the median line, which enclose between them a thinner portion of the ectoderm. In a superficial view, the latter appears as a neural groove, although it is not actually sunk below the surface. The lateral halves of the ventral ganglionic chain become the future longitudinal commissures, which thicken segmentally to form the ganglia, and become detached from the ectoderm from before backward. The transverse commissures seem to arise by the invagination of the enclosed median ectodermal area (neural groove),

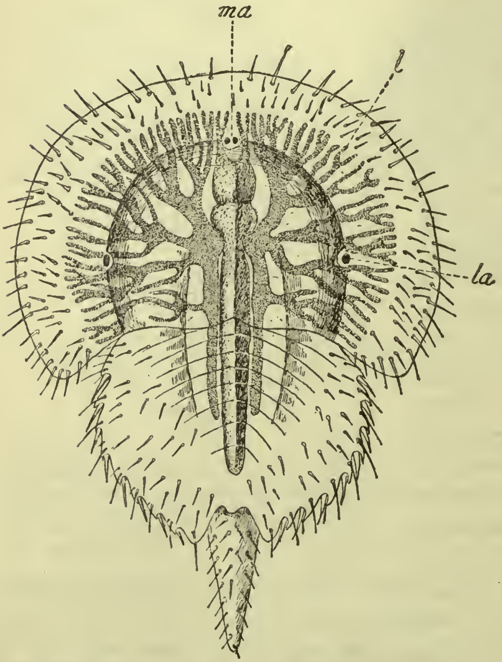

Fig. 161.—Older larval stage of *Limulus* (after Watase). *l*, hepatic diverticula; *la*, lateral eye; *ma*, median eyes.

KINGSLEY. The ventral chain of ganglia thus develops essentially in the manner described above as typical for the Crustacea (p. 160), and apparently for all Arthropoda. There are, in all, eight distinct pairs of ventral ganglia in the embryo, the six anterior pairs occurring on the six thoracic segments. As the oral aperture shifts back, the anterior pair of post-oral ganglia, those belonging to the chelicerae, moves gradually forward, so that finally these ganglia become incorporated with the oesophageal commissures proper, the nerves which run to them originating close to the edge of the brain. The thoracic portion of the ventral chain of ganglia is at first elongated. Only in later stages does it become concentrated anteriorly, the circular form characteristic of the adult arising at the same time by the shifting apart of its two halves. Nothing is as yet accurately known as to the origin of the vascular sheaths of this part of the nervous system in *Limulus*, but KINGSLEY (No. 15) states that they pass through a stage in their development which, in the Scorpiones, persists throughout life, where they are found lying upon the oesophageal commissures without completely enveloping them.

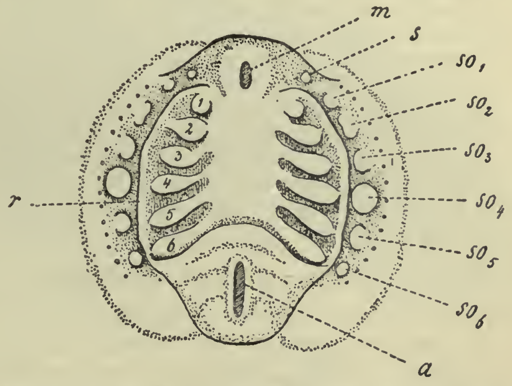

FIG. 162.—Diagram of the germ-disc of *Limulus* with the lateral, segmental sensory organs (after PATTEN). *a*, anus; *m*, mouth; *r*, margin of the cephalo-thoracic shield; *s*, sensory organ of the third cerebral segment, so_1–so_6 first six lateral, segmental sensory organs; so_4, dorsal organ, *1–6*, the six pairs of thoracic limbs.

