J. F. Urbatt

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TEXT - BOOK

OF THE

EMBRYOLOGY OF INVERTEBRATES

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OF THE

EMBRYOLOGY OF INVERTEBRATES

BY

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WITH ADDITIONS BY THE AUTHORS AND TRANSLATORS

PART I

PORIFERA, CNIDARIA, CTENOPHORA, VERMES, ENTEROPNEUSTA, ECHINODERMATA

ARDVA·QVÆ·PVLCRA

London

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1895

TRANSLATORS' PREFACE

The value of the *Lehrbuch der vergleichenden Entwicklungs-geschichte der wirbellosen Thiere* for students of animal morphology is too well understood by those who are familiar with its scope and execution to require any statement of our aims in undertaking an English translation of it.

In presenting to zoologists the First Part of this work we consider ourselves fortunate in having had the valuable aid of the authors in supplementing the original text by numerous additions, made desirable by the rapid advance of the science since the date of first publication. Although the scope of the work has permitted the addition of only the most succinct statement of the results reached by embryologists in the last five years, these additions must prove to be of assistance to all students, and will, we believe, be especially acceptable to those who are already familiar with the original edition.

In order to spare the reader the labor of comparing original and translation for the purpose of ascertaining what is new, the plan has been adopted of enclosing in brackets [ ] all new matter, which, so far as practicable, has been put in the form of footnotes. Each of these additions is followed by the initial of the author, or by the word " Translators," to indicate the persons responsible for the new matter. Owing to an oversight, the initial has been omitted from several of the additions in the earlier chapters. It should be stated, therefore, that, unless otherwise indicated, the additions to Chapters I.—III. were made by Professor Heider, those to Chapters IV.—XIV. by Professor Korschelt. Brackets have also been freely used in the text to enclose such words or brief explanations as the translators deemed

useful supplements to the more literal translations of the
original. In such cases an indication of the authority has
been omitted, since no uncertainty is likely to result from
the omission.

To avoid confusion in citation and to indicate at a glance
the *additions* to the *Literature* of the several chapters, the
references not included in the original have been put in the
form of *Appendices* and numbered with *Roman* numerals. It
has been the aim to make these additions include all the
important papers which have appeared since this Part was
first issued.

In translating *Anlage* we have employed the word *funda-
ment*—a use which one of us has suggested and defended in
the Translators' Preface to *Text-book of the Embryology of
Man and Mammals*, by Dr. Oscar Hertwig, etc. (Swan
Sonnenschein & Co : London, 1892).

We are under deep obligation to our colleagues Doctors
C. B. Davenport and G. H. Parker for their friendly and
self-sacrificing assistance, and we desire to thank both of
them for their aid—Dr. Davenport for having rendered us
valuable service in revising the whole of the manuscript;
Dr. Parker for assistance in revising parts of the manuscript
and reading the whole of the proof.

It is with reluctance that we have felt compelled by the
pressure of other duties to relinquish to others the task of
completing the translation of this admirable work. We
trust that one of the advantages of this change will be the
more rapid publication of the translation of the remaining
parts than could possibly have been hoped for from us.

                                        THE TRANSLATORS.

Cambridge, Mass., U.S.A.

AUTHORS' PREFACE

THE facts that the comparative embryology of Invertebrates has not had a broad and comprehensive presentation since the appearance of BALFOUR's *Treatise on Comparative Embryology*, and that the special literature of this subject has undergone an enormous increase since that time, have forced upon every one who has been concerned with questions of comparative embryology the pressing need of a more modern treatment of the subject. Inasmuch as we had occasion to go over a considerable part of the literature of this subject during the last few years—partly for the purpose of courses of lectures to be given, partly from the requirements of special investigations—it was natural that the idea should have occurred to us to utilize this preliminary work, and by arranging the material acquired and further elaborating it to issue the whole in book form—a venture which was undertaken, and the first results of which have assumed the form of the present part.

Since it has been our plan in writing the present work to proceed from the special to the general, and since naturally some time will elapse before the completion of the whole, we have thought that we should secure the gratitude of the reader if we published the first half of the special part at once. The second half of this part, embracing the Arthropods, Molluscs, Molluscoidea, Tunicates, and Amphioxus, will appear shortly, while we hope to finish the general part, and therewith the whole book, in the course of the year 1890.

Not to begin the special part of this work too abruptly, we have prefaced it with a short general introduction.

Our decision to limit the subject matter to the *so-called*

invertebrate animals may require an explanation, and perhaps also an excuse. We have been guided exclusively by practical considerations, especially the fact that the comparative embryology of Vertebrates has very recently been comprehensively treated in an excellent manner, and further the reflection that, with the limitation of our field to the Invertebrates, the treatment of them might be so much the more thorough.

We take the liberty of expressing here our best thanks to Herrn Geheimrath F. E. SCHULZE, who has aided us in the most amiable manner, both by his advice and by his assistance in procuring literature; and likewise to our publisher, who has made it possible to issue the book in its present form.

<div align="right">THE AUTHORS.</div>

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CORRIGENDA

INTRODUCTION

ZOOLOGICAL research of the last decade has led to a sharp
separation of two chief divisions of the animal kingdom:
the *Protozoa* and the *Metazoa*. In the group *Protozoa* the
individual can, from its structure, be referred to the funda-
mental type of a cell. These unicellular individuals exist
either separately or united in great numbers to form colonies
or corms. In the latter case, however, the different indi-
viduals remain equivalent to one another in structure and
function. In the group *Metazoa*, or *Germ-layer animals*,
on the contrary, there always results a multicellular or-
ganism (cell-community or cell-corm), in which the single
cells give up their independence for the good of the com-
munity, and accommodate themselves to a division of labour,
in consequence of which there is brought about a diversity
in the structure and function of the cells of the Metazoan
organism. While the development and differentiation of
distinct tissues with specific functions result from this poly-
morphism of the cells, the entire colony gains a higher
functional capacity and a more complete unity. In this
way there arises an individual of higher rank or second
degree, which we designate as *person*. These Metazoan in-
dividuals also may, through incomplete separation after
budding, remain united in colonies, and then there results
an individual of the third degree, the *stock* or *corm*. By
adaptation of the stock-forming persons to various functions,
accompanied with their polymorphous development, a higher
functional unity may be reached in this case also.

As a result of the division of labour which is effected
among the cells of the Metazoan organism, it comes about

that the ability of reproducing the entire organism does not
belong alike to all the cells. It is confined rather to very
special cells, which are known as *reproductive cells* (egg-cells
and sperm-cells); these are cells which for the most part
are developed only in definite regions of the organism (*genital
organs, gonads*). The development of the Metazoan begins
with the fusion of two morphologically different reproductive
cells derived, as a rule, from two different individuals
(*fertilization*). This kind of reproduction, known as *sexual
reproduction*, is typical for all Metazoa. In many forms,
however, non-sexual modes of reproduction (by division or
budding) are interpolated in the life-history. If such an
interpolation is the rule, so that two morphologically differ-
ent generations, one of which multiplies by sexual and the
other by non-sexual reproduction, regularly alternate with
each other, then this condition is known as *metagenesis* or
alternation of generations. It may also happen, however, that
there is a regular alternation of sexual generations, in one
of which reproduction is hermaphroditic or parthenogenetic,
while in the other it is by means of separate sexes. Here
also there occurs a heteromorphous development of the two
generations. We call this condition *heterogeny*.

Inasmuch as the individual Protozoan has the morpho-
logical value of a single cell, the embryology of the Protozoa
belongs to the province of cell morphology. For this reason
it is usually excluded from the domain of comparative em-
bryology of animals in the stricter sense; in this book, too,
it will receive no consideration. Comparative embryology
accordingly has to do with the development of the Metazoa,
and, above all, with their development from the fertilized
egg. Its chief problems consist in the investigation of the
formation of the germ-layers, the origin of organs, and the
development of the general form of the body. Its purpose
is the recognition of the laws of development, the determina-
tion of the homologies of organs, and the deduction of the
ancestral history of the Metazoa.

The Metazoa constitute a single stem of the animal king-
dom. It is very probable that all Metazoa can be referred
to a common ancestral form, and that certain correspond-

ing features in the mode of development are the result of this common descent. The earliest stages of development in the Metazoa can readily be reduced to a uniform plan characterized by the appearance of the *blastula-* and *gastrula-*stages at the end of cleavage. One is justified in the assumption that in these two stages there exists a repetition of ancestral forms which are common to all the Metazoa.

In the first stages of development of the Metazoa the existence of a *chief* or *primary axis* can be recognized, the ends of which are distinguished as the *animal pole* and the *vegetative pole*, because in the differentiation of the two primary germ-layers, which soon follows, the layer arising in the vicinity of the animal pole (*ectoderm*) presides over the animal functions (sense perception, locomotion), while the germ-layer at the opposite pole (*entoderm*) is mainly devoted to the functions of vegetation (*e.g.*, nutrition). The Metozoa accordingly at first show a monaxial, heteropolar structure. Frequently the chief axis can be recognized in the egg-cell of the Metazoa before the beginning of development, since the germinative vesicle (nucleus of the egg-cell) and a dense accumulation of protoplasm are situated near the animal pole, whereas in the region of the vegetative half of the egg a great accumulation of yolk particles can be recognized. The animal pole, furthermore, is characterized by being the place at which the expulsion of the *polar globules* takes place before fertilization.

The process of the *cleavage of the egg*, by which, after fertilization has taken place, the embryonic development is initiated, is essentially an ever-progressing division of the egg, which takes place according to fixed laws, and by which the egg is divided into a number of cells (*cleavage spheres, blastomeres*), which at first are still undifferentiated. According to the direction which the planes of cleavage occupy in this process, we distinguish *meridional* and *equatorial* furrows, the former coinciding with the chief axis, the latter being perpendicular to it. In this manner there arise blastomeres that are at first spherical, but in later stages more or less pyramidal in form, and which are arranged radially about a point occupying the centre of the egg. By

separation of the cells there soon arises a central cavity, the *clearage cavity* or *Von Baer's cavity* (*blastocœle*), which continually increases during the succeeding cell divisions, while the blastomeres arrange themselves about this cavity in a single-layer epithelium (*blastoderm*). The stage of development thus reached is known as the *blastula* or *blastosphere*. In the one-layer blastula an arrangement of the parts of the egg about the chief axis is also clearly recognizable. The cells in the vicinity of the animal pole are, as a rule, smaller and not so rich in nutritive yolk particles; whereas the cells of the vegetative portion are larger and richer in yolk, and, in consequence of the impeding influence offered by the nutritive yolk, divide more slowly.[1] The wall of the single-layer blastosphere represents the first of the primitive organs of the Metazoan body.

In the simplest cases a *gastrula-stage* is developed out of the blastula-stage by the cell-layer of the vegetative half becoming flattened and gradually depressed, so that there arises an ever-deepening invagination at the vegetative pole. In this way the cleavage cavity (primitive body cavity) becomes gradually reduced, and often is preserved only as a narrow cleft between the two layers of the body-wall produced by the metamorphosis already described. The gastrula-stage has substantially the form of a sac. It encloses a cavity which has arisen by invagination, called the *archenteric cavity*, and opens to the exterior in the region of the vegetative pole by means of the *primitive mouth* or *prostoma* (*blastopore*). The wall at this stage consists of two cell-layers: an outer, the *ectoderm*, which is derived from the cells of the animal portion of the blastosphere, and an inner, the *entoderm*, which consists of the cells of the former vegetative half, and which has reached the inside of the embryo by the process of invagination. In the region of the blastopore the ectodermal and entodermal layers become continuous with each other. Ectoderm and entoderm

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[1] There are reasons for thinking that the rate of cleavage is not wholly dependent on the proportion of nutritive yolk in the blastomere. (See KOFOID, C. A., "On Some Laws of Cleavage in Limax," *Proc. Amer. Acad. Arts and Sciences*, vol. xxix., p. 180, 1894) [TRANSLATORS].

represent the two primitive organs—or, as they are called, the two *primary germ-layers*—resulting from the differentiation of the simple blastosphere. The gastrula-stage, which recurs under various modifications in all the Metazoa, appears as the recapitulation of a hypothetical ancestral form (*Gastrea*), which was characterized by the development of the archenteron. Among the Metazoa now living many of the Cnidaria have retained essentially the structure of this hypothetical ancestor. In the more highly developed forms the two primary germ-layers undergo various modifications, whereby additional organs are differentiated. A third layer, the *mesoderm* or *middle germ-layer*, also grows in between the two cell-layers. Concerning the origin of this we shall speak farther on. Of the primary germ-layers, the entoderm retains, even in the higher Metazoa, the function originally belonging to it: that of receiving and digesting food. In general it constitutes the epithelium of the mid-gut. From the ectoderm, on the other hand, arise usually the epidermis, and the nervous system, and sense organs, as well as the epithelial lining of the stomodeal and proctodeal invaginations.

We have described above a method of origin of the blastula- and gastrula-stages as it occurs in some, but by no means all, Metazoa. It was chosen as the type because, with due regard to the disturbing influences present, many of the aberrant modes of development can readily be reduced to the plan here presented. Frequently cleavage, the formation of the blastosphere, and the process of gastrulation are modified by the presence and definite arrangement of large masses of food-yolk.

Certain eggs with little food-yolk approach most nearly to the plan presented above (*e.g.*, those of Amphioxus, Sagitta, and the Echinoderms). In such cases cleavage results in the production of blastomeres which are nearly uniform in size, so that in the completed blastosphere only a slight difference can be detected between the size of the blastomeres of the animal and vegetative poles. However, even here those of the vegetative pole are, as a rule, a little more voluminous. This kind of cleavage is called *total and equal* cleavage. It

is called total because the entire mass of the egg is separated
by the division into blastomeres, and it is called equal on
account of the approximately equal size of the resulting
blastomeres.   The blastula-stage which, with large central
segmentation cavity, is produced by this cleavage, is called
a *cœloblastula* or *archiblastula*, whereas the gastrula arising
from the latter by a process of enfolding is called an *inva-
gination gastrula* or *embolic gastrula*.

In the eggs of some Cnidaria, especially Hydroids, whose
earliest development is accomplished exactly in the manner
described above—that is, by total and equal segmentation
and subsequent development of a cœloblastula—there exists
a method of entoderm formation (gastrulation) which differs
somewhat from the method by invagination just described,
although it can be reduced to the same. This is the forma-
tion of the entoderm by *polar ingression*. In this case the
entoderm does not arise by an invagination of the cells of
the vegetative pole, but the latter detach themselves from
the blastoderm and migrate into the blastocœle, which in
this way gradually becomes filled with a closely packed mass
of entoderm cells. It is only secondarily that the archenteric
cavity arises in this mass as a fissure, and that a mouth is
formed by dehiscence of the wall. One sees that this kind
of entoderm formation can readily be derived from that by
invagination, inasmuch as the essential difference from that
method of formation consists in the fact that the entoderm
cells give up their epithelial continuity at the beginning of
the ingrowth.

Closely allied to the above-described type of total and
equal cleavage are forms in which a more or less con-
siderable amount of food-yolk is deposited in the vegetative
half of the egg. On account of this accumulation the vege-
tative portion of the egg considerably exceeds the animal
portion in mass. It follows from this that in the course of
cleavage, which here also is total, the cleavage cavity appears
relatively small, and occupies a very eccentric position near
the animal pole. The wall of the blastosphere, which can
still be called a cœloblastula, in this case presents a con-
siderable difference in thickness at the animal and vegetative

poles. We call this kind of cleavage *total unequal cleavage*, and group together as *holoblastic* eggs the forms belonging to this type and those previously mentioned. The unequal-walled blastula that has arisen through total unequal segmentation can in its further progress lead to the formation of a gastrula by invagination, but in this case the gastrula cavity will be relatively shallow, corresponding to the small size of the segmentation cavity.

In some other cases, on the contrary (*e g.*, in some Annelids), after the conclusion of the process of total unequal cleavage, there is formed a blastula in which the cleavage cavity is reduced to a minimum. Accordingly there results from segmentation a more or less solid cell-mass (*sterroblastula*), in which we can distinguish a portion composed of large entodermic elements rich in food-yolk from an ectodermic portion consisting of small cells. The latter is placed upon the former like a small cap in the region of the animal pole. Here gastrulation by invagination cannot take place ; but the gastrula-stage is formed by the growth and consequent increase in size of the cap-shaped ectodermic part, whereby its edges push themselves more and more over the entodermic mass, so that finally the latter is entirely included within the ectodermic sac. We designate the solid gastrula-stage arising in this manner as a *circumcrescent* or *epibolic gastrula* (*sterrogastrula*). By this means a gastrula cavity is not formed primarily, but arises only secondarily as a fissure in the entodermic cell-mass. The edges of the spreading ectodermic layer must be regarded as the blastopore, which accordingly is filled by a so-called yolk-plug.