As to the development of the *supra-oesophageal ganglion* proper, or brain, which gives off the optic and some integumental nerves (the frontal nerves), we have only a few short statements by PATTEN (Nos. 28 and 29) and KINGSLEY (No. 15), which throw but little light on the actual facts concerning the complicated processes which here appear. According to PATTEN, with whom KINGSLEY agrees, the rudiment of the brain consists of three consecutive pairs of ganglia, which represent a pre-oral continuation of the ventral chain of ganglia lying in the cephalic region of the body. (This is in agreement with the scheme drawn up by PATTEN for the Scorpiones and *Acilius*, and described in the section on the nervous system of the Insecta, Vol. iii.) Each of these three pairs corresponds to a pair of ectodermal invaginations which originally lie on the outer sides of the ventral chain, and give rise to the optic ganglia. In *Limulus*, the two anterior pairs of invaginations are said to unite to form the median eyes and the nerves connected with them, while the third pair, in *Scorpio*, yields the optic ganglia of the lateral eyes, but, in *Limulus*, is related to a small sensory organ (Fig. 162, *s*). The lateral eyes belong to the third (PATTEN), fifth (KINGSLEY), or, according to other authors, the fourth thoracic segment, and thus represent post-cephalic structures. Each optic ganglion is continued posteriorly into a nerve strand, a kind of lateral nerve running along the outer side of the limb-rudiments, and connected with a sensory organ in each segment (Fig. 162, so_1–so_6). According to PATTEN, these sensory organs (with the exception of the rudiments of the lateral eyes) have usually only a temporary importance, and soon disappear. KINGSLEY, on the contrary, holds that the first pair (so_1) yields the median eyes, the second a peculiar and as yet undescribed sensory organ, while the third disappears; from the fourth is developed the dorsal organ (so_4) of WATASE, which persists for a long time; the fifth passes into the compound lateral eyes, and the sixth, finally, degenerates. Until these statements have been confirmed by more detailed observations, they must be regarded with some scepticism.* We must refer the reader to PATTEN's treatise cited above for details as to the development of the brain in *Limulus*, his account of which, in the absence of satisfactory figures, is hardly comprehensible. We are also unable, on account of the fragmentary character of the statements made on the subject, to decide how far PACKARD's more recent researches (No. 27) as to the structure of the brain in *Limulus* can be brought into agreement with PATTEN's views. PACKARD emphasises the fact that the cheliceral ganglion in *Limulus* does not fuse with the brain, but remains distinct. The brain proper sends off only the nerves to the median and lateral eyes, and two pairs of integumental nerves (frontal and inferior frontal nerves). It consists of three pairs of lobes: those of the lateral eyes, the median eyes, and the cerebral lobes proper. In the absence of figures, it is impossible to obtain a clear idea of the true relationships of these cerebral lobes.

PATTEN considers that the development of the *median eyes* in *Limulus* closely resembles the processes observed in *Scorpio*. Here, as in the latter, there are two (or perhaps, according to PATTEN, four) invaginations which, shifting backward, unite in the median line to form a sac with a common posterior aperture. This sac gives off anteriorly two tubular processes, the blind ends of which, becoming apposed to the hypodermis of the cephalo-thorax, are transformed into the median eyes, while the parts of the processes that remain change into the optic nerves.

The development of the lateral eyes, now made more fully known by WATASE (No. 30), is much simpler. We can trace the lateral eyes back to a highly-differentiated part of the ectoderm (hypodermis). The actual rudiment of the compound lateral eye (Fig. 163, *la*) is a thickened point of the ectoderm (hypodermis) near the so-called dorsal organ (*do*), which apparently belongs to

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* [KINGSLEY, in his latest work, withdraws his account of the segmental sense organs, and would now regard those structures as glandular. KISHINOUYE (No. III.) finds four parts in the developing brain, and regards the lateral eyes as cephalic, not thoracic.—ED.]