The presence of large quantities of yolk matter in the region of the vegetative half of the egg presents obstacles to the progress of cleavage in that region. The accumulation of large masses of yolk can go so far that this portion of the egg does not at first take part in the segmentation ; but only a small portion, situated in the vicinity of the animal pole and consisting principally of formative yolk, is divided into blastomeres. Such, which undergo only a partial cleavage, are known as *meroblastic eggs*, in contradistinction to holoblastic ones. There is developed in this

way a disc-shaped embryonal part which is situated on the
unsegmented yolk-mass at the animal pole. We call this
type of segmentation, which represents the most extreme
case of unequal cleavage, *discoidal cleavage*. It occurs, for
example, in the Cephalopods.

A particular type of cleavage, which does not fit into the
above series, occurs in the class of Arthropods. Whereas
all eggs thus far considered were characterized by a more
or less considerable accumulation of yolk in the region of
the vegetative half (*telolecithal eggs*), the distribution of
the yolk being accordingly eccentric, the eggs of Arthro-
pods exhibit a regular distribution of the yolk masses of
such nature that their centre coincides with the middle
point of the egg (*centrolecithal eggs*). The first cleavage
nucleus here lies in the centre of the egg, where by divi-
sion it separates into a large number of nuclei, which are
distributed uniformly at the periphery of the egg, and thus
give rise to the formation there of a layer of small uniform
blastomeres. This cell-layer represents the blastoderm,
while the cleavage cavity of the blastula-stage produced in
this way is filled with the unsegmented yolk-mass. This
kind of cleavage is known as *superficial cleavage*.

The modifications of development hitherto considered ap-
pear to be dependent principally upon the amount and mode
of distribution of the yolk matter. We have still to consider
some forms which in the mode of distribution of the yolk
recall the centrolecithal eggs, but which by their peculiar
mode of entoderm formation prove to be aberrant forms. In
the first place, there should be mentioned in this connection
the kind of *entoderm formation* (*by delamination*) occurring in
the Cnidaria (Hydroids). The typical case of this kind
exists in the development of the Geryonidæ. A cœloblastula
is here formed by total and equal cleavage, and there follows
a division of the cells in such a manner that an inner portion
rich in yolk becomes separated from a superficial part with
little yolk matter. In this way there arises out of the one-
layer sphere an arrangement of the cells into two concentric
hollow spheres, of which the inner contains the elements of
the entoderm, and the outer those of the ectoderm. One

sees that in this mode of formation, which cannot be compared to the plan of gastrulation by invagination, the gastrula cavity arises from the cleavage cavity.

Apparently a transition between the formation of the entoderm by delamination and by polar ingression is effected by a kind of entoderm formation which has been observed by METSCHNIKOFF in different Hydroids, and which is designated as *multipolar ingression* (*i.e.*, ingression from all sides), in which single cells of the blastoderm migrate into the blastocœle from different points of the surface and here form an entodermic cell-mass. Nevertheless the process of forming entoderm by delamination remains, in contrast with the other types of entoderm formation, somewhat isolated and unexplained.

Closely related to delamination is a kind of entoderm formation which was formerly held to be of frequent occurrence, but whose range of distribution has become more and more restricted by careful investigation of the individual cases. They are the cases in which the blastomeres present no radial arrangement about a point within and no definite relation to a cleavage cavity. Such a stage, which is an apparently irregular solid mass of cells, without cleavage cavity, has been designated as *morula*; and it is assumed that by a rapid division of the cells at the surface an outer cell-layer is differentiated from the inner cell-mass, so that here also the separation of ectoderm from entoderm would be brought about by a splitting off which takes place uniformly over the entire circumference. We shall see that examples of such a mode of origin of the two primary germ-layers are still ascribed to many Hydroids and Anthozoa, though probably the greater part of the cases referred to this method can be reduced to epibolic gastrulation, in which event the morula-stage, as being a Schema founded on erroneous assumptions, would have to be omitted.

Even though the last-mentioned modes of entoderm formation, restricted as they are to a few kinds of Metazoa, place many difficulties in the way of the conception that there is uniformity in this process, it is probable that more careful investigation may succeed in bringing them into accord with the less aberrant types already mentioned.

We have seen that the chief axis of the gastrula-stage unites the anterior or apical (animal) and the posterior or prostomial poles with each other. In the lowest types of the Metazoa—the Porifera, Cnidaria and Ctenophora—this primitive axis becomes the permanent chief axis of the body; therefore these groups have been contrasted by HATSCHEK [1] as *Protaxonia* with the rest of the Metazoa, which he terms

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[1] Compare Hatschek's *Lehrbuch der Zoologie.* Jena, 1888, p. 40, as well as p. 69 *et seq*.

Heteraxonia or *Bilateria*. In the latter the blastopore
undergoes a secondary shifting, so that the later chief axis
can no longer be identified with the primitive axis.

The layered structure of the Metazoa becomes more com-
plicated by the appearance of a cell-layer introduced between
the ectoderm and entoderm, which takes a position in the
primitive body cavity, the remnant of the cleavage cavity,
and is designated as *mesoderm* or *middle germ-layer*. This
name is applied to any cell-layer introduced between ecto-
derm and entoderm and separated from both by a sharp
boundary, but it is not intended thereby to maintain the
homology of this layer for all the Metazoa. On the contrary,
it appears that in the Protaxonia mesodermic layers were
independently acquired in various ways. Even in the
Bilateria the homology of the mesoderm in all groups is
not absolutely established, although it may be assumed as
probable.

The mesoderm of the Bilateria arises as a rule out of the
primary entoderm, which in such cases is divided into two
parts: mesoderm and secondary entoderm. In regard to
the mode of origin, we can distinguish two sharply separated
types: the formation out of *two primitive mesoderm cells*
and the formation by the production of *diverticula of the
archenteron*.[1] The first type is widely distributed among the
Bilateria. At an early period there become conspicuous at
the prostoma of the gastrula-stage two peculiar cells, by
whose position the median plane, which passes between the
two, is determined. These cells are known as the primitive
mesoderm cells. They move into the space between the
ectoderm and entoderm (therefore into the primitive body
cavity), and by proliferation give rise to two paired cell-
bands, which are called the *mesoderm bands*, and out of
which the organs of the mesoderm are constructed. The
formation of the mesoderm by the production of diverticula

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[1] As a third type of mesoderm formation one might perhaps cite the
formation of a *mesenchyma* (compare p. 11) in those cases in which, as
in the Nemerteans and Echinoderms, numerous wandering cells migrate
into the blastocœle at an early period. Yet this type could perhaps be
reduced to one of those mentioned above.

of the archenteron, as it occurs in the Chætognatha, Brachio-poda, and Chordonia, consists in the development of paired sac-like diverticula of the archenteron, which become constricted off, and then as independent cœlomic sacs give rise to the systems of organs of the mesoderm. Different as these two kinds of mesoderm formation appear to be, they nevertheless can be reduced, like the processes of gastrulation by invagination and by polar ingression already described, to a uniform plan, if we assume that in the first case the mesodermic elements at an early period abandon (as primitive mesoderm cells) epithelial continuity with the entoderm, whereas in the second case the mesodermic cell-mass retains provisionally its epithelial continuity, and only later becomes separated from the entoderm by the formation of the diverticula.

As regards the subsequent fate of the mesoderm, we can, if we disregard the formation of the individual organs, distinguish two types. In the one case the union of the mesodermic elements is loosened, and these distribute them-selves in the manner of amœboid wandering cells in the space of the primitive body cavity, which eventually they completely fill with a tissue consisting of stellate migratory cells embedded in a gelatinous stroma. This tissue is known as *mesenchyma* (O. and R. HERTWIG). By separation of the cells of the mesenchymatous tissue, spaces (lacunæ) may be formed in it, which may coalesce to form larger spaces, and so apparently represent a kind of body cavity. To such spaces the name of *pseudocœle* is given.

In other cases the largest part of the mesoderm is employed in the formation of paired sacs, the *cœlomic sacs*, the walls of which consist of a continuous epithelium of mesoderm cells. The cavities contained in them represent the *true body cavity* or *cœlom*. The paired cœlomic sacs entirely surround the intestinal canal, so that the walls of the sacs come together in the middle line above and below the intes-tine to form the so-called *mesenteries*. The body cavity divides the mesoderm into two layers. The outer layer, the one applied to the ectoderm, is known as the *somatic layer*, the inner one, applied to the entoderm, as the *splanchnic layer*.

There are a number of animals in which the mesoderm produces, in addition to the specific organs that have arisen from it (genital organs, excretory organs), only mesenchyma. Such is the case in the Platyhelminthes. In the great majority of the Bilateria, on the contrary, the formation of mesenchyma and cœlom occurs together, and there is therefore a sort of competition between the two methods of mesoderm development, so that in one case (Annelids, Sagitta, Phoronis) the formation of a cœlom predominates, in the other (Mollusca, Arthropoda) that of a pseudocœle (mesenchyma).

In the Bilateria there arise from mesoderm the musculature, the genital organs,[1] the excretory organs known as nephridia, the connective tissue, and fatty tissue.

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[1] [The statement that the fundament of the genital organs of the Bilateria comes from the mesoderm ought to be considerably restricted. In recent times the observations have been increasing which appear to support the Weismannian doctrine of the continuity of the germ cells. GROBBEN some time ago observed the early differentiation of the sexual cells in Moina. The same has been known for a long time to be true of Diptera and Aphidæ. Recently HEYMONS (*Sitz.-Ber. Gesell. Nat. Freunde, Berlin Jahrg.*, 1893, p. 263) has found similar conditions in various Orthoptera. The investigations of FAUSSEK on Phalangidæ (*Biol. Centralbl.*, Bd. xii., p. 1, 1892) and the very recent observations of A. BRAUER (*Zeitschr. f. wiss. Zool.*, Bd. lvii. 1894) on the scorpion have shown the early independence of the genital fundaments in these forms. Special importance in the present question is to be attached to the observations of BOVERI on Ascaris (*Sitz.-Ber. Gesell. f. Morph. u. Physiol. München*, Bd. viii., 1892), according to which the sexual cells are distinguished from the somatic cells even in the first stages of cleavage owing to the special structure of the chromatic elements of their nuclei.]

CHAPTER I.

PORIFERA.

SPONGES reproduce by sexual and non-sexual means. To the non-sexual kinds of reproduction belong—(1) *sprouting* or *budding*, which may lead to the formation of complicated stocks or colonies; (2) the formation of small *buds* which separate from the parent body and grow up independently into new individuals; (3) reproduction by means of *gemmulæ*.

The investigations on the development of sponges from the fertilized egg have not up to the present time yielded a uniform plan for the embryology of this group, and they frequently contradict one another. The following may be mentioned as features common to the development of all sponges.

(1) The sexual products arise in the connective tissue of the so-called mesoderm out of cells which at first are not to be distinguished from the connective tissue cells of this layer.

(2) The eggs are not surrounded by any cuticular envelope (chorion) or vitelline membrane. They lie naked in a cavity lined with endothelium (Fig. 1 *e*) in the mesoderm of the parent body. Here the expulsion of the polar globules, fertilization, and early development take place.
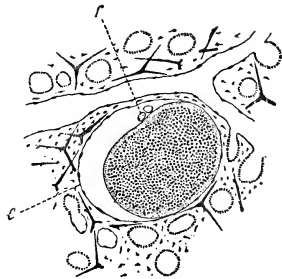
FIG. 1.—Egg of *Placina trilopha* in the parent body (after MAGDEBURG). *r*, polar globules; *e*, endothelial lining.

The polar globules of the sponges have been overlooked up to the present time. According to recent observations by MAGDEBURG, not yet published, they present in *Placina* the appearance typical for most of the other Metazoa (Fig. 1 *r*). Also the processes of their formation may well find place in the general plan, while, according to FIEDLER's communication (*Zeitschr. f. wiss. Zool.*, Bd. 47) on Spongilla, it would almost seem as if there existed here a peculiar type of formation.

(3) The eggs undergo total cleavage, and develop in the parent body into spheroidal or ovate embryos covered on the surface with flagella.

(4) When the embryos have reached the stage of the oval, flagellate, so-called *planula larva*, they emerge and pass through a swarming stage, during which development makes but little progress.

(5) After attachment to a fixed support is effected there follows a rapid transformation into a young sponge, resembling substantially the parent.

We may best arrange the types of sponge development hitherto known in accordance with the characteristic condition of the swarming stage.

I.—Type of development through a so-called Amphiblastula-stage.

The development of *Sycandra raphanus*, which has been described by METSCHNIKOFF (Nos. 12 and 13) and F. E. SCHULZE (Nos. 19 and 22), serves as an example of this type.

The egg of this calcareous sponge undergoes a total and nearly equal cleavage, but the course of cleavage is somewhat modified by the relation which the embryo acquires to the wall of one of the radial tubes of the parent (Fig. 2).

The egg is a naked cell, and lies in the parenchyma close to the wall of a radial tube. It is first divided into two blastomeres of equal size (Fig. 2 *A*) by means of a furrow which is perpendicular to the radial tube, and in relation to the orientation of the developing embryo must be considered as meridional. By means of another meridional furrow perpendicular to the first one, the two cleavage spheres separate into four blastomeres, now arranged in the form of a cross (Fig. 2 *B*), which are applied to the radial

tube with a flattened basal surface; and since they do not come into close contact with one another at the centre, they enclose between them a cavity (cleavage cavity) open above and below. With the next act of cleavage each of these four cells is divided into two equal parts by a new meridional furrow (Fig. 1 C and D). The embryo now consists of a circle
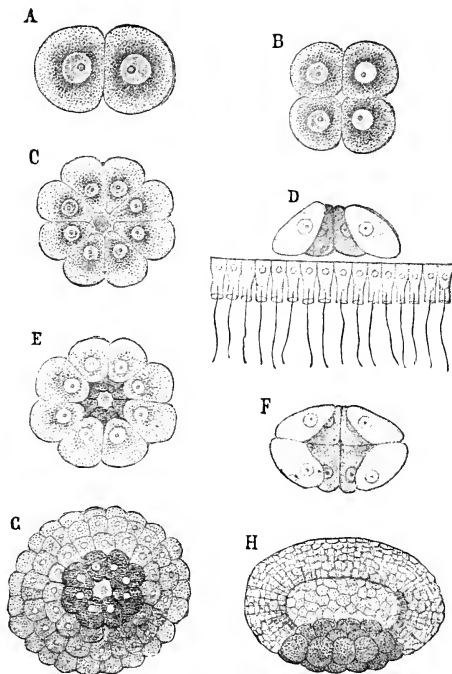
FIG. 2.—Cleavage stages of *Sycandra raphanus* (after F. E. SCHULZE). *A*, two-cell stage; *B*, four-cell stage; *C* eight-cell stage; *D*, the same in vertical section in its relation to the collared epithelium of the maternal radial tube (diagram); *E*, sixteen-cell stage; *F*, the same in vertical section (diagram); *G* later stage of cleavage with eight granular (ectodermal) cells at the lower pole; *H*, blastosphere stage in side view. In the interior the cleavage cavity; granular cells below, otherwise an epithelium of tall columnar cells.

of eight cells, which enclose the cleavage cavity. Since the cells
are applied to the wall of the tube with their broad bases,
and taper conically in the opposite direction, the embryo has
nearly the form of a cup-cake (Fig. 2 *D*). By means of a
subsequently appearing equatorial furrow each of these
8 cells is separated into an upper smaller [entodermal] and
a lower larger [ectodermal] segment; and at the same time the
whole shape of the embryo changes in this 16-cell stage,
taking on the form of a biconvex lens by the bulging out of
its basal surface (Fig. 2 *E* and *F*). The cleavage cavity is
still open at both poles, although the opening of the upper
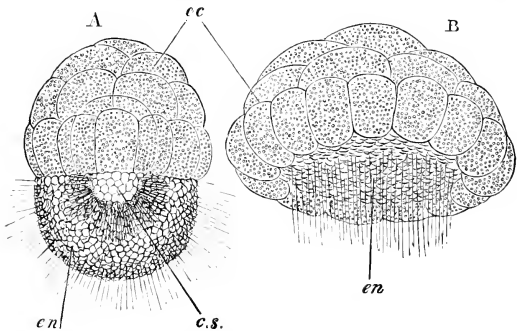
FIG. 3.—Swarming larval stage of *Sycandra raphanus* (after F. E. Schulze, from
Balfour's *Comparative Embryology*). *A*, amphiblastula-stage; *B*, stage at the
beginning of the gastrula invagination; *cs*, cleavage cavity; *cc*, future ectoderm
cells; *en*, future entoderm cells. [The orientation of the larva in this figure is the
reverse of that in Fig. 2 *D*, *F* and *H*, the entodermal pole being there the upper
one.]—Translators.

side is already considerably narrower than that of the lower
one. By means of new meridional and equatorial furrows
the embryo gradually passes into a multicellular stage,
which has an almost spherical shape, corresponding to which
there is an extensive cleavage cavity within. The opening
at the upper pole has disappeared by the apposition of the
cells, while the one corresponding to the former basal sur-
face is still retained (Fig. 2 *G*). It is surrounded by eight
[ectodermal] cells, which are soon distinguished by increasing

size and by their granular plasma. With the closure of this lower opening the embryo becomes a spherical blastosphere.

The granular cells now enlarge and multiply to the number of about thirty-two; the other cells meanwhile increase in numbers, and lengthen out into tall columnar prisms (Fig. 2 *II*), each of which develops a flagellum at the surface. The large, richly granular cells now fold into the segmentation cavity, and the last stage to be passed in the body of the parent, the so-called *pseudo-gastrula stage*, is thus reached. It has nothing to do with the true process of gastrulation, but represents a transient condition, which was perhaps acquired in connection with the mechanism of hatching.
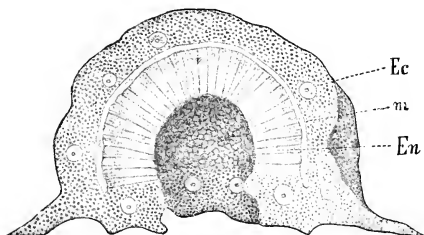
Fig. 4.—Attached gastrula-stage of *Sycandra raphanus* (after F. E. Schulze). *Ec*, ectoderm; *En*, entoderm; *m*, gelatinous secretion between the two layers (remnant of the cleavage cavity).

When the embryo is hatched the invaginated part (ectoderm) returns to its former position, and an elongation in the direction of the chief axis follows. The ovate swarming stage now reached is known as the *amphiblastula* (Fig. 3 *A*). It consists of histologically differentiated halves. The half of the body directed forwards in swimming is composed of tall columnar flagellate cells, whereas the large granular cells of the posterior half of the body bear no flagella. Within is seen the considerably reduced cleavage cavity (*cs*)[1].

[1] [According to recent investigations of Dendy (Appendix to *Literature on Porifera*, No. II.), small cells, which perhaps become mesoderm cells, make their appearance in this cavity at an early period.]

After the completion of the swarming stage, and shortly
before the attachment of the larva, a shortening in the
direction of the chief axis takes place, which is accomplished
principally by a flattening of the flagellate, formerly bulging
cell-layer; and an invagination of this layer quickly follows
the flattening, the result being that the cleavage cavity is
entirely obliterated. In this way a cap-shaped *gastrula-stage*
(Fig. 3 *B*) is reached. The outer granular layer of cells can
henceforth be considered as the ectoderm, and a circle of
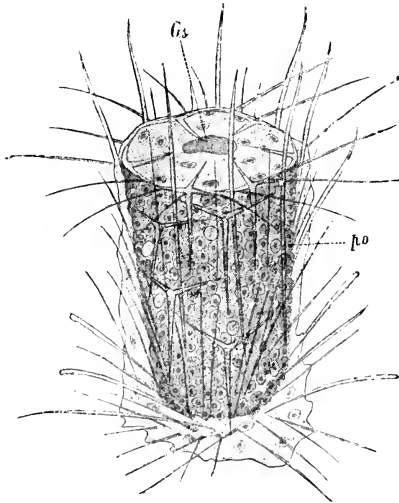
Fig. 5a.—Young, mortar-shaped Olynthus stage of *Sycandra raphanus* (after
F. E. Schulze). *Os*, osculum; *po*, lateral inhalent pores of the body-wall.

about sixteen of these cells, which are particularly prominent
and are known as marginal cells (*Randzellen*), surrounds the
wide gastrula mouth or blastopore, while the invaginated
flagellate layer represents the entoderm.

The attachment of the larva now takes place by the
fixation of the edge of the gastrula mouth by means of
pseudopodia-like processes of the marginal cells to some

support (Fig. 4). The entire process of gastrulation and attachment proceeds with uncommon rapidity.

In the gastrula-stage ectoderm and entoderm are not closely applied to each other; but one notices between them a space which must be interpreted as the remains of the segmentation cavity (Fig. 4 m), and which is filled with a gelatinous hyaline mass. According to METSCHNIKOFF, individual cells of the granular ectodermal layer migrate into this mass, and lead to the formation of the mesenchyma, the so-called mesoderm, between the two primary layers. The first skeletal structures arise in these cells in the form of small rod-like needles; triradiate ones are formed later, and finally quadriradiate ones.

After the gastrula mouth has become narrowed and finally closed, the hollow body of the larva, which has no external opening, elongates in the direction of the chief axis, and grows out into a cask-like or cylindrical form (Fig. 5a), the upper surface of which consists of a thin membrane, which acquires at its centre a circular opening, the beginning of the exhalent orifice (*osculum*, *Os*), which soon enlarges. At the same time the inhalent openings or *pores* (*po*) appear as perforations in the lateral walls. Since, moreover, the epithelial layer of the entoderm acquires the character of
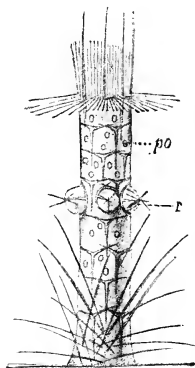
FIG. 5b. — Older, attached stage of *Sycandra raphanus* with the fundaments of the first radial tubes, *r*. Po, inhalent pores.

flagellate collar-epithelium, the characters typical of the Porifera are completed in this ascon-like stage (Fig. 5a, *Olynthus*). The development into the Sycon takes place by the radial tubes becoming established as simple evaginations of the body-wall (Fig. 5b); at first a circle of radial tubes makes its appearance at about the middle of the body; to this a second is soon added, and so on.

The amphiblastula-stage seems to occur in the life-history of many Calcarea. It has also been found in *Ascandra contorta* (BARROIS), in *Ascandra Lieberkühnii* (KELLER), and *Leucandra aspera* (KELLER, METSCHNIKOFF). The genus Ascetta develops according to another type.

II.—Type of Development through a Swarming Cœloblastula-stage.

The egg of *Oscarella lobularis* (*Halisarca lobularis*) develops in the trabeculæ of the tissue in the internal parts of the parent, which are without flagellate ampullæ, and undergoes total and equal cleavage, by which there are formed at first two, then four, eight, sixteen, etc., blastomeres of equal size. At the sixteen-cell stage a distinct cleavage cavity can be recognized within. By further cell proliferation there is formed a hollow sphere (*cœloblastula* or *archiblastula*), the wall of which is composed exclusively of cubical cells of equal size arranged in a single layer (CARTER, No. 3; BARROIS, No. 2; F. E. SCHULZE, No. 20).

Shortly before swarming, the elements of the body-wall lengthen out into columnar epithelial cells, each of which acquires a flagellum at its outer end. The swarming larva (Fig. 6 A) possesses an approximately ovate form, and exhibits a blunt yellowish pole, which is directed forwards in swimming, and a posterior, more pointed brownish-red pole. The wall of the blastula consists of a single layer of cylindrical flagellate cells. The internal cavity contains no cells, and is filled with an albuminous fluid (F. E. SCHULZE).

By the invagination of one pole of the larva this stage passes into a hemispherical gastrula-stage, which, like that of *Sycandra*, now attaches itself by its gastrula mouth to a support (Fig. 6 B). Thus there arises a shallow, cap-shaped larva, the wall of which consists of two layers (ectoderm and entoderm) and the inner cavity of which must be considered as the archenteron. The gradual closure of the wide gastrula mouth now follows; and, at the same time, by a complicated process of folding, the first flagellate ampullæ arise as diverticulæ of the archenteron (Fig. 6 C). The mesodermal connective-tissue layer originates by the migration of cells into the space embraced between the

ectoderm and entoderm.   Lastly, there occurs at the apical
pole an evagination of the body-wall like a chimney-pot, at
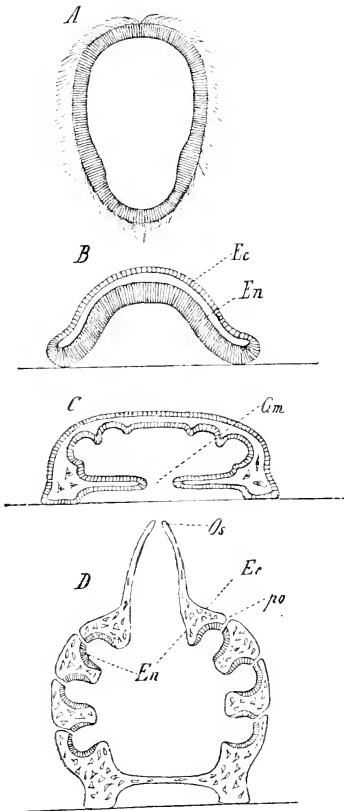
FIG. 6.—Development of *Oscarella*, diagrammatic (after HEIDER). *A*, swarming
blastula larva; *B*, attached gastrula-stage; *C*, stage initiating the closure of the
gastrula mouth (*Gm*) and the folding of the entodermic sac; *D*, young sponge; *Os*,
osculum *po*, inhalent pores; *Ec*, ectoderm; *En*, entoderm.

the apex of which the osculum (*Os*) breaks through (Fig. 6 *D*)
The inhalent pores (*po*) are formed as perforations at places
where the ampullæ lie close to the ectoderm. The system
of inhalent canals, which arises later, must be referred to
invaginations of the ectoderm, that of the exhalent canals to
evaginations of the entoderm. The larva is not attached by
its entire base, but rests upon a few foot-like supports
(K. HEIDER, No. 8).

The development of the Plakinidæ appears to be closely related to that
of *Oscarella*. The swarming larvæ can on the whole be included in the
type just described. The metamorphosis into the attached stage has
not been accurately investigated; it is certain, however, that here also
the ampullæ arise as diverticula of a common central cavity (F. E.
SCHULZE).

III.—Type of Development through a Parenchymula Stage.

The superficial layer of the swarming larva consists of a
cylinder epithelium, composed of long flagellate cells, and
encloses an internal space filled with embryonic connective
tissue.

(*a*) The superficial layer presents on all sides cells of
nearly uniform condition.

Ascetta.—By total and equal cleavage there is first produced a
cœloblastula-stage, which is similar to that of Oscarella. But even
before the hatching of the embryo, which attains an ovate form in
later stages, the immigration of cells into the internal cavity takes
place; and this occurs at the posterior pole of the larva. In this
manner the primitive body cavity becomes filled with a connective-tissue
mesenchyma, the common fundament of the mesoderm and entoderm,
in which the permanent gastral cavity subsequently appears as a fissure.
The entoderm cells arrange themselves about this in the form of a
unilaminar epithelium (O. SCHMIDT, METSCHNIKOFF).

(*b*) The superficial layer in the region of the posterior
pole of the larva presents an altered condition of the cells.[1]

[1] [The investigations of DELAGE (No. I., Appendix to *Literature*) and
those of MAAS (Nos. IV. and V.) on the development of the Cornacuspongia
(Ceratosa and Silicea) are of great importance. A satisfactory founda-
tion for the interpretation of the development of sponges in general has

Ceratosa.—The embryos of Spongelia pallescens (Fig. 7) which are ready to swarm possess a cylindrical form with one end convexly rounded and with a shallow depression at the other. In the region of this shallow invagination the flagellate cells are pigmented brownish red. The inside of the embryo is filled with a gelatinous connective tissue. The embryo of Euspongia officinalis before swarming presents a very similar struc-
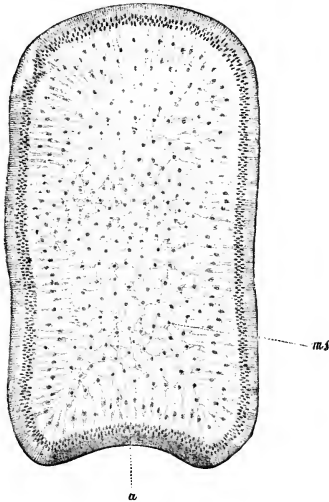
Fig. 7.—Longitudinal section through a larva of *Spongelia pallescens* (after F. E. Schulze). *a*, pigmented epithelial cells of the posterior pole of the body; *ms*, gelatinous connective tissue inside the larva.

(The superficial covering of flagella has been omitted in the illustration.)

thereby been acquired, inasmuch as the development of the Cornacu-spongia fits in completely with that of Sycandra. The free-swimming larval stage corresponds to the pseudo-gastrula stage of Sycandra. The superficial flagellate epithelial cells of the larva subsequently become the collared entoderm cells of the adult sponge; whereas the inner cell-mass, which in many cases is exposed at the posterior pole of the larva, represents the common fundament of the ectoderm and mesoderm. The ectoderm and mesoderm of sponges must be regarded as an undivided whole. The larvæ attach themselves by the anterior pole, and at the same time occurs that inversion of the layers which must be compared with the process of actual gastrulation in Sycandra.]

ture, save that the parenchyma filling the internal cavity is of a different histological character ; it consists of a tissue comparable to hyaline cartilage. The cleavage in this form is total and equal, although a cœloblastula-stage is never developed (F. E. SCHULZE, Nos. 23 and 24).

Chalinidæ.—The egg of Chalinula fertilis segments totally and un-equally, according to C. KELLER (No. 9). The first act of cleavage results in a larger and a smaller blastomere. The next stage which has been observed shows three small and one large blastomere. By the succeeding division of the small cells there results a stage in which six small cells rest like a cap upon the large undivided blastomere, which also soon divides. The small cleavage spheres are said to represent the fundament of the ectoderm, the large ones that of entoderm and mesoderm together. In the further course of cleavage, the small cells, having the form of a shell, grow around the large ones in such a manner that there results an epibolic gastrula, the mouth of which is entirely filled by the solid cell-mass of the primary entoderm, which is plainly visible at this point. The embryo now develops flagella on its entire surface, acquires a more elongated form, and emerges as a planula larva. At its posterior pole it presents a darker-coloured area of the superficial flagellate layer, and this corresponds to the superficial entodermic portion. The earliest spicules are very soon developed in the cells of the internal parenchyma. The larva now attaches itself by its posterior pole, but very soon turns over, so that it adheres to the support by the entire broad side of the body. It now acquires the form of an irregular flat cake. The forma-tion of the ampullæ within is said to proceed in a different manner from that described for Oscarella (p. 22) ; that is to say, individual entodermic cells unite into compact groups, within which a cavity appears later. The fundaments of the ciliated chambers (ampullæ), which at first were independent, then establish relations with a large central cavity arising in the parenchyma, which soon breaks through to the outside at the apex of the larva, thus producing the osculum. The larvæ of most siliceous sponges appear to belong to a type similar to that of the swarming larva of Chalinula, thus the larvæ of Esperia, Amorphina, Raspailia, and Reniera (O. SCHMIDT, METSCHNIKOFF), further those of Isodyctia and Desmacidon, made known by CH. BARROIS.

Reniera.—The larva of Reniera filigrana resembles the ones previously described. It consists of a flagellate columnar epithelium and an in-ternal cellular parenchyma. In the course of the further development the layer of columnar cells ruptures at the anterior and posterior ends, so that the internal parenchyma is exposed. The larva attaches itself by the anterior pole, loses the covering of flagella belonging to the super-ficial layer, and takes on the form of a flattened cake, while in the internal parenchyma, the common fundament of entoderm and meso-derm, a cavity appears in the form of a fissure, about which the nearest cells group themselves in the form of an epithelium. In this manner the entodermic epithelium is separated from the mesoderm. The first

ampullæ and all of the canals arise as evaginations of this inner cavity. Later the osculum breaks through, and siliceous spicules are formed in the cells of the mesodermic layer (W. MARSHALL, No. 10).

Halisarca.—By total and equal cleavage (F. E. SCHULZE, No. 20) there originates a blastula, into which migrate cells that entirely fill the cleavage cavity, and there form a connective-tissue mesenchyma. Upon emerging the larva presents at the posterior pole an area consisting of large granular flagellate cells. After the larva has attached itself and assumed a cake-like form, the ectoderm loses the flagella, and is changed into a pavement epithelium. In the internal parenchyma there now arise fundaments of the ampullæ and canals which at first are separate, but subsequently unite into a common system (METSCHNIKOFF, No. 14).

A unique type of development, which perhaps most resembles Reniera, appears to exist in *Spongilla*. The de-
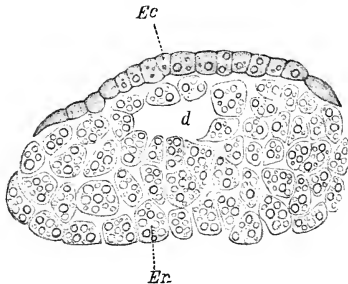
Fig. 8.—Late stage of cleavage (beginning gastrulation) of *Spongilla* (*Ephydatia*) *fluviatilis* (after GOETTE). *Ec*, ectoderm cells; *En*, entoderm cells; *d*, central entodermic cavity.

velopment of this fresh-water sponge has been described by GANIN (Nos. 4 and 5) and GOETTE (No. 6); but in many points the statements of these investigators do not altogether agree. In our presentation we follow the detailed description of GOETTE without forming any preliminary judgment as to the way in which the development of Spongilla is related to that of other sponges. A final judgment will be possible only when new observations have been made on the development of sponges of the most widely differing groups.