a posterior thoracic segment (according to PACKARD and PATTEN the third, according to KINGSLEY the fifth; *cf.* also Fig. 157, *au* and *do*). The optic area proper (Fig. 163, *la*) is bounded at its dorsal (median) and ventral (lateral) margins by folds (*df* and *vf*), which, converging posteriorly till they meet, form the letter **V**. At the point at which the two folds meet, a short tubular invagination of the ectoderm is formed, extending below the surface, so that the **V**-shaped rudiment becomes **Y**-shaped. These folds, which are composed of very large cells (Fig. 164, *df* and *vf*), yield new cell-material for the formation of younger ommatidia at the margin of the optic area. Each ommatidium (*om*) arises in the form of a simple depression of the ectoderm (hypodermis), over which the cuticle becomes thickened to form a conical lens (*c*). The manner in which the optic nerve of this lateral eye arises is not quite clear. PATTEN and KINGSLEY trace it to the nerve-strand of the lateral sensory organs (p. 350).

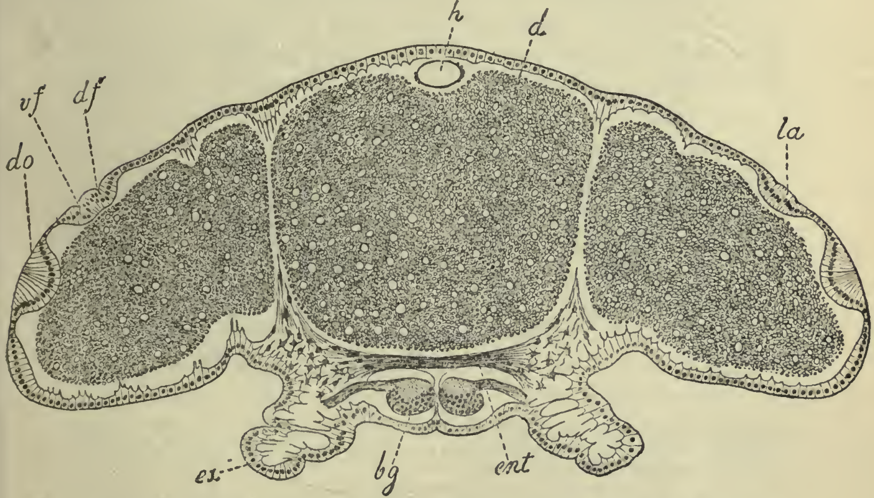

FIG. 163.—Transverse section through the Trilobite stage of *Limulus* (after WATASE). *bg*, ventral chain of ganglia; *d*, food-yolk (rudiment of enteron); *do*, dorsal organ; *df*, dorsal fold, and *vf*, ventral fold of the rudiment of the lateral eye (*la*); *ent*, endosternum; *ex*, limb-rudiment.

The position of the lateral eyes of *Limulus* must be considered as very remarkable. Authors are unanimous in attributing these eyes to a post-oral thoracic segment of the body. They would thus have a position altogether exceptional among the Arthropoda. Although the statements of PATTEN and KINGSLEY just given would to a certain extent explain this, it must appear remarkable that, in spite of this position, the innervation of these eyes takes place, not from the corresponding ventral ganglia, but from the brain. Taking into account the close relationship between *Limulus* and the Scorpiones, which can hardly be denied, we should feel inclined to homologise the lateral eyes of *Limulus* with those of the Scorpiones. The latter belong, without doubt, to the pre-oral cephalic region of the body. This homology, however, was disputed by PATTEN, who regarded the small sensory organ (Fig. 162, *s*) just described, and discovered by him, as corresponding to the lateral eyes of the Scorpiones. If we consider the distribution of the nerves in the adult *Limulus*, however, we shall hesitate a little before regarding the lateral eyes as belonging to that thoracic segment in which they appear to lie. Not only do the optic nerves of the lateral eyes come from the brain, but a large branch of the integumental (frontal) nerves arising from the brain runs far back in the lateral parts of the cephalo-thorax. We are thus justified in asking whether the lateral parts of the cephalo-thorax which carry the lateral eyes do not correspond to lateral portions of the pre-oral cephalic region which, during growth, have been secondarily shifted backward.* According to this view, only the middle part of the cephalo-thorax or the glabella, together with the parts of the cheeks bordering on the limbs, could be attributed to the thoracic segments. The position of the facial suture in the Trilobites could also be brought into agreement with this view (p. 337).