The egg of Spongilla (Ephydatia) fluviatilis undergoes

total unequal cleavage, by means of which there arises an embryo consisting for the greater part of large blastomeres rich in yolk (entodermic portion, Fig. 8 *En*), and presenting only at its upper pole a cap of small blastomeres containing little yolk (ectodermic part, Fig. 8 *Ec*). Since the cap of ectoderm cells gradually grows around the entire embryo, there is formed in this way a kind of epibolic gastrula. At an early period there appears in the entodermic mass an eccentrically placed irregular cavity, which can be referred neither to a cleavage cavity nor to an archenteron, and is known as the entodermic cavity. The chief axis of the embryo is recognized by the eccentric position of this cavity, for it always lies close to the apical pole (the subsequent anterior pole). The embryo, which at first is comparable to a plano-convex lens, now elongates in the direction of the chief axis, and is covered on the surface with a coat of cilia. The swarming larva (Fig. 9) is generally ovate in form, and in floating in the water has the broadened anterior end of the body, in which the spacious entodermic cavity is situated, always directed upwards. The larva possesses a superficial, unilaminar, flagellate epithelium, all the cells of which present the same character. Within the posterior half of the body is found a solid entodermic mass, which, in the course of the further development, takes on the character of embryonic connective tissue. The cells lying in the vicinity of the cavity are flattened, and form a reticulated layer of amœboid elements. A similar layer of flattened cells is found at the surface of the solid entodermic core, where it is in close contact with the ectoderm. At an early period spicules are developed in certain cells of this core.

The larva attaches itself by the apical pole, the layer covering the entodermic cavity being split open, and the edges of the breach thus formed bending outward. In this way the cells of the entodermic layer come in contact with the support, to which they adhere by means of pseudopodia-like processes. In the majority of cases the larva after this first attachment bends over in order thus to attach itself by a broader surface. According to Goette, there ensues the

complete loss of the ectoderm, which breaks up and is detached from the surface in shreds, so that the entire body of the young sponge consists of entoderm. In this now solid mass (for the entodermic cavity has disappeared in the process of attachment) ampullæ arise as separate fundaments; they are produced by groups of cells (each of which has arisen from a single cell) acquiring cavities within them. The canals and cavities of the body develop in the same manner in many separate regions, and afterwards unite with one another and with the ampullæ. The most superficial layer of the body acquires the character of a pavement epithelium,
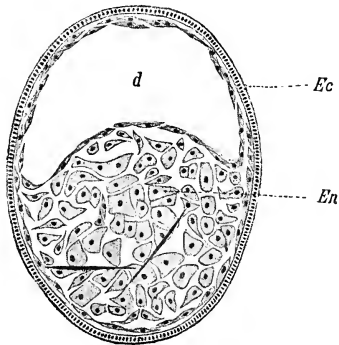
FIG. 9.—Free-swimming larva of *Spongilla fluviatilis* (after GOETTE). The covering of flagella has been omitted. *Ec*, ectoderm; *En*, entoderm; *d*, entodermic cavity.

and forms the permanent epidermis of Spongilla. All organs therefore arise by histological differentiation from a single layer, the primitive entoderm.

In GOETTE's account, which we have given here, several points must appear to be still doubtful, thus, above all, the alleged complete casting off of the ectoderm. To be sure, a rupture and partial loss of the ectoderm has also been maintained for other sponges (Reniera, Esperia) by earlier observers, to which attention has already been called (p. 24). But such appearances are probably for the most part to be referred to pathological or abnormal processes. GANIN has assumed that in Spongilla the ectoderm of the larva becomes the permanent epidermis of the sponge; and

that statement has recently been confirmed by the observations of O. Maas (*Zool. Anz.*, 1889), who has convinced himself on the same object that the ectoderm of the larva is not cast off, but gradually passes over into the superficial pavement epithelium of the adult sponge. Also in regard to the origin of the ampullæ and canal system Ganin does not agree with Goette. According to Ganin, the entodermic cavity is to be explained as an archenteron, and represents the earliest fundament of the canal system, from which the ampullæ arise as diverticula. A mode of origin for the ampullæ similar to that communicated by Goette for Spongilla has recently been maintained by Dendy (*Quart. Jour. Micr. Sci.*, 1888) for one of the horn sponges (Stelospongia).

The distribution of the recognized types of development among the different groups of sponges, then, is represented as follows: In the calcareous sponges (Calcarea) the amphiblastula is found in most of the cases observed up to the present time. Perhaps this larval form is confined to the Calcarea. The cœloblastula appears in Oscarella and in the family of the Plakinidæ, whereas the parenchymula seems to be present generally in the Ceratosa and siliceous sponges. Furthermore Halisarca and Ascetta exhibit a parenchymula stage.

As is to be seen from the preceding, a uniform plan of development for sponges cannot at the present time be formulated.[1] The statements differ too widely. In certain cases we find a cœlogastrula-stage, which attaches itself to some support by the circumference of the large gastrula mouth. This is of importance as a distinguishing characteristic in contrast with the Cnidaria, in which the attachment is always effected by the aboral pole of the two-layer planula larva. In other cases there is formed a parenchymula, the genesis of which for many forms is as obscure as the further development of this stage into the adult sponge. We can only assume conjecturally that this stage is in all cases brought about by epibolic gastrulation or by the process of migration of certain cells from the entodermic pole. The most obscure point in the development of sponges is the metamorphosis accomplished at the moment of the attachment of the swarming larva. Even the statements regarding the pole by which the larva attaches itself vary for the different forms. Authors likewise differ in regard to the organogeny, above all as regards the origin of the canal system and the flagellate ampullæ. In certain

[1] Compare footnote, p. 22 [Translators].

cases the common fundament of the ampullæ and exhalent canal system is affirmed to have the form of a central cavity (archenteron), from which the ampullæ and exhalent canals arise by repeated foldings of the wall. Opposed to this are the observations of other authors, according to whom the different ampullæ are formed independently, and become united by means of the canals which appear later on, and which only gradually unite into a common system of canals.

In such a condition of affairs it is hardly possible to arrive at any general conclusions without in one way or another doing violence to the individual statements. This much, however, seems with some certainty to result from all the observations : that we have before us in the sponges an independent stem of the Metazoa, which is connected with the other types only at its roots. We adhere to the view that the sponges have a common origin with the rest of the Metazoa. In the embryology of the sponges we find true blastula- and gastrula-stages, which appear to point to an ancestral form common to the Porifera and all other Metazoa. Characteristics of histological differentiation (the formation of columnar and pavement epithelium, of connective tissue and cartilaginous tissue) likewise point to this community of origin. As opposed to these characteristics, the single fact of the occurrence of the collar-bearing flagellate cells of the entoderm does not seem sufficient to warrant the derivation of the Porifera as an independent group from the Choanoflagellata and the denial of their phylogenetic relationships to the rest of the Metazoa (Sollas, No. 15 ; Bütschli).

That the Porifera do not stand in any close relationship to the Cnidaria (Cœlenterata in the stricter sense) (Marshall, No. 11) appears to be beyond doubt. We lay less stress upon the absence of nettling capsules, as being a purely histological character, than on tectonic points. The attempts to reduce the structure of sponges to the fundamental form of the Polyp must lead to contradictions. Above all must be emphasized the fact that the exhalent opening of the canal system, the so-called osculum, is not homologous with the

mouth of Cœlenterates, furthermore that the Porifera in
general are derived from a monaxial, heteropolar funda-
mental form in which the production of secondary axes in
definite numbers has not yet taken place, whereas the radial
type with four rays lies at the foundation of the Cnidaria
(compare F. E. Schulze, No. 12; A. Goette, No. 6; Heider,
No. 8). The absence of movable processes of the body
(tentacles) and the low grade of histological differentiation
serve as substantiating facts in support of this view.

The Porifera possess no true muscle fibres. The property of con-
tractility appears rather to belong to all the cells in about the same
degree, and the "contractile fibre-cells" occurring in the mesoderm of
many sponges are distinguished from true muscle fibres by the fact that
the contractile substance in them has not yet become separated as a
distinct portion of the cell. The absence of a nervous system has not
yet been proved, it is true; but the presence of such a system does not
appear to be firmly established, for up to the present time the groups of
cells claimed by Lendenfeld as the nervous system of sponges have
remained doubtful as regards this interpretation.

In respect to the origin of the canal system of sponges,
reference must be made to those primitive forms which are
found more especially among the calcareous sponges, and
by comparison of which it is most clearly proved that the
complicated canal system of the siliceous and horny sponges
has been evolved by a continuous process of folding of the
wall of the sacular olynthus-like primitive form, whereby
the collar epithelium eventually becomes localized in
particular parts (ampullæ) of the canal system. If the
diagram Fig. 10 *A* represents the wall of a simple ascon
perforated by pores, and if we bear in mind that the entire
inner surface is covered with collar-cells, then Fig. 10 *B*
shows the origin of the radial tubes of a sycon by means
of a folding of this wall. At the same time the entoderm
lining the common central cavity is transformed into a pave-
ment epithelium; and alternating with the evaginations of
the radial tubes, enfoldings (*a*) of the outer surface of the
body lined with ectoderm have also been formed, the funda-
ments of the inhalent canal system. Fig. 10 *C* shows how,
by a repeated process of folding, diverticular spaces (*b*) of
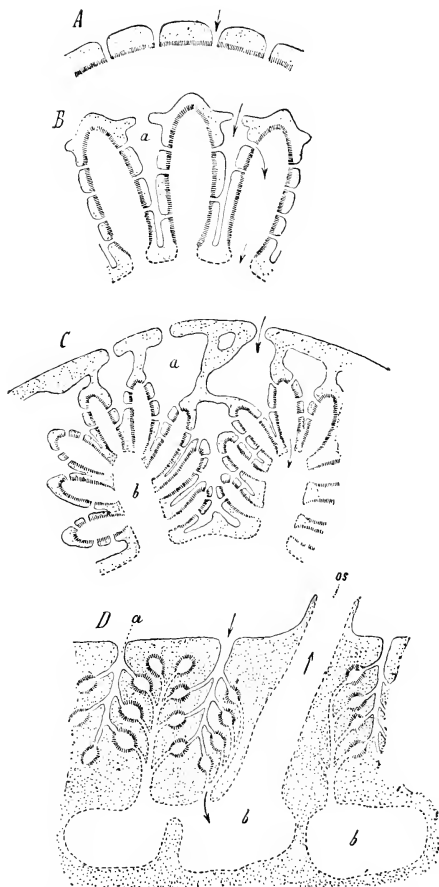
Fig. 10.—Diagram of the development of the canal system in various sponges. The ectoderm is indicated by a continuous, and the entoderm by a broken, line. The collar epithelium of the entoderm is expressed by perpendicular striations. *A*, cross section through a part of the wall of an ascon; *B*, cross section through the wall of a sycon; *C*, cross section through the wall of *Leucilla connexiva* (after POLÉJAEFF); *D*, vertical section through Oscarella; *a*, spaces of the inhalent canal system; *b*, spaces of the exhalent canal system; *os*, osculum.

the central cavity arise, in which the fundaments of an exhalent canal system, lined with entoderm, are to be recognized, so that in this manner we arrive by gradual transitions at the distribution of the canals shown in Fig. 10 *D*, which serves as a plan for most sponges.

This series, resulting from the comparison of different genera, makes it probable that the ontogenetic origin of the gastro-canal system by the formation of diverticula from a single common central cavity, as it has been observed in many forms, represents the original mode of development. As to the development of the calcareous or siliceous spicules, it appears to be certain that they are formed within skeleto-genous mesoderm cells. The circumstance that the forms of the spicules frequently merge into one another, and that in many of the rod-like spicules an axial cross has been observed in connection with the central canal, suggesting their origin from triaxial spicules, gave rise to certain specula-tions on the fundamental form of the spicules occurring in the different groups and their derivation from the soft parts of the body through simple mechanical conditions. Thus F. E. SCHULZE (*Abh. kyl. Acad. Berlin*, 1887) found that the fundamental form of the regular triaxial spicules of the cal-careous sponges was determined by the regular alternating position of the pores in the wall of the original ascon-like animal, and that the peculiar initial quadriradiate form of the Tetractinellidæ (as well as that of the sponges derived from them, the Monactinellidæ and the horn sponges) were explain-able by the closely crowded position of the spherical ampullæ and the resulting forms of the soft parts of the body, whereas in the Hexactinellidæ the arrangement of the trabeculæ of the soft parts led to the fundamental form of the regular sexi-radiate spicules.

Whereas the hard parts just mentioned develop within cells, the horn fibres must be considered as cuticular secre-tions, for, according to F. E. SCHULZE, they are deposited on the inner surface of mesoderm cells (*so-called spongioblasts*) arranged like an epithelium.

Non-sexual Reproduction of Sponges.—In this con-nection is to be mentioned the formation, by means of budding,

of new individuals, which remain united to the parent
organism throughout life, thereby permitting the formation
of extensive colonies.   In many cases (Sympagella nux,
Hexact.) the single individuals of the colony can readily be
recognized as such (No. 4), whereas in the majority of cases
their connection becomes so intimate that it is only the pre-
sence of the oscula which makes the recognition of the
individuals to a certain extent possible.

FIG. 11.—*Lophocalyx* (*Polylophus*) *philippinensis* with buds (after F. E. SCHULZE).
a, young bud;   *b*, older bud constricted off from the parent and attached to it by
the siliceous spicules of the parent only.

Furthermore, a kind of reproduction occurs in many
sponges by means of buds, which separate from the parent
in a partially developed condition, and grow up into a new
sponge organism.   A comparatively simple case of this kind
appears to exist in Leucosolenia (VASSEUR, No. 36.)   The
young bud is here a simple outfolding of the body-wall, which
is soon separated as an independent sac-like body, and after
becoming attached, grows up, and by the production of an
osculum becomes a young Leucosolenia.   In a similar man-

ner the budding in Tethya, Tetilla, Rinalda, etc. (Désö, No. 29; MEREJKOWSKY, No. 31; SELENKA, No. 34), and also in Lopho-calyxi. e. Polylophus (F. E. SCHULZE, No. 33), appears to de-pend upon the outgrowth and abstriction of a portion of the parent body, in which is included a part of the canal system of the latter, while the tissues exhibit an active cell-proliferation. The separation from the parent frequently takes place in these cases by an emigration along projecting siliceous spicules (Fig. 11). After separation has taken place, the bud grows up into a young animal resembling the parent organism. To this class belong also the transportable brood-buds of Oscarella described by F. E. SCHULZE (No. 32), which are very similar in structure to the larva of this form (Fig. 6 D), since they contain a considerable internal cavity. These vesicular bodies, after they have become separated from the parent, are for a time carried about by currents, and then fall to the bottom, where they grow into young sponge-crusts.

Reproduction by budding in these forms depends upon the fact that the superficially located parts of the sponge tissue become separated and acquire the power of reproducing the entire form of the parent organism. If we consider a simi-lar process to take place within the tissues of the sponge, whereby the separation of such a group of cells is accom-plished by an encystment, then perhaps the manner is indi-cated by which we are to consider the first formation of gemmulæ to have taken place. Reproduction by means of gemmulæ occurs principally among the fresh-water sponges (Spongilla), although the occurrence of gemmula-like structures has also been affirmed for a few marine forms (TOPSENT, No. 35). The fully developed gemmula (Fig. 12) consists of a multicellular germ (d), whose large cells, poly-gonally flattened by mutual pressure, are filled with yolk particles, and present one, frequently two or more, nuclei (PETR, WELTNER). This germ-body is surrounded by an envelope often very complicated in structure, which opens to the exterior by means of a pore (p) provided with an oper-cular apparatus. There is always found a thick cuticular layer (c), to which there is generally added externally a

porous meshwork containing air (air-chamber layer), in which skeletal elements (needles or amphidiscs) are often found embedded (*b*), while outside of all there may be added still another cuticular layer (*a*). Furthermore the germ-body is said to be immediately enveloped in a delicate membrane (CARTER).

The gemmulæ are found in the midst of the mesodermal tissue of the parent body. Many views have been advanced in regard to their origin. According to GOETTE (No. 6), there is a kind of cell-proliferation that affects a particular territory and also involves the ampullæ and canals of this region, whereas, according to MARSHALL (No. 30), certain mesodermic cells, filled with reserve food-stuff, creep together in groups to form the gemmulæ. The earliest fundament of the gemmula, which is essentially a mass of cells having embryonic characters, soon exhibits a differentiation of two layers (GOETTE, WIERZEJSKI). The central mass is composed of large cells in which yolk particles become embedded in ever-increasing quantities. The cells of the outer layer, according to GOETTE, become club-shaped, and arrange themselves into a kind of elongated epithelium enveloping the central mass. This layer, like the spongioblasts, at first secretes a thick cuticula on the inside (the fundament of the inner cuticular membrane, Fig. 12 *c*) ; the amphidiscs are then formed in the cells of this layer, whereupon it moves outward in order to secrete, likewise from its inner surface, the outer cuticular membrane, Fig. 12 *a* (GOETTE). According to WIERZEJSKI (No. 39), the amphidiscs are not formed in the layer of cylindrical cells mentioned, but in the surrounding tissue, and only later move into this epithelial layer, in which they become arranged in a definite manner.

FIG. 12.—Gemmula of Spongilla (Ephydatia) fluviatilis (after VEJDOVSKY). *a*, outer cuticular layer ; *b*, amphidisc layer ; *c*, inner cuticular layer ; *d*, germ-body ; *p*, pore.