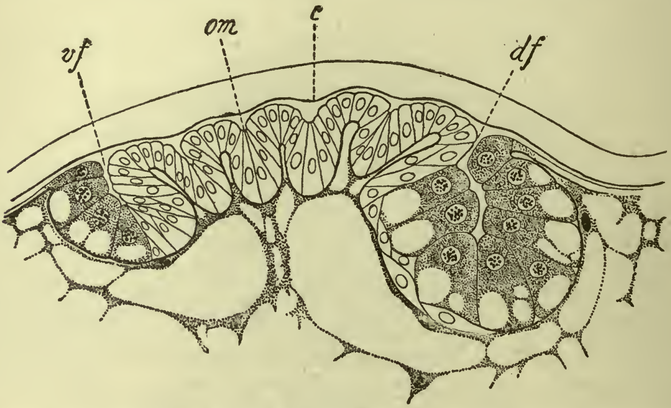

FIG. 164.—Transverse section through the rudiment of the lateral eye of *Limulus* (after WATASE). *om*, rudiment of an ommatidium ; *c*, rudiment of a corneal lens : *df*, dorsal fold, and *vf*, ventral fold of the optic rudiment.

B. The Alimentary Canal.

The anterior and posterior portions of the alimentary canal arise from ectodermal invaginations (stomodaeum and proctodaeum), which only become connected with the enteron after the first larval moult. We have already (p. 344) referred to the backward shifting of

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* [KISHINOUYE regards the lateral eyes as belonging to the second brain segment, and as true cephalic structures, thus entirely supporting the above.—ED.]

the oral aperture above which projects an "upper lip." The stomodaeum runs upward and forward, becomes dilated (anterior stomach), and then bends sharply backwards to join the enteron. Its strongly cuticularised inner wall is longitudinally folded. The anal aperture lies immediately in front of the insertion of the caudal spine; the proctodaeum is short throughout life.

The enteron here attains its final form unusually late, a peculiarity which recurs in the Scorpiones. During the whole of embryonic life the rudiment of the enteron consists of the mass of food-yolk (Fig. 163, *d*) which has undergone cleavage, and is divided up into polygonal cells, and the surface of which in later stages appears covered with a splanchnic layer arising from the mesoderm. At first this mass of entoderm retains the spherical shape, but it adapts itself later to the form of the embryo. Its anterior region, however, which lies in the cephalo-thorax, very soon becomes divided up into lobes by mesodermal septa, which grow in laterally; these lobes are the first rudiments of the digestive gland. There are, at first, six of these primary lobes on each side (p. 346), but these soon present a branched appearance by the formation of secondary lobes (Figs. 160 and 161).* In consequence of the development of these mesodermal septa and of paired hepatic lobes, the organs lying within the cephalo-thorax show a segmentation corresponding to the six thoracic segments.

The transformation of the solid entoderm into the hollow enteron takes place by the increase in number of the yolk-cells near the surface, and by their arrangement as a single-layered epithelium, which very soon separates from the central mass of yolk, liquefied yolk-substance collecting between the latter and the epithelium. The stomodaeum breaks through into the enteron earlier than does the proctodaeum. The hepatic lobes become grouped about two pairs of efferent ducts, which open into the anterior part of the metenteron. Although the greater number of the hepatic lobes belong to the cephalo-thorax, one pair of hepatic tubes which opens into the second pair of efferent ducts extends back into the abdomen.