The formation of the gemmulæ takes place principally in the fall in parts of the sponge which generally die after gemmulation has taken

place. In the following spring the germ-body crawls out hrough the pore, to become attached and metamorphosed into a young sponge, by means of processes of development which have not yet been accurately studied.[1]

From what has been said it follows that in the gemmulæ we have to do with an encysted portion of the parent body, provided with food-yolk and retrograded to an embryonic condition, which acquires the power to regenerate the parent organism. On this account gemmulation has also been designated as a kind of internal budding. In support of another current interpretation, according to which the gemmules would represent the winter eggs of Spongilla, evidence is as yet entirely wanting, for in this case it would be necessary to prove that the germ-body originates by the division of a single original cell, but all observations made up to the present time are opposed to this.

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[1] [Compare ZYKOFF (Nos. VIII. and IX., Appendix to *Literature* on Porifera).]

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CHAPTER II.

CNIDARIA.

I. HYDROZOA.

I.   Hydroidea.

The sexual products of the Hydroidea are usually matured in specially organized individuals, which are either free-swimming, and then attain to the high degree of organization of the *hydroid medusa*, or remain united throughout life with the polyp colony, and then, as sessile *medusoid gonophores* (*Sporosacs*), exhibit that organization only in a degenerated condition. In Hydra, on the contrary, the sexual products develop in the ectoderm of the body-wall of the polyp.

The eggs of the hydroid medusæ are generally extruded, by the dehiscence of the wall of the gonad, into the sea-water, where they are fertilized and undergo development. But in those forms which possess sessile gonophores the first stages of development take place within the gonophore, and the embryo does not become free until it attains the stage of a *planula* or *actinula*.

In the following account we separate as *metagenetic forms* those which produce free-swimming medusæ (forms with alternation of generations) from those whose sexual individuals remain sessile, as medusoid buds (forms with masked alternation of generations, Hatschek). A third group embraces those Hydroids in which there is developed out of the

egg not a polyp, but a free-swimming larva, which passes into the form of a medusa by a simple metamorphosis (*hypogenetic forms* with suppressed alternation of generations).

Metagenetic Medusæ.—We begin with the description of the better-known cases of development of the eggs of *hydroid medusæ*, and follow principally the accounts of CLAUS (No. 3) and METSCHNIKOFF (No. 12). The spheroidal eggs of the craspedote medusæ are for the most part colourless, transparent, and destitute of a membrane. There may be distinguished in them a layer of ectoplasm, consisting of a viscid formative yolk, and an endoplasm filled with coarse
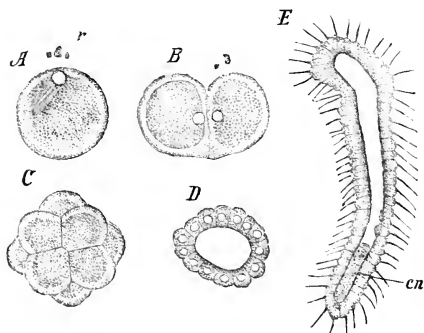
FIG. 13.—Development of the egg of *Rathkea fasciculata* (after METSCHNIKOFF). *A*, an egg immediately after deposition ; *r*, polar corpuscles ; *B*, stage of first division ; *C*, eight-cell stage ; *D*, blastula-stage in optical section ; *E*, planula-stage with formation of entoderm, *en*.

granules of nutritive yolk (Fig. 13 *A*). After fertilization they undergo a total, and in most cases a nearly equal, cleavage. By the formation of the first two meridional and mutually perpendicular furrows (extending from the animal to the vegetative pole, Fig. 13 *B*), there arise four blastomeres placed in the form of a cross, and by a succeeding equatorial furrow there is produced an eight-cell stage (Fig. 13 *C*), while two additional meridional furrows lead to the formation of a sixteen-cell stage. Only in certain cases (Æquorea) is the cleavage more unequal, the blastomeres of the animal

zone being less voluminous than those of the vegetative.   In
early stages the blastomeres move away from the centre, so
that there is formed a gradually enlarging *cleavage cavity*
within.   By additional but less regular cleavages the blasto-
meres increase in numbers, and arrange themselves into a
single layer of epithelial cells surrounding the cleavage
cavity, thus attaining the typical *blastula-stage* (Fig. 13 *D*).
This cell-vesicle now elongates, so that it becomes ovoid, or
sausage-shaped ; and its surface becomes covered with flagella
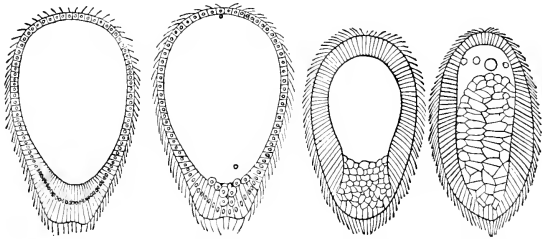
Fig. 14.—Formation of the entoderm by polar ingression in the planulæ of
Aequora (after CLAUS, from HATSCHEK'S *Lehrbuch*).

(Fig. 13 *E*), by the motions of which it swims about with
the broader end of the body directed forward.   The forma-
tion of the entoderm now takes place by *polar ingression*, at
first a few, and then numerous, cells migrating from the
posterior end of the body into the cleavage cavity, so that,
advancing from behind forward, they gradually fill it up
(Fig. 13 *E*, Fig. 14).   In this way there arises a larva which
is eminently characteristic for the Hydroids, and was named
by DALYELL the *planula* (Fig. 15 *A*); it has also been called
a *parenchymula*, on account of the embryonic cell-mass filling
its interior (METSCHNIKOFF).   During further development
there are formed in the ectoderm nettle-capsules, which seem
to be especially concentrated about the posterior pole, while
within the mass of entoderm cells there arises a fissure, the
first trace of the *gastral cavity*, around which the entodermal
cells assume an epithelial arrangement.   Preparation is now

made for the process of attachment.[1]   The larvæ sink to the
bottom, their motions become slower, and finally they attach
themselves by means of the disc-like enlargement of the
anterior end of the body (Fig. 15 C).   They then lose their
cilia ; and the surface becomes covered with a thin cuticular
secretion, the perisarc (Fig. 15 D).   The disc-shaped region
of attachment often acquires a lobed appearance, due to the
formation of notches (Fig. 15 E).   The disc constitutes the
first fundament of the hydrorhiza, while the posterior end of
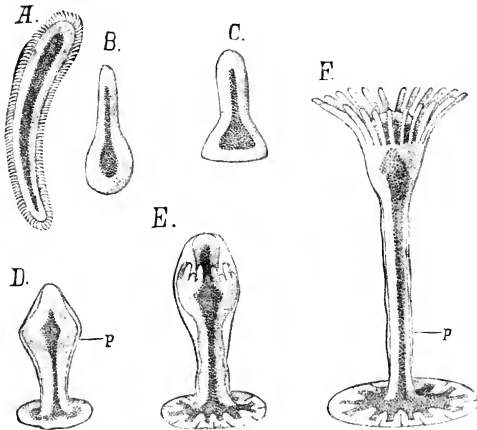
FIG. 15.—Attachment and growth of the larval planula of *Eudendrium* (after
ALLMAN). *A*, planula ; *B* and *C*, stages of attachment by means of the disc-like
enlargement of the anterior end ; *D*, beginning of the formation of the hydranth
and perisarc, *p* ; *E*, formation of the tentacles ; *F*, expansion of the hydranth.

the larva, now directed upward, grows up into the first
hydranth of the young polyp colony.   The fundaments of the
tentacles (Fig. 15 E) arise as lateral diverticula, and the
mouth-opening is formed at the apex by a breaking through

[1] The development of the eggs of medusæ and of hydroid polyps with
gonophores is from the planula-stage onward alike, so that Eudendrium
may serve in this place as an example.

of the body-wall. Finally, the perisarc is ruptured at this place, and the polyp becomes fully expanded (Fig. 15 *F*).

The origin of the polyp stock does not always take place exactly according to the plan here given. In certain cases the larva becomes attached by its side, and is almost wholly employed in the formation of the hydrorhiza, while the first hydranth grows out of it by a kind of budding (Mitrocoma, METSCHNIKOFF).

The *hydroid polyp* thus produced propagates principally by means of lateral budding. There is formed at first a hernia-like protrusion of the body-wall, the cavity of which communicates with the gastral cavity of the parent animal, and the wall of which consists of the same layers as that of the parent (ectoderm, entoderm, and the sustentative lamella between them).[1] The bud is converted into a hydranth by the progressive abstriction of this protrusion from the parent animal, by the production of a crown of tentacles, and by the acquisition of a mouth-opening through dehiscence at the anterior end. Only rarely do the hydranths thus produced detach themselves from the parent, and become independent (Hydra); in most cases extensive polyp colonies are formed by continued budding. The laws of budding, by which the extraordinarily manifold shape as well as habit of the polyp colonies is determined, have recently been subjected to a critical study by WEISMANN (No. 49) and by H. DRIESCH (*Inaug.-Diss.*, Jena, 1889).

The individuals produced by budding do not always have the same form as that of the first hydranth. A more or less pronounced polymorphism often arises among the individuals of a colony. There are produced defensive polyps (spiral zoöids), abundantly supplied with nettle-capsules, but destitute of tentacles and oral opening, hard-shelled spiny protective polyps, nematophores, etc. The so-called blastostyle, which occurs in many Hydroids, is also to be interpreted as a metamorphosed, non-tentacular polyp, upon the lateral walls of which the gonophores are produced by budding.

The formation of the individuals destined to become sexually mature (medusæ, sessile medusoid buds) is the

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[1] [Recently ALB. LANG (No. IX., Appendix to *Literature* on Cnidaria) has maintained that the whole of the bud in Hydroids is derived from the ectoderm of the parent.]

result of a lateral budding, which during its earliest stages
pursues a course quite similar to that described above. Here
too there is formed at first a small spheroidal bilaminar
bud (Fig. 16 *A*), between the two cell-layers (ectoderm and
entoderm) of which there can be recognized a hyaline sus-
tentative membrane. The next change, which takes place
at the same time with the progressive abstriction of the
bud, is the formation of an ectodermal thickening at the
free distal pole, which is developed (Fig. 16 *B*) into a knob,
the so-called *nucleus of the bud* (*nucleus of the bell*). By the
growth of the latter into the interior of the bud, the ento-
dermal sac is invaginated, so that it now assumes the form
of a cup (Fig. 16 *B*). While a fissure (the beginning of the
cavity of the bell) makes its appearance (Fig. 16 *D*) in the
nucleus of the bud, the two facing layers of the cup-shaped
entoderm sac come into close contact, and fuse along
four meridians (Fig. 16 *E*), so that of the cavity of the
entoderm sac only four perradial regions (*i.e.* places cor-
responding with the four chief radii) remain open ; they are
the fundaments of the four radial canals. It is to be
observed that these four radial canals are connected with one
another through the remnant of the obliterated entoderm sac
(Fig. 16 *E*, *i*), in other words through the originally bila-
minar so-called *vascular lamella* (*cathammal plate*) (L. AGASSIZ,
No. 2 ; CLAUS, No. 62). While with the further enlargement
of the bud the bell-cavity increases in size and breaks through
to the outside, and while the manubrium grows out at the
bottom of it, the sustentative lamella of the wall of the
bell is converted into the gelatinous substance of the
umbrella. The radial vessels have become relatively nar-
rower and farther separated from one another. The ring-
canal at the margin of the bell appears to arise by a
secondary separation of the two layers of the vascular
lamella. With these metamorphoses and with the breaking
through of the mouth-opening and the formation of the
velum,[1] the medusa is essentially completed and ready to be
detached (Fig. 16 *F*).

[1] The velum does not arise by the formation of a fold, but directly
from that ectodermal membrane which in early stages (Fig. 16 *D*) sepa-

"Alternation of generations" in Hydroids depends upon the regular alternation of non-sexual generations (hydroid polyps), increasing by lateral budding, with a sexually developed generation (hydromedusa or sessile gonophore).

The account of the development thus far affords some
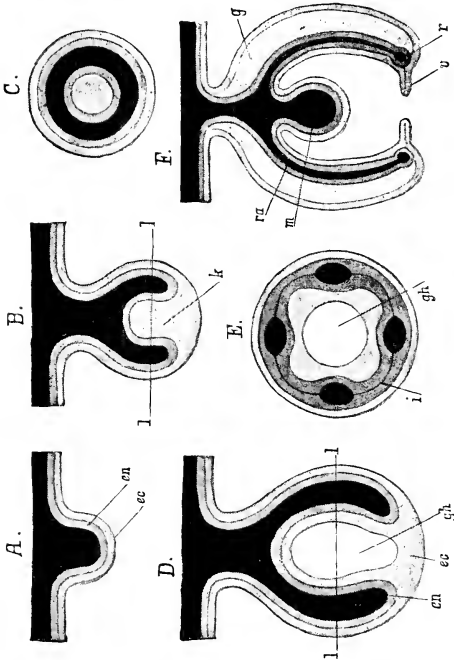
FIG. 16.—Diagrammatic representation of the budding of medusæ. *A*, very young bud; *ec*, ectoderm; *en*, entoderm; *B*, bud with solid nucleus, *k*; *C*, cross-section of *B* at the level of the line *ll*; *D*, bud with the beginning of the cavity, *gh*, of the bell; *E*, a cross-section through *D* at the level of the line *ll*; *gh*, cavity of bell; *i*, interradial region of fusion between the two entodermal layers (vascular plate); *F*, the nearly completed fundament of the medusa; *m*, manubrium; *m*, radial canal; *r*, cross-section of the ring-canal; *v*, velum; *g*, gelatinous layer of the umbrella.

suggestions of the manner in which the hydroid polyps and the hydromedusæ may be referred back to one and the

rates the cavity of the bell from the outside world and in which a two-layer arrangement of the ectodermal cells can be recognized at an early epoch (WEISMANN, No. 49, p. 260).

same initial form. For if we assume that the alternation of generations in Hydroids has arisen as a result of division of labour, whereby the capabilities of sexual and non-sexual reproduction have been distributed to different individuals (LEUCKART, No. 11), we must regard the different shapes of these individuals as having been evolved from the same fundamental form (ALLMAN, No. 15; CLAUS, No. 62; O. AND R. HERTWIG, No. 8), the sessile individuals, which are reproduced exclusively by budding, having undergone development more in the vegetative direction, while the free-swimming medusæ, which become sexually mature, have allowed the systems of organs pertaining to the animal functions to attain to complete development. Various circumstances [1] indicate that in the sessile form of the hydroid polyp we have to do with the primitive condition, so that we may characterize the hydromedusa as a metamorphosed hydroid polyp which has acquired the power of independent locomotion. Then the mouth of the medusa would be homologous to
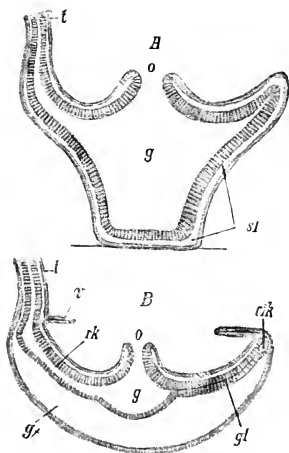
FIG. 17.—A, diagram of a hydroid polyp; B, of a craspedote medusa (after O. UND R. HERTWIG, from LANG's Lehrbuch). o, mouth; g, gastral cavity; t, tentacle; sl, sustentative lamella; gt, gelatinous mass between ectoderm and entoderm; rk, radial canal; gl, vascular lamella or cathammal plate; v, velum; rik, ring-canal.

[1] As such is to be considered the fact that the sequence in budding is from hydroid polyp to medusa, and never the reverse, further the total absence of the production of organs, especially sensory organs, on the exumbrellar side of the medusa-bell, which points to an antecedent sessile condition; this is of importance in comparison with the condition in Ctenophores.

that of the polyp (Fig. 17 *o*), and the manubrium of the former to the oral cone (peristome, hypostome) of the latter. The cavity of the medusa-bell would be represented by a concavity of the peripheral part of the peristome, which exists in many hydroid polyps, while the polyp's crown of tentacles would be equivalent to the marginal tentacles of the medusa (Fig. 17 *t*). According to this interpretation, the aboral part of the polyp, broadened and flattened, would be metamorphosed into the exumbrella of the medusa, while the gastral cavity of the latter is differentiated into a central stomach cavity and a *peripheral intestine* (*Kranz-darm*), consisting of radial canals and circular canal, together with the vascular lamella lying between them (Fig. 17). The velum, produced by a fold of the ectoderm, would be a new structure, not present in the polyp. To the differentiations which characterize the medusa belong the greater development of the musculature and the nervous system (double nerve-ring of the margin of the bell) and the evolution of sensory organs.