C. Formation of the Mesoderm.

The mesoderm arises, as we have already seen (p. 342), as a proliferation of cells proceeding from the primitive groove and spreading out beneath the ectoderm. When the rudiments of the limbs appear, the mesoderm splits along the middle line, so that it now consists of two mesodermal bands running above the attachment of

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* On the development of the mesodermal septa, *cf.* p. 354.

the limbs, but connected together anteriorly and posteriorly. The space within the limb-rudiments is completely filled with mesoderm-cells. Paired, segmental coelomic cavities soon appear, as in the Arachnids, and are continued into the limb-rudiments. Many small spaces arise between the mesoderm-cells, and these unite to form the coelomic cavities. The enlargement of these cavities divides the mesoderm into a splanchnic and a somatic layer. Laterally, however, these two layers pass into one another, and this single layer grows up dorsally; this dorsal continuation only splits into a somatic and a splanchnic layer at a later stage, after the appearance of the heart. A paired, longitudinal thickening develops very soon in the single dorsal mesoderm-layer; this is the rudiment of the dorsal longitudinal muscle, and, at the same time, of the points of insertion of the limb-muscles which run up from the ventral side. These latter muscles develop in the mesodermal septa which grow in from the ventral and lateral surfaces, and divide the mass of food-yolk into a number of lobes (originally into six); this gives rise to an apparent segmentation of the internal organs of the cephalo-thorax.

As soon as the mesodermal plates meet in the middle dorsal line, a longitudinal thickening, the rudiment of the heart, arises at their point of junction. KINGSLEY was unable to decide whether the cells which combined to form this thickening belonged exclusively to the mesoderm, or whether they should be considered as immigrating yolk-cells. A lumen soon appears within the rudiment of the heart, into which a few cells which have become detached from the walls wander, and these change later into blood-corpuscles. The wall of the tubular heart now separates from the splanchnic layer, but only later from the somatic layer of the mesoderm.

In later stages of development, the coelom undergoes degeneration, all the spaces of the body-cavity becoming traversed by reticular connective tissue. These processes have, however, not yet been accurately described.

Limulus, like the Arachnids, is distinguished by the possession of an inner skeletal body, lying between the ventral chain of ganglia and the alimentary canal, and consisting of tissue resembling fibro-cartilage. This is the *endosternum* (Fig. 163, *ent*, and p. 356), which serves for the attachment of many groups of muscles. According to BROOKS and BRUCE (No. 10), the endosternum arises as a thickening of the splanchnic mesoderm on the ventral side of the mass of food-yolk (rudiment of the enteron).

PACKARD'S "brick-red gland," which we agree with RAY LANKESTER

(No. 17) in regarding as the homologue of the coxal gland of the Scorpiones, and which is probably to be considered as a modified nephridium, is also a derivative of the mesoderm. This paired gland which, in the adult, seems to have no external aperture,* is situated on either side of the endosternum, close to the coxal joints of the thoracic limbs (second to fifth); it consists of coiled anastomosing tubes, massed together, but divided into a longitudinal body and four vertical lobes. In the young stage observed by Gulland (No. 13), these latter are wanting, but the glands open outward on the coxae of the fifth pair of limbs. According to Kingsley, this organ develops in the embryo from the mesoderm, and includes part of the coelomic cavity of the fifth post-oral segment. Its inner end opens out into the coelom of the fifth post-oral somite. The cubical epithelium of the gland passes into the pavement epithelium of the coelomic cavity; the latter represents the end-sac. It thus appears essentially to resemble in structure the nephridia of *Peripatus.* The tubular portion of the gland first bends anteriorly, the outer part of this coil forming four more loops. These new secondary loops develop in each segment into the four lobes of the adult gland mentioned above. At the points where the coils come into contact, fusion and perforation take place.

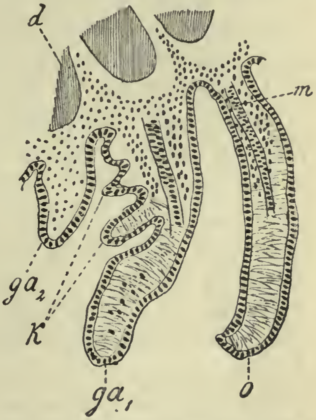

Fig. 165.—Longitudinal section through the abdominal appendages of a *Limulus* embryo, to illustrate the origin of the branchial lamellae (after Kingsley). ga_1, ga_2, first and second gill-bearing limbs; *o*, operculum; *K*, branchial lamellae; *m*, muscle; *d*, food-yolk.