In many Hydroids, *pari passu* with an acceleration of sexual maturity accomplished by a dislocation of the germarium (WEISMANN, No. 50), the sexual persons have lost the power of free locomotion, and have been metamorphosed into sessile medusoid buds (gonophores). They must be regarded as reduced medusæ (v. KOCH, No. 34), in which the marginal tentacles, the sensory bodies, and the velum—and often the opening of the bell also—have disappeared, while the peripheral intestine has undergone considerable reduction (Fig. 18). According to the degree of degeneration, there may be distinguished with WEISMANN (No. 49) the following five stages:—(1) *medusoids* with canals in the bell, but without marginal tentacles, usually also destitute of velum and sensory bodies, manubrium without mouth, usually becoming detached at maturity (Pennaria); (2) *sessile medusoids*, bell usually without canals or with incomplete ones, but with bell-cavity and bell-mouth (Tubularia); (3) *sessile gonophores*, the wall of whose bell—still retaining the entodermic lamella and two layers of ectoderm, but without canals or bell-mouth—immediately encloses the manubrium (Clava, Hydractinia); (4) *sessile gonophores*, the medusa-layers of whose wall are incomplete (female Campanularia); (5) *sporophores*, *i.e.* sessile gonophores without any trace of medusoid structure (Cordylophora).

It is still questionable whether the sexual organs of Hydra are related to the last of these groups, according to which Hydra would be an extremely modified form, or whether we are not perhaps to regard

Hydra as a polyp that has reached sexual maturity, and therefore as a
very primitive form of hydroid.

In general the sexual organs, both in the medusæ and in the sessile
gonophores, lie in the ectodermal wall of the manubrium (Fig. 18) or
(Leptomedusæ, HAECKEL) on the inner wall of the bell in the course of
the radial canals.

The investigations of WEISMANN have yielded new results concerning
the early stages in the formation of the sexual products. In the
original condition the sexual cells were developed and reached maturity
in the ectoderm of the manubrium of the medusa. In other cases (in
forms with sessile gonophores) the development of the sexual cells took
place even before the gonophore itself was fully formed; there ensued
therefore a secondary displacement (phyletic) of the germarium, first
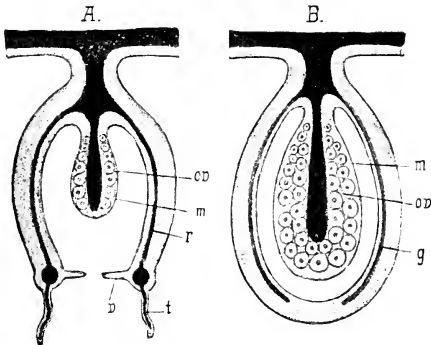
Fig. 18.—Diagrammatic section through two sexual hydroid individuals. *A*,
young medusa, still attached; *B*, sessile gonophore; *ov*, gonads (ovarium); *m*,
manubrium; *r*, radial vessel; *t*, tentacle; *v*, velum; *g*, vascular lamella.

into the ectoderm of the bud, then into the entoderm of the same, and
finally into the entoderm of the stem and the branches before the de-
velopment of the bud. From this location the sexual cells are compelled
to migrate (ontogenetically) to the seat of their maturation. It is to be
seen that this displacement of the germarium was established in the
interest of the greatest possible acceleration of sexual maturity. In this
case the displacement (phyletic) of the germarium is in centripetal
direction. In the Leptomedusæ (HAECKEL), on the contrary, the seat of
maturation is displaced in centrifugal direction, for HARTLAUB has been
able to show in Obelia that the sexual cells arise in the manubrium, and
reach the radial canals only secondarily.

Reproduction by *budding* occurs not only in hydroid polyps, but also

in hydromedusæ. In the case of the latter the buds may be developed on the manubrium (Sarsia siphonophora, Lizzia), at the base of the tentacles (Sarsia prolifera, Codonium codonophorum), on the ring-canal, or at other places. Concerning budding in the Cuninas consult p. 58. A remarkable kind of reproduction by budding has been observed by BROOKS (No. 18) in a Eucopid, Epenthesis McCradyi. In this case numerous blastostyles enclosed in a chitinous gonangium sprout out from the surface of the four gonads belonging to the radial canals; by further budding small medusæ are produced on the blastostyles. Accordingly, if the interpretation of these blastostyles as metamorphosed hydranths should be definitely established, we should have in this case an exception to the rule that by the budding of a medusa there can never be produced anything but a medusa.

From the form of non-sexual reproduction—lateral budding—thus far treated of, must be distinguished the reproduction of a hydranth from the free end of the stalk, such as has been observed after injuries, after the spontaneous detachment of the hydranths, as in Tubularia (DALYELL, No. 4 ; ALLMAN, No. 15), and after the death of the polyps in consequence of their being overgrown by algæ, as in the case of Campanularians (v. LENDENFELD, No. 38).

In addition, reproduction by *division* has been observed in Hydroids in certain cases, thus by METSCHNIKOFF (No. 12) in the blastula-stage of Oceania armata, by USSOW (No. 48) in the buds and in the mature animals of Polypodium hydriforme, which is parasitic in its early stages in the eggs of the sturgeon, and also as the only method of reproduction hitherto observed in the North American fresh-water Microhydra Ryderi and in Protohydra (GREEFF). Furthermore the occurrence of spontaneous division in Hydra has been maintained by the earlier observers.

Reproduction by means of division has also been observed in the young of certain medusæ ; it is introduced by the budding of a new stomach ; this is followed by a grouping of the radial vessels around the two existing manubria as centres and a fission of the disc, which begins at the margin. Such is the case with Stromobrachium mirabile (KÖLLIKER, No. 37), Phialidium variabile (DAVIDOFF, No. 23), and Gastroblasta Raffaeli (LANG, No. 39). The newly formed radial canals grow out from the marginal canal as centripetal vessels. Owing to the fact that in later stages the budding of the gastral sacs continues and the division of the individuals does not keep pace with it, in fact ceases altogether, colonies are produced (Gastroblasta Raffaeli and timida—KELLER).

Another method of non-sexual reproduction, which has been called *frustulation* (ALLMAN, No. 15), may best be defined as an early abstriction of an only slightly developed lateral bud. In the case of Schizocladium ramosum, a Campanularian, there are on the polyp colony lateral branches which bear no hydranths. From the ends of these are constricted off small portions, which, except for the absence of cilia, resemble a planula ; for they attach themselves, become surrounded

with a perisarc, and grow out as the hydrorhiza of a new colony, the first hydranth arising from them by a process of budding. In the remarkable Corymorpha, which does not produce colonies, but remains solitary, a very similar abstriction of frustules takes place from the lower part of the polyp. Perhaps we should recognize in this process the last trace of stock-formation.

Hydroid Polyps with Sessile Gonophores.—The

course of the development of embryos which are formed in sporosacs is, according to ALLMAN (No. 15), F. E. SCHULZE (No. 46), HAMANN (No. 27), and METSCHNIKOFF (No. 12), somewhat different from that just described, especially in the formation of the entoderm, and is more closely related to the development of the hypogenetic medusæ (see p. 53). It is maintained that in the case of sessile gonophores there arises, by a total and usually equal cleavage, at first a spheroidal solid embryo destitute of a cleavage cavity (a so-called morula stage), the superficial cells of which by more rapid division become separated off as a distinct layer (ectoderm) from the internal cell-mass (entoderm). As is evident, this process is closely related to the formation of entoderm by delamination, which is to be described further on. The bilaminar embryo thus formed elongates and acquires a coat of flagella and, by the dissociation of the entoderm cells, the beginnings of a gastral cavity. In most instances it becomes free as a planula.

A distinctly unequal cleavage and subsequent formation of a gastrula-stage by epiboly has been described by CIAMICIAN (No. 22) for *Tubularia*.[1]

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[1] [The development of Tubularia has recently been thoroughly investigated by A. BRAUER (No. II., Appendix to *Literature* on Hydroidea). There are two types of cleavage. In the one case it is approximately regular. There are, however, differences in the size of the blastomeres ; but no regular distribution of these is recognizable. At length a cœlo-blastula arises. The entoderm is produced by division of the blastoderm cells according to the multipolar type, so that finally the cleavage cavity is filled with entodermal elements given off from the inside of the blastula. This stage looks like a morula, but it is already a bilaminar germ. (Compare also GERD, No. III., Appendix to *Literature* on Hydroidea.)

The second method of cleavage exhibits at first only a multiplication of the nuclei ; then the cleavage, beginning at the animal pole, progresses toward the opposite side.]

But his investigations have been refuted by HAMANN (No. 27), METSCHNI-
KOFF (No. 42), and CONN (No. 21), according to whom the development of
the egg of Tubularia takes place in accordance with the type described
above. On the other hand, it appears as though TICHOMIROFF (No. 47)
had expressed himself in favour of CIAMICIAN's observations. The bi-
laminar embryo has at first the form of a cake, then soon becomes spindle-
shaped, owing to the budding forth of two tentacles at opposite points.
Then follows the formation of the gastral cavity and of new tentacles in
the equatorial plane. The latter are at first curved toward the aboral
side. The embryo now generally undergoes an elongation in the direction
of the chief axis; and while at its oral pole the beginnings of the oral
tentacles appear and the mouth-opening breaks through, and while the
main tentacles curve orally, the posterior end becomes narrower and to a
certain extent constricted off from the main body by a circular furrow.
With this the so-called *actinula-stage* (Fig. 19) is reached, and the small
polyp quits the mother (gonophore) for the purpose of attaching itself and
growing up into a new colony. The agreement with the development of
the larva of the Æginidæ to be described further on (p. 57) is note-
worthy.

The egg of *Hydra* [1] develops in an ovarium which belongs to the
ectodermic layer of the body-wall of the polyp, and which has arisen by
an increase of the cells of the so-called interstitial tissue. Of the cells
composing the ovarium only one (in rare cases two) is developed into a
mature egg, whereas the remaining ones serve as food for it, and are in-
corporated into the egg by means of its pseudopodia. The mature egg,
which contains numerous yolk elements called pseudo-cells, escapes by
the rupture of the enclosing ectodermic layer of the parent, to which it,
however, remains attached for a long time. The part of the egg which
is directed away from the body of the mother marks the animal pole,
that which adheres to it the vegetative pole, of the egg. Then follow the
detachment of the polar globules and fertilization. The development of
the egg has been studied by KLEINENBERG (No. 32), KOROTNEFF (No. 35),
and KERSCHNER (No. 33). According to KERSCHNER, a solid morula is not
formed; but there is produced by total and tolerably equal cleavage a
blastula, from the lower (vegetative) pole of which there is a migration
into the cleavage cavity of cells which go to form the entoderm. In this
case, then, the entoderm arises by polar ingression; and since in Halecium

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[1] [In regard to the development of Hydra the reader is referred to the
important recent investigations of A. BRAUER (No. I., Appendix to *Litera-
ture* on Hydroidea). A cœloblastula with a large central cavity is pro-
duced by total and equal cleavage. The formation of the entoderm is
multipolar, and results from the inward migration or the division of the
blastoderm cells. The ectoderm secretes an outer and an inner germinal
membrane; it is itself preserved, however, and persists as the permanent
ectoderm. The layer of interstitial cells arises from the ectoderm. The
future oral pole is identical with that of the polar bodies.]

tenellum HAMANN (No. 27) and in Campanularia caliculata (?) METSCHNI-
KOFF (No. 12) have observed the formation of the entoderm by immigra-
tion, this type appears to be more wide-spread among the hydroid polyps
than has been assumed hitherto.

After the cleavage cavity is completely filled with entoderm cells, a
double egg-membrane is secreted,
an inner germ envelope and an
outer, harder chitinous shell.
Whereas, according to KLEINEN-
BERG and KOROTNEFF, the ectoder-
mic layer is wholly consumed in
the formation of the latter, KER-
SCHNER was able to show that the
ectoderm persists. The egg now
detaches itself from the body of the
mother and sinks to the bottom.
The mass of entodermic cells, by
the formation of numerous con-
necting cords of protoplasm and interstices between them, then assumes an
appearance similar to that of connective tissue (KERSCHNER); and then
the gastral cavity makes its appearance in this mass. Finally, the outer
(chitinous) shell of the germ goes to pieces; and the embryo, still enclosed
in the inner envelope, emerges from it. The tentacles now arise as
evaginations of the wall, and the mouth-opening is formed by a breaking
through of the wall at a place which corresponds to the vegetative pole
(KERSCHNER), so that after the dissolution of the inner membrane the
young Hydra becomes free in a form that resembles an actinula.

FIG. 19.—Actinula of *Tubularia* (after
CIAMICIAN). *m*, incipient oral tentacles.

Statements concerning the laws which govern the appearance of the
tentacles in Hydra have thus far disagreed. KLEINENBERG maintains
that all the tentacles appear at the same time, whereas KOROTNEFF asserts
that they arise in pairs, as MEBESCHOWSKY has affirmed for buds. While
JUNG (No. 31) was unable to recognize in the latter any definite law,
HAACKE (No. 28) believed that he had observed that the Hydras, apart
from the green form, were divisible into two species, which he dis-
tinguished as H. Tremblyi and H. Roeselii. On the buds of the former
all (six) tentacles arise simultaneously; the appearance of the tentacles
on the buds of H. Roeselii, on the contrary, discloses a definite orienta-
tion in relation to the maternal organism, inasmuch as (the insertion of
the bud being perpendicular) the two tentacles first to appear lie in a plane
dividing the maternal organism transversely, while the third sprouts out
in a plane perpendicular to the first and toward the oral side of the
mother, the fourth opposite the latter, etc. Such examples prove
that in stock-forming radiate animals the bilateral symmetry of the bud
is caused by its relation to the parent organism. We must therefore
attribute the bilateral structure of many Cœlenterates (Anthozoa, young
Scypho-polypi) to stock-formation.

Concerning the development of *Hydrocorallia* there are as yet only scattered observations. Moseley (No. 44) found in the Stylasteridæ well-developed planulæ within the gonophores. The larvæ of Millepora also appear to become free at this stage. In this case the very small eggs, with scanty yolk, pass through the first stages of development in the entoderm of the cœnosarc, where they are often attached by a stalk-like pseudopodium to the supporting lamella. Subsequently they migrate into the entoderm of the basal plate of the gastrozoöid, where they develop into planulæ. It is remarkable that the early development is here accompanied by a considerable increase in the number of the embryonic nuclei, but without distinct cleavage (Hickson, No. 30, and Nos. VI. and VII., Appendix to *Literature* on Hydroidea).

Hypogenetic Medusæ.—In the groups of the *Tracho-medusæ* and *Narcomedusæ* the alternation of generations, consisting in the regular recurrence of polyps and medusæ, is wanting, since in these instances the polyp-generation appears to be suppressed. The young medusæ are developed from the egg directly, but in many cases still have to pass through a metamorphosis. In the Cuninas, however, there is a secondary introduction of alternation of generations, the larva developed from the egg giving rise by a process of budding to medusæ (parasitic bud-spikes [*Knospenähren*] of the Cuninas).

The development of the egg of the *Geryonidæ* has been studied in several species by Metschnikoff (Nos. 42 and 12), Fol (No. 25), and Brooks (No. 17). The Geryonid egg, which is expelled from the mother's mouth, is surrounded by a mucilaginous envelope, and shows a distinct separation into a granular ectoplasm and a foam-like, clearer endoplasm. By total and equal cleavage there are produced two, four, eight, etc., blastomeres, in which a superficial ectoplasmic and an inner endoplasmic portion can be recognized (Fig. 20 *A*). In the sixteen-cell stage there is usually to be seen a cleavage cavity (Fig. 20 *A*, *h*) produced by separation of the blasto-meres. If this represents the blastula-stage, the following stages inaugurate the formation of the entoderm, which, according to the concurrent testimony of the investigators mentioned above, takes place by means of a so-called delamination process.

By a transverse division of each of the cleavage spheres

the ectoplasmic portion is separated from the endo-
plasmic (Fig. 20 *B*). The latter constitutes the ento-
dermic elements. The result of this process, which takes
place over the whole periphery, is the formation of a closed
two-layer cellular sac (Fig. 20 *C*), the outer layer of
which represents the ectoderm, the inner the entoderm,
while the central space, the former blastocœle, now becomes
the gastrocœle or archenteron. Soon there is a secretion of
a transparent jelly between the two layers (Fig. 20 *C, g*).
Since the embryo from this time forward swims about by
means of the flagellate motion of the ectodermal cells, this
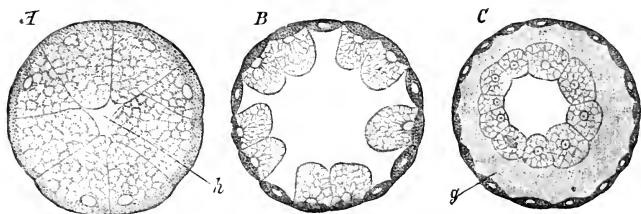
Fig. 20.—Three stages in the development of Geryonidæ : *A* and *C* from *Liriope
mucronata* (after Metschnikoff); *B* from *Geryonia fungiformis* (after Fol). *A*, six-
teen-cell stage ; *h*, cleavage cavity ; *B*, beginning of delamination ; *C*, after com-
pletion of delamination ; *g*, gelatinous substance.

stage may be compared with the planula-stage of the other
Hydroids.