D. Respiratory Organs.

The branchial lamellae (Fig. 165, *K*) arise at the posterior dorsal side of three of the abdominal limbs (second to fifth) as simple outgrowths of the body-surface. At first they are few in number, but, as development progresses, new rudiments of lamellae are continually added to the basal segments of these appendages. Kingsley has pointed out that, in the early stages of the development of the gills, the whole region appears slightly sunk below the surface, as if foreshadowing the formation of the invaginate lung-books of the Scorpion (Fig. 165, *ga*).

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* [See Tower, App. Lit. Xiphosura, No. VI.—Ed.]

4. General Considerations.

We have already (p. 352) pointed out that the Xiphosura are evidently somewhat closely related to the Trilobites. Certain characters which tend to connect the two are specially apparent in the young larvae of *Limulus* (Trilobite stage), their presence in the adult also being undeniable. Here, as in the Trilobites, the anterior region of the body is divided by two longitudinal furrows into a middle and two lateral portions. The position of the lateral eyes agrees in the two groups, but the occurrence of ocelli (median eyes) has not yet been fully established in the Trilobites. The two groups further agree in the general configuration of the cephalo-thorax, in the bending under of the anterior part of the cephalic shield, and in other points. Our present knowledge of the cephalic limbs of the Trilobites seems to indicate that they resembled in structure those of the Gigantostraca.* Four pairs of jaw-feet have been found in the latter, the last pair having been specially developed, and having grown out into broad, oar-like limbs. Various fossil forms of Xiphosura connect *Limulus* with the Trilobites; among these, *Belinurus*, by the shape of its cephalo-thoracic (cephalic) shield, which is continued into long cheek-spines, strikingly recalls the Trilobite family, *Trinucleidae.*

Although the Palaeostraca thus appear to form a single group based upon natural relationship, a certain distant relationship to the Crustacea is, as we have already pointed out (p. 315), undeniable. This is supported chiefly by the structure of the Trilobite limbs, described more in detail by WALCOTT (No. 5),* and by the biramose character of the abdominal limbs of *Limulus.* We have already stated why we regard the Palaeostraca and the Crustacea as groups of equivalent value, but have abstained from uniting them. We, however, think ourselves justified in assuming that they both had their origin in a common racial group, the Protostraca, which may perhaps also be regarded as the racial group of the Onychophora—Myriopoda series.

The relationship which appears to exist between the Palaeostraca and the air-breathing Arachnida deserves closer consideration. As early as 1829, STRAUSS-DÜRKHEIM emphasised the near relationship between *Limulus* and the Arachnida. He based his view chiefly on the radial arrangement of the limbs, on the common sternal plate, and on the presence of an inner endoskeleton (the endosternum),

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* See Editorial note, pp. 333 and 360.

lying between the ventral cord and the intestine, which affords attachment to numerous groups of muscles. The views of STRAUSS-DÜRKHEIM were supported on embryological grounds by ED. VAN BENEDEN (No. 8) in 1871, and J. BARROIS in 1878. CLAUS also, in 1876,* expressed his belief that "the air-breathing Arachnida may have been derived from the polygnathan Merostomata (Trilobites, Eurypterida, and Xiphosura)." HUXLEY had also expressed himself in a similar way as to the genealogical connection between the Arachnida and the Merostomata. The near relationship of the two groups has been recently demonstrated in more detail by RAY LANKESTER (No. 16), by means of a careful comparison of the structure of *Limulus* with that of *Scorpio.* Although RAY LANKESTER, as we think, goes decidedly too far in insisting that *Limulus* should be regarded as an Arachnid, he still deserves credit for having established on a broader base the view that the two forms belong to the same phylogenetic series. It appears to us that the structure of the limbs used for respiration and adapted to aquatic life, the absence of the Malpighian vessels, and, moreover, their connection with the Trilobites, which are further removed from the Arachnida, afford sufficient cause for giving the Xiphosura a more independent position.