The next change consists in the increase of the gelatinous
secretion, whereby the ectoderm sac is greatly distended.
Inasmuch as this secretion does not take place uniformly on
all sides, the entoderm sac becomes more and more eccentric
until it touches the ectoderm at one point, the oral pole
(Fig. 21 *A*). The cells of the ectoderm and entoderm at
this place become thickened, and here the mouth-opening is
subsequently formed by the breaking through of these layers.
On the thickened ectodermic plate surrounding the mouth
there is soon established a special thickening of the peripheral
parts, whereby a circular wall is produced, on the outer side
of which the four (or six) primary tentacles are developed

as slight elevations, in the interior of which are to be recognized cords of entoderm cells continuous with the wall of the gastral cavity (Fig. 21 *B*).   This tentacle-bearing stage,
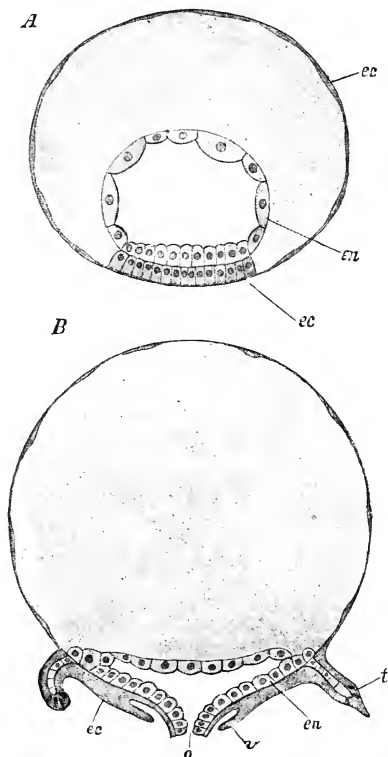
Fig. 21.—Two stages in the development of *Liriope mucronata* (after METSCHNI-KOFF), diagrammatic. *A*, a larva of the fifth day ; *B*, a seven-day larva in optical section ; *ec*, ectoderm ; *en*, entoderm ; *o*, mouth-opening ; *v*, fundament of the velum; *t*, that of the primary perradial tentacle.

which does not yet reveal the peculiarities of the medusa, may well be regarded as a modified actinula-stage.

In the further course of development the larva, hitherto
spherical, undergoes a flattening, and at the same time the
entoderm sac becomes depressed.   Then the velum (Fig. 21
B, v) is developed from the ring-like wall of the ectoderm.
By the enfolding of the area surrounding the mouth-opening
the beginning of the sub-umbrellar cavity is established
(Fig. 22), which soon increases in size.   Since the flattened
gastral cavity likewise undergoes an enfolding, it now has
the form of a double-walled cup inverted over the sub-
umbrellar cavity.   According to BROOKS, its two walls (in
Liriope) come together and fuse with each other at four
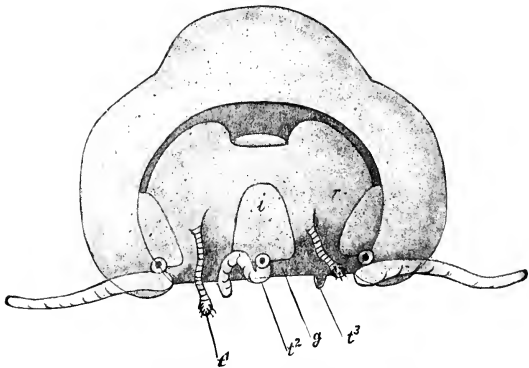
FIG. 22.—Larva of *Liriope scutigera* (after BROOKS). i, interradial area of fusion
of the peripheral intestine (cathammal plate); r, radial vessel; g, circular vessel;
t^1, primary perradial larval tentacle, migrated upward ; t^2, interradial larval ten-
tacle ; t^3, bud of a permanent perradial tentacle.

interradial places (Fig. 22 i), thus forming the cathammal
plates of the vascular lamella, while the regions that
remain unfused represent the four, at first very broad,
radial vessels (r) and the ring-canal (g).   The further
changes, through which the larva approaches the structure of
the adult, consist in the establishment of the interradial (t^2)
and the permanent perradial (t^3) tentacles (while the primary
tentacles disappear), the development of otocysts, the out-

growth of the gastrostyle, and a general flattening of the bell (BROOKS).

Upon these metamorphoses, above all upon the loss of the solid larval tentacles—of which the perradial are always resorbed, while in some forms the interradial are retained alongside the later-developed, hollow, permanent (perradial) ones—is based the metamorphosis of the Geryonidæ, accurately described by LEUCKART, FR. MÜLLER, and E. HAECKEL.

In *Aglaura* and *Rhopalonema* the entoderm is not produced by delamination, but like that of the hydroid polyps, since there is formed at first a solid so-called morula-stage destitute of cleavage cavity, the superficial cells of which are converted into the ectodermic layer, while those within represent the entoderm (METSCHNIKOFF, No. 12).
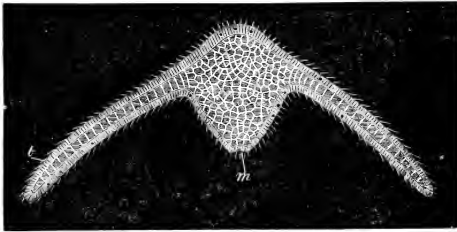
FIG. 23.—Larva of *Æginopsis* three days old, with two tentacles (after METSCHNIKOFF, from BALFOUR'S *Comparative Embryology*). *m*, mouth; *t*, tentacle.

The development of the *Narcomedusæ* from the egg has become known principally through METSCHNIKOFF (Nos. 12 and 13). In Æginopsis mediterranea the formation of the entoderm is accomplished by *multipolar ingression*. In the course of cleavage there is no distinct cleavage cavity produced, but from a very early period cells migrate into the interior from any point whatever of the surface, and these constitute the entodermic cell-mass. Since the ectoderm becomes flagellate, there is produced an elongated, rod-like planula, which has almost the appearance of a detached tentacle of a hydroid, for its interior is filled with entodermal cells, which are arranged in a single row at either end, being more crowded in the middle portion only. Soon, however, these afterwards bent ends are seen to grow out

into the first tentacles of the larva, while the middle part becomes the body of the medusa (Fig. 23). The gastral cavity is produced by the dissociation of the entoderm cells, the mouth breaking through later. There is developed a second pair of smaller tentacles, which with the first pair forms a cross. By the development of the sensory bodies, the mesoglœa, the umbrellar cavity, and the velum, the larva is gradually converted into the form of the medusa (J. MÜLLER, METSCHNIKOFF).

Although the development of the Æginidæ thus consists of a simple metamorphosis, much more complicated relations have been found in the life-history of the Cuninas, which are produced by the parasitism of the larva and the simultaneous tendency to early budding.[1] The conditions in Cunoctantha octonaria are, according to McCRADY and to BROOKS (No. 17), comparatively simple. In this case the ciliate larvæ get into the umbrellar cavity of one of the Tiaridæ (Turritopsis), and there, through stages similar to those described above for Æginopsis, grow up into an actinula-like creature, which attaches itself by means of its four tentacles to the outer wall of the stomach of Turritopsis, while it introduces its long proboscis through the mouth-opening into the stomach of its host. This larval stage multiplies by budding until finally both the original larva and the individuals thus produced acquire the form of medusæ by a gradual metamorphosis, and become young Cunoctanthæ. Similar are the cases in which free-swimming planulæ of Cuninas migrate into the stomach of Geryonidæ and there attach themselves, and grow up into a spike of buds [*Knospenähre*]. Since in these cases, however, the buds alone possess the capability of being metamorphosed into medusæ, whereas the polypoid stolon developed out of the larva does not undergo further development, the outcome is the establishment of an alternation of generations. There have often been observed in the gastral cavity of Cuninas themselves parasitic larvæ of Cuninas, which became metamorphosed into medusæ, but at the same time multiplied asexually by budding at the aboral pole (METSCHNIKOFF). Since the individuals thus produced often differ essentially in structure, especially in the number of the antimera, from the forms in whose stomachs they are found, it has remained doubtful whether one had to do in this case with a brood differing from the parent in form or with descendants of another species of Cunina, which in the free-swimming stage migrate into the gastral cavity of the host. Recently a Cunina larva (?) parasitizing the mantle-jelly of Salpa fusiformis has been described by KOROTNEFF (No. 36) as Gastrodes parasiticum.[2]

[1] [Compare O. MAAS, No. X., Appendix to *Literature* on Hydroidea.]

[2] [In regard to the position of Gastrodes, compare KOROTNEFF, No. VIII., and HEIDER, No. VII., Appendix to *Literature* on Hydroidea.]

METSCHNIKOFF (No. 12) has described and designated as *sporogonia* a remarkable method of reproduction in Cunina proboscidea. This would be the only case of parthenogenetically developing eggs among Cœlenterates. There are developed in the sexual organs of this form (in addition to the reproductive elements) neutral amœboid sexual cells, which soon migrate out of their places of origin and penetrate into the entoderm of the gastral pockets and of the ring-canal, and also into the gelatinous layer of the sub-umbrella. These amœboid cells, which occur in males as well as females, at first divide, and then one of the cells closes around the other. The enclosed cell is converted into the embryo, while the enveloping cell, as an enormously enlarged amœboid cover-cell, provides for the nutrition, the motion, and the attachment of the embryo. With the further growth of the ciliate embryo it hangs free in the gastral cavity of the parent animal, while the cover-cell alone effects the attachment to the entoderm. Finally, the embryos become free in the gastral space of the parent, where they are metamorphosed into medusæ, and at the same time produce buds from their aboral pole. The medusæ thus produced are already sexually mature at the moment of their emergence from the body of the parent. They are, however, essentially different from the parent. They have the characters of the Solmaridæ in so far as they possess a simple gastral sac and a ring-shaped gonad, whereas " otoporpæ " are wanting. Here, therefore, there is an alternation in the cycle of development of two differently constructed sexual generations, one of which has arisen in a parthenogenetic manner (or by budding). These conditions require further investigation and confirmation.

II. SIPHONOPHORA.

Systematic : I.   *Physophoridæ.*
          1.   Physonectæ (Haeckel).
          2.   Pneumatophoridæ (Rhizophysa,
                        Physalia).
          3.   Tracheophysæ (Vellela, Porpita).

     II.   *Calycophoridæ.*

The eggs of the Siphonophora are developed in sessile gonophores, or in small, ultimately free, primitively quadriradiate craspedote medusæ, and are fertilized in the sea-water after their deposition. They are spherical, usually naked (with the exception of Hippopodius gleba), and resemble the eggs of the Geryonidæ and Ctenophora in so far as a dense homogenous exoplasm and a vacuolated,

frothy-looking endoplasm can be distinguished in them.
Cleavage is always total and equal, and leads first to a
morula-stage, which shows no cleavage cavity within it. By
the development of a layer of small ciliated cells on its
outer surface, there is produced a two-layer spherical or
somewhat elongated *planula-stage*. Nothing more accurate
concerning the separation of the two germ-layers is known
up to the present time.

The development of the Siphonophora has been investi-
gated chiefly by GEGENBAUR (No. 67), HAECKEL (Nos. 68 and
70), METSCHNIKOFF (No. 13), FEWKES (No. 66), and CHUN
(Nos. 54—58). Considerable differences prevail among the
various groups regarding the further development (meta-
morphosis[1]) of the young Siphonophore stock.

Physophoridæ.—A comparatively simple type is repre-
sented by the development of Halistemma (Stephanomia)
pictum. The first change noticeable in the planula is an
elongation in the direction of the subsequent chief axis
(Fig. 24 *A*) and the accumulation of red pigment at the
lower (oral) pole. Certain small cells, which have ap-
parently proceeded from a metamorphosis of the large
nutritive entoderm cells, then make their appearance under
the ectodermal cell-layer, and soon arrange themselves in a
second layer of cells (the permanent entoderm) under the
ectoderm. In the further course of development the large
nutritive entodermal elements become more and more ab-
sorbed, so that an internal cavity, the gastrovascular cavity,
is developed (Fig. 24 *B*). The fundament of the first
organ to be formed is seen at the upper (aboral) pole. The
ectoderm here exhibits a thickening, which very soon, like
the bud nucleus [*Knospenkern*] of a medusa, grows inward
(Fig. 24 *A*, *ep*), and by a dehiscence of the cells develops

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[1] We here regard the entire Siphonophore stock as a unit (individual
of the third or higher degree, *corm*). Just as the metamorphosis of an
individual of the second degree (*person*) usually takes place by the loss
of larval organs and their replacement by permanent ones, so the meta-
morphosis of the Siphonophore stock is frequently accompanied by the
loss of larval parts, to which the value of a person must be ascribed, *e.g.*,
nectocalyces, hydrophyllia, etc.

a cavity at the centre. This is the earliest trace of the *pneumatophore*, which consequently is formed as a solid ingrowth of the ectoderm. After this the fundament of the first larval tentacle becomes noticeable as a lateral evagination of both body-layers (Fig. 24 *B*, *t*). The fundament of a second deciduous larval tentacle soon follows. The bilaterally symmetrical structure of the larva is indicated by the appearance of the tentacle, since that side of the body to which the above-mentioned organ belongs corresponds to the zone from which subsequently all the newly
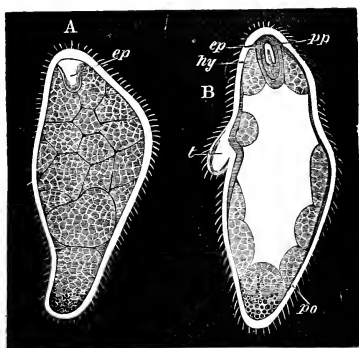
FIG. 24.—Two stages of development of *Halistemma* (Stephanomia) *pictum* (after METSCHNIKOFF, from BALFOUR's *Comparative Embryology*). *A*, ciliated planula-stage; *ep*, fundament of the pneumatophore as an ectodermal ingrowth ; *B*, older stage with central gastric cavity ; *po*, fundament of the first polypite ; *t*, fundament of tentacle ; *pp*, pneumatocyst ; *ep*, its ectodermal envelope (pneumatosaccus) ; *hy*, entoderm in the region of the pneumatophore.

appearing buds grow forth, the so-called *ventral side* of the Siphonophore stock.[1] At the same time, by a transverse constriction at the base of the tentacle, a separation into an upper portion of the body, which becomes the stem and pneumatophore, and a lower portion is indicated. The first

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[1] The designation of this as the ventral side can only be established by comparison with other Siphonophore larvæ. On the other hand, HAECKEL (No. 70, p. 315, Taf. xxii.) has pointed out that the primary tentacle of similar larvæ has a dorsal position.

nutritive polyp, polypite, is developed from the latter by
the breaking through of a mouth-opening at the lower pole.

Thus a larval form is reached in Halistemma pictum, which recurs
frequently among the Physophoridæ, and consists of the apical pneumato-
cyst and a polypite with accompanying tentacle. In it we recognize the
Auronectid larva described by HAECKEL (No. 70), and referred to Stephalia
corona, which, in addition to the extensive pneumatophore, also exhibits
the fundament of the remarkable apparatus for the elimination of air
(aurophore). Moreover, it appears to occur among the Pneumatophoridæ
(CHUN). Thus the youngest Physalid larvæ, which have been made
known through HUXLEY and HAECKEL (No. 70), are constructed after this
type (Fig. 25). Not until a later period do the air-sac, which increases
considerably in size, and the rudiment of the stem, assume a more
horizontal position, whereby the formerly apical pore of the pneumato-
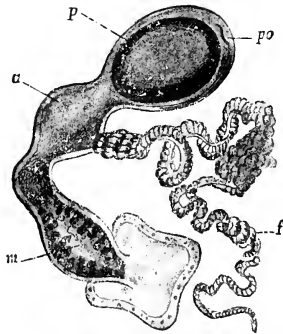
FIG. 25.—Youngest larval stage of a Physalid (*Alophota Giltschiana*) (after
HAECKEL). *p*, pneumatophore; *po*, its apical stigma; *a*, rudiment of the stem;
m, polypite; *f*, tentacle.

cyst comes to occupy the anterior end, the insertion of the primary
polypite, on the contrary, the posterior end, of the body, on the under
(ventral) side of which new groups of individuals (polypites, dactylo-
zoöids, with tentacles and gonophores) now bud forth. Later the so-
called pneumatic plate is developed on the inner side of the air-sac
(modified pneumatic funnel), and also the dorsal comb (CHUN, No. 58).