We cannot here undertake to enter further upon the palaeontological evidence in favour of the genealogical connection between the Arachnida and the Palaeostraca. We can only mention that among the Gigantostraca, which are nearly related to the Xiphosura, forms are found which, in appearance and in the segmentation of the posterior region of the body, stand still nearer to the Scorpiones than does *Limulus* itself. We must confine ourselves to a short consideration of the points of comparison between *Limulus* and the Scorpiones.

In both forms we recognise an anterior region of the body (cephalo-thorax) carrying six pairs of limbs, and covered by a dorsal shield, having on its upper side two median eyes, and, nearer the edge, paired lateral eyes. The median eyes of *Limulus* and of *Scorpio* agree so closely in structure, that we cannot doubt that they are homologous. We might take the same view of the lateral eyes, even though the numerous unicorneal lateral eyes of *Scorpio* essentially differ from the remarkable lateral eyes of *Limulus*, the composition of which is very primitive. In this case we should have to regard the lateral eyes of *Scorpio* as of a modified type.

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* *Unters. zur Geneal. Grundl. der Crustac. Systems.*

Of the six pairs of limbs belonging to the cephalo-thorax, the most anterior (the chelicerae) shift during development in front of the oral aperture, while the pair of ganglia belonging to them enter into closer connection with the brain. The five pairs of limbs behind these serve for locomotion and mastication. While, in *Limulus*, the coxae of all the limbs appear enlarged and have toothed masticatory ridges, in *Scorpio*, only the pedipalps and the first two pairs of ambulatory limbs have basal blade-like structures. An upper lip (rostrum, camerostome), lying in front of the mouth between the chelicerae, is common to the two forms; as also is an original paired projection behind the sixth pair of limbs, which, in *Limulus*, is represented by the chilaria, but, in *Scorpio*, fuses to form a small pentagonal plate found in front of the operculum.

Behind the cephalo-thorax, in *Scorpiones*, comes a pre-abdomen consisting of seven segments, which is followed by a post-abdomen of five segments, with a terminal poisonous spine. If we regard the long caudal spine of *Limulus* as the representative of the poisonous spine, we shall consider the region usually described as the abdomen to be the equivalent of the pre-abdomen and the post-abdomen of *Scorpio*. This region, in *Limulus*, consists of eight fused segments. Taking into account certain fossil forms (*Belinurus*), however, we may conjecture that the last of these segments, strictly speaking, corresponds to several segments which have not separated. The resemblance between *Limulus* and *Scorpio* finds expression in the development of the abdominal limbs. In both forms, rudiments of limbs appear in the embryo on the six anterior abdominal segments. Of these, the most anterior pair changes, in *Limulus*, into the large plate-like structure known as the operculum, which is also slightly developed in *Scorpio*, and on the inner side of which lie the genital apertures. The five posterior pairs of limbs, in *Limulus*, are leaf-like, and carry gills, and thus serve for respiration. In *Scorpio*, the most anterior pair develops into pectines, while the four other pairs seem to disappear at the time when the lung-sacs develop.

In the assumption of a near relationship between *Limulus* and *Scorpio*, an important part is played by the supposed transformation of the gills of the former into the lungs of the latter. In structure the two organs show remarkable agreement. While, however, careful consideration shows how a transition may well have taken place from the book-like gills of *Limulus* to the lung-book of *Scorpio*, there are certain difficulties which RAY LANKESTER (Nos. 16 and 20), KINGSLEY (No. 14), and MACLEOD (No. 21) have sought to set aside by means of various hypotheses. RAY LANKESTER himself gave up his original, very artificial theory, and has since derived the lung of *Scorpio* from the gill of

Limulus by complete invagination. The limb was not only, according to this view, invaginated as a whole, but each single branchial lamella was separately invaginated, the limb, as it were, growing into the body instead of growing out, so that the interstices between the lamellae then became the lamellae of the book-lung. This view somewhat resembles that of KINGSLEY. It appears to us that MACLEOD'S view is the simplest explanation, and the one best agreeing with the facts. MACLEOD (No. 21) starts from the assumption that the lamellae of the book-like gills are homologous with those of the book-like lungs. The gill-bearing limbs of *Limulus* are usually closely pressed against the ventral side of the abdomen. The branchial lamellae develop only on those upper surfaces which are pressed against the body. The ventral side of the limbs, in *Limulus*, already shows a depression corresponding to the branchial lamellae. If we imagine the respiratory limbs shifted further apart than they are in *Limulus*, and the edges of the depression just alluded to fused with the edges of the leaf-like limb, a closed space, the lung-sac, will thus be formed. The free posterior edge of the limb would then become the anterior margin of the stigma belonging to this sac. By this assumption, MACLEOD is able to explain certain features in the structure of the Arachnid lung: *e g.*, the facts that some of the lung-lamellae are free not only at their posterior edges, but at their lateral edges also, and that the corresponding lung-sacs of the two sides are connected, etc.*

The agreement in the internal anatomy of the two forms is no less remarkable than that in the outer segmentation of the body and in the structure and functions of the limbs. The presence of an endosternum has already been mentioned. We shall here merely recall to mind the large, branched liver, opening through several efferent ducts into the intestine, the retiform rudiment of the genital glands, the presence of a circum-oesophageal, arterial vascular ring accompanying the oesophageal commissure (and in *Limulus* developing into an actual vascular sheath), and, finally, the presence of a gland (brick-red gland of *Limulus*, coxal gland) on the coxae of the fifth pair of limbs (third ambulatory limbs).

The agreement which we have thus pointed out in the structure and development of *Limulus* and of the Arachnida is so remarkable that we can hardly avoid the conclusion that the two forms are genetically related. We therefore accept the view that the Arachnida have developed from the Palaeostraca through adaptation to terrestrial life.

It may be further mentioned here that adaptation to life in fresh water, and possibly on land (?) had, perhaps, taken place even in the Gigantostraca themselves. According to ZITTEL (No. 7), they are found in the coal formations associated with land plants, scorpions, insects, fish, and fresh water amphibia.

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* [BERNARD (App. to Lit. on Trilobita IV.), on the other hand, has endeavoured to show that the lung-books of *Scorpio* developed *in situ*, as adaptations to the circulatory system. He further claims that the Arachnids originally had more stigmata than there were respiratory limbs in *Limulus*.—ED.]

A striking feature in some of the forms (Eurypterida) in this group is the scale-like marking of the body-plates.

A homology is naturally suggested, and has been carried out by Ray Lankester, between the coxal glands of the Arachnida and Xiphosura and a pair of Crustacean nephridia. This could only apply to the shell-gland, which belongs to the segment of the second maxillae, *i.e.* to the fifth limb-bearing segment. We should then have to homologise the chelicerae of the Arachnida with the first pair of antennae of the Crustacea, an assumption which seems to us somewhat daring, and not sufficiently supported by the structure and development of the brain in the two groups. There is the less need for a homology between the shell-gland of the Crustacea and the coxal gland of *Limulus* and *Scorpio*, as we have to imagine each body-segment originally provided with a pair of glands of this kind, an assumption which appears to be justified by a comparison with *Peripatus.**

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[* The new discoveries of the antennae and limbs of a Trilobite (*Triarthrus*) have advanced our knowledge of these fossils and of their affinities so greatly, that the student must not rest content with the foregoing. The recent observations of Beecher and Bernard (App. to Lit. on Trilobita, Nos. I., II., III., IV.) have taken the point off many of the author's comments on the valuable information given above. The text is translated as it stood on account of the matter it contains, and the reader is merely referred to the more recent works on the subject. This seems to be the only alternative to re-writing the whole chapter.—Ed.]

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