The development of Halistemma rubrum takes place, according to
METSCHNIKOFF (No. 13), in a similar way to that of H. pictum, differing
from it principally in the early appearance of the buds of the nectosome
[*Schwimmsäule*], which are developed on the ventral side between the
fundament of the pneumatophore and the first tentacle. The first
nectocalyx bud is established very early, at the same time as the pneumato-

cyst, and both fundaments at first have almost the same appearance. In the further course of development, however, the fundament of the nectocalyx protrudes out over the surface of the larva, and is constricted off from it like a bud, whereas the pneumatophore remains sunk in the
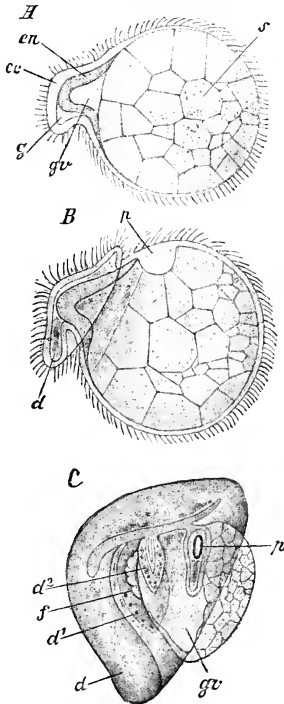
FIG. 26.—Three stages of development of *Agalma Sarsii* (after METSCHNIKOFF). *A*, first fundament of the cap-shaped hydrophyllium on the ciliated larva ; *B*, abstriction of this fundament and development of the pneumatophore ; *C*, stage with fundaments of three hydrophillia. *d*, primary cap-shaped hydrophillium ; *d¹, d²*, first and second heteromorphous hydrophillia ; *ec*, ectoderm ; *en*, entoderm ; *f*, bud of tentacle ; *g*, mesoglœa ; *gv*, gastrovascular cavity ; *p*, fundament of pneumatophore ; *s*, nutritive cells.

apical end. A further difference from H. pictum results from the eccentric position of the gastrovascular cavity, which is crowded quite

to the ventral side by a dorsal accumulation of nutritive entodermal cells. This condition affords a transition to the larvæ of Agalma, Crystallodes, and Atorybia, in which, by an accumulation of still greater masses of large nutritive cells on the dorsal side of the larval body, a structure almost like a yolk-sac may be developed (Crystallodes).

The development of Agalma has been described by METSCHNIKOFF (No. 13) and FEWKES (No. 66). The ciliated planula-stage here retains the spherical shape of the egg, but soon exhibits a thickening of the ectoderm at one spot. At this place, which corresponds to the subsequent ventral side of the embryo, an accumulation of small cells soon takes place, which forms a second cell-layer under the ectoderm (Fig. 26 A, en). Both layers separate somewhat from the underlying large nutritive cells, thereby forming the gastral cavity (gv), while the projection arising in this way is constricted off from the rest of the larval body by a circular furrow, and is to be recognized as the fundament of the first primary hydrophyllium (Fig. 26 B, d). It develops further by the secretion of a gelatinous mass (g), lying between the ectoderm and entoderm, which soon increases greatly, so that the entodermic diverticulum extending into the hydrophillium becomes a comparatively small plug-shaped organ. A short time after the establishment of the primary cap-shaped hydrophillium, the pneumatophore is formed as an ectodermic ingrowth (Fig. 26 B and C, p), which is soon surrounded by an ectodermic duplicature, while the pneumatocyst is developed inside of it. Next there bud forth on the ventral side two new fundaments of hydrophillia (Fig. 26 C, d^1, d^2), which develop into the heteromorphous, leaf-shaped, serrated larval hydrophillia, and meanwhile a new ventral bud is developed into the provisional tentacle (f). By the enlargement of the gastrovascular cavity (gv), the remains of the larval body, which is filled with nutritive cells, are gradually metamorphosed into the polypite. The further development is accomplished by the loss of the primary cap-shaped hydrophillium, which is replaced by a circle of foliaceous, likewise provisional, hydrophillia, so that in this way a larval stage is reached which resembles the condition which persists throughout life in Atorybia (CLAUS).

The development of *Physophora*, which in general is like that of Halistemma, is also characterized by the early development of a larval hydrophillium which subsequently disappears, the earliest fundament of which, as it seems, precedes that of the pneumatophore. In the further progress a larva is developed in which the bilateral hydrophillium, which is provided on one side with a fissure, envelops like a spathe the fundament of the polypite, the pneumatophore, and the provisional tentacle. The general resemblance of this larva to certain bilaterally symmetrical medusæ (Hybocodon) has already been pointed out by HAECKEL (No. 68), and later by BALFOUR, and has been made use of in support of the medusa theory (see p. 73).

According to this view, the larva of this stage would represent an individual of a medusoid organization, in which the manubrium of the medusa would be represented by the polypite, and the umbrella of the

medusa by the larval hydrophillium, whereas the tentacle would have
to be explained as the only remaining marginal tentacle of the medusa.
This primary individual of the Siphonophore stock, referable, from
HAECKEL's point of view, to the fundamental form of a Hydromedusa,
would in the language of the medusa theory (see pp. 70 and 73) be
called a *medusom*, and the corresponding larval form a *Siphonula-stage.*

Only portions of the development of the *Vellelidæ* (Tracheophysæ,
CHUN) are as yet known. A number of young larvæ have been de-
scribed by A. AGASSIZ (No. 52), HAECKEL (No. 70), BEDOT (No. 53), and
CHUN (No. 57). The youngest larval stage observed by HAECKEL, perhaps
belonging to the developmental cycle of Porpita, was named *Disconula*;
it exhibits a distinctly octoradial structure (Fig. 27). From the under-
surface of the discoid stem there hangs a central polypite (*c*), the cavity
of which is united by means of eight radial canals to a peripheral ring-
canal and eight simple tentacles (*t*). In the apical part of the gelati-
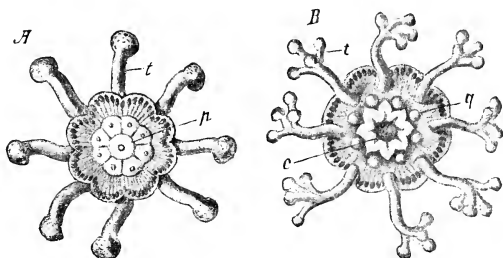
FIG. 27.—Two *Disconula*-stages (after HAECKEL). *A*, younger stage, seen from
the upper side; *B*, somewhat older stage with ramified tentacles, seen from the
lower surface; *p*, pneumatophore; *q*, buds of the blastostyle; *c*, central polypite
with mouth-opening; *t*, tentacle.

nous disc is found a central lentiform pneumatocyst (*p*), surrounded by
a circle of eight radial air-chambers, each of which opens to the ex-
terior by means of a dorsal pore. HAECKEL interprets this stage as the
ontogenetic reproduction of an octoradial ancestral form which would
have to be sought for among the Trachomedusæ; consequently all the
Siphonophores assignable to this group must be separated as an inde-
pendent sub-class (Disconanthæ) from all the remaining ones, which are
descended from a bilateral ancestral form, of which the *Siphonula* larva
is the expression. In opposition to this hypothesis of the diphyletic de-
rivation of the Siphonophora, CHUN has contended that the octoradial
Disconula-stage is probably preceded in the development of the Por-
pitidæ and Vellelidæ by a bilateral Siphonula-stage. Young *Rataria*
(larvæ of Vellelidæ), still with a simple, unchambered pneumatophore,
exhibited four bilaterally arranged tentacles, for a larger tentacle and

three smaller ones arranged symmetrically were to be noticed. The
Rataria are characterized by the possession of a sail which stands ver-
tically on the upper surface of the elliptical disc, and the base of which
originally occupies the direction of the long axis of the disc, so that in
general the Rataria possess a biradial structure. It is only in subse-
quent stages that the amphitectal (klinoradial) fundamental form of the
Vellelidæ is brought out by the sail turning at an angle of forty-five
degrees to the above-mentioned axis.
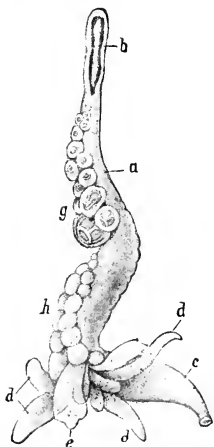
FIG. 28. — Young *Agalmopsis*
(after GEGENBAUR). *a*, stem; *b*,
pneumatophore; *c*, only polypite
developed; *d*, buds of tentacles
and dactylozoöids belonging to
the group of individuals of the
first polypite; *e*, hydrophillium;
g, buds (nectocalyces) of the nec-
tosome; *h*, buds of the lower
portion of the stem.

We have still to add something
on the laws of growth of Sipho-
nophore stocks. In those forms
which are characterized by an
elongated stem, the different indi-
viduals do not bud on the entire
circumference, but only along a
longitudinal line (Fig. 28). Since
the wall of the stem exhibits a
different structure along this line,
a cross-section of the stem pre-
sents a bilaterally symmetrical
arrangement. That side of the
stem from which the individuals
bud is known as the *ventral side*
(CLAUS). The fact that the indi-
viduals of the stem appear to be
oriented in various directions re-
sults from a spiral twisting of the
stem, by which, for example, the
biserial or multiserial arrange-
ment of the nectocalyces on the
nectosome is brought about. It
was shown by CLAUS (No. 62)
that in the Physophoridæ the
spiral twisting of the nectosome takes place in the opposite
direction to that of the lower portion of the stem.

As appears from Fig. 28, a budding point for the indi-
viduals of the nectosome is found at the upper end of the
stem. Another budding point, at the base of the necto-
some, supplies in general the buds for the rows of individuals
of the stem. Accordingly those groups of individuals which

lie at the lowermost end of the stem are the oldest. In nearly all of the Calycophoridæ and some of the Physophoridæ (Apolemia) the individuals of the stem are arranged in definite groups (*cormidia*), which are separated from one another by free portions of the stem (*internodes*). In many other forms, on the other hand, the limits of the successive internodes are indicated merely by the attachment of the polypites with their tentacles (Fig. 29 *A*, *B*, *C*, *D*), whereas the parts of the stem lying between the polypites are occupied by groups of individuals (consisting of hydrophyllia, dactylozoöids, and gonophores). (In the accompanying figure, for the sake of simplicity, instead of these groups of individuals, only their dactylozoöids are indicated.) Here the law that growth progresses uniformly from above downwards applies only to the polypites (*A*, *B*, *C*, *D*), whereas each internode presents its own zone of growth for the groups of individuals (*a*, *b*, *c*, *d*) belonging to it, for which in turn the uppermost end of the internode must be looked upon as the budding point, so that likewise in the series of groups of individuals in each single internode the lowermost (*a*) is the oldest. Each internode of the stem is divided by these groups of individuals into internodes of the second order (*Aa*, *ab*, *bc*, *cd* . . .); and each such internode of the second order may, in the further growth of the stem, become a zone of growth for a series of new groups of individuals (*a*, *β*, *γ* . . .) (CHUN, No. 57).

For the other groups [of Physophoridæ] the details of the laws of budding are as yet little known. In the *Vellelidæ* the formation of the individuals takes place in concentrically arranged circles.
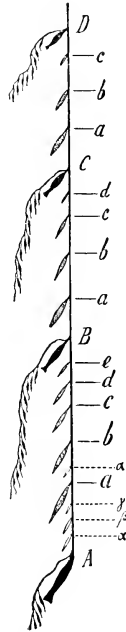
FIG. 29.—Diagram of CHUN's law of budding of the groups of individuals on the stem of *Halistemma*. In place of the groups of individuals only the corresponding dactylozoöids are shown.

Calycophoridæ.—The development of Epibulia auran-
tiaca (family of the Diphyidæ), which has been very accurately
followed by METSCHNIKOFF (No. 13), will be described as the
type. The ovate planula larva exhibits a thickening of the
ectoderm at the posterior pole and on one side (the subse-
quent ventral side). Here the fundaments of the first
nectocalyx (Fig. 30 B, nc) and of the tentacle (Fig. 30 B, t)
are developed. The former is developed by the invagination
of a solid bud-nucleus (Knospenkern), in which the cavity
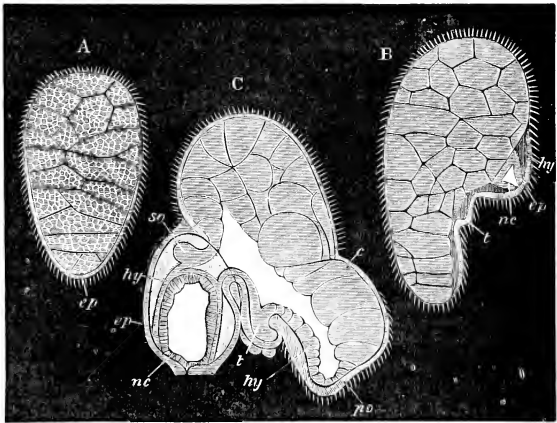
FIG. 30.—Three larval stages of Epibulia aurantiaca (after METSCHNIKOFF, from
BALFOUR's Comparative Embryology). A, planula; B, stage six days old with funda-
ments of nectocalyces (nc) and tentacles (t); C, somewhat older stage with gastral
cavity; nc, nectocalyces; t, fundament of tentacle; po, polypite; c, nutritive cells;
so, fundament of the so-called somatocyst; hy, entoderm; ep, ectoderm.

of the bell is soon formed; the fundament of the tentacle
at first consists of a simple invagination of the body-wall,
in which two layers take part, the development of an
ectodermic layer (Fig. 30 B, hy) along the ventral side, con-
sisting of small cells, having already taken place at this
stage. The next important change consists in the establish-
ment of the gastrovascular cavity (Fig. 30 C), which is

correlated with the disappearance of the nutritive cells. By
means of it the posterior part of the larval body (Fig. 30 C,
po) is characterized as the fundament of the first polypite,
whereas the upper dorsal part is retained for a considerable
time as an embryonal remnant, which gradually diminishes
and is converted into the stem (like the yolk-mass of the
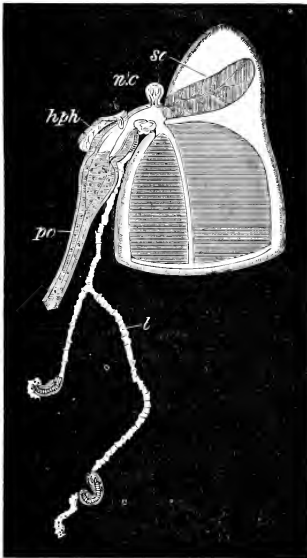
Fig. 31.—Older larval stage of *Epibulia aurantiaca* (after MЕТSCHNIKOFF, from
BALFOUR's *Comparative Embryology*). *so*, somatocyst ; *nc*, second nectocalyx bud ;
hph, hydrophillium ; *po*, polypite ; *t*, tentacle.

Agalmidæ). At the same time the fundament of the necto-
calyx (Fig. 30 C, nc) has made considerable progress. The
hollow core of the bud is enveloped by a layer of entoderm
(hy), into which a part of the gastrovascular cavity is pro-
longed as the fundament of the vessels of the bell. Another
entodermal process (Fig. 30 C, so) becomes the so-called
somatocyst (*Saftbehälter*). Between the entoderm and the

outer ectoderm mesogloea has been secreted. In general the development of the nectocalyx is quite like the budding of a Hydromedusa described above (p. 43). On the fundament of the tentacle (*t*) the individual nettling tubercles can be seen developing as secondary evaginations (Fig. 30 *C*).

The further changes (Fig. 31) consist in a considerable enlargement of the first nectocalyx, which now, after the reduction of the nutritive cells, is the most voluminous structure of the young colony. The polypite (*po*) now acquires its permanent structure by the breaking through of the mouth at its distal end, while the tentacle (*t*), in this case persisting (not larval), attains its complete development. Of interest is the appearance of new buds on the rudiment of the stem, first of all that of a hydrophillium (Fig. 31 *hph*), with the development of which is established the first group of individuals (cormidium) of the subsequently elongated stem—consisting of a polypite, a dactylozooid, and hydrophillium—which is afterwards developed into the Eudoxia. At the same time we see two smaller buds arising, one of which must be considered as the second nectocalyx (Fig. 31 *nc*), whereas from the other the elements of the second group of individuals of the stem bud forth.

In the stage Fig. 30 *B*, which in Fig. 30 *C* and Fig. 31 undergoes its further development, is shown a larval stage exceedingly characteristic of the Calycophoridæ, which has been designated by HAECKEL as the *Calyconula*, and which represents essentially the *Siphonula-stage* of the *Calycophoridæ*. HAECKEL (No. 70) regards this stage as an individual of the second degree (person), and recognizes in its component parts the constituent organs of an Anthomedusa, which here present a remarkable dislocation. For if the nectocalyx corresponds to the umbrella and the polypite to the manubrium of the medusa, then it is evident that the polypite is here attached to the ex-umbrellar side of the medusa-bell. HAECKEL explains this dislocation by the assumption of a ventral fissure in the umbrella of the ancestral forms, through which a gradual emigration of the manubrium was possible. Furthermore the only marginal tentacle of the medusa present has moved from the margin of the nectocalyx to the base of the polypite.

The assumption that the Siphonula thus characterized actually corresponds to an ancestral form acquires an apparent support from the circumstance that the same type of form is found again in the groups of individuals of the stem (*cormidia*). For the individuals of the stem in

the Calycophoridæ are united into groups and separated by intervals of the stem (*internodes*). They bud in such a way that the group of individuals (*cormidium*) occurring at the lowermost end of the stem is the oldest. In many cases (Polyphyidæ, Desmophyidæ, Praya, Galeolaria, etc.) the groups of individuals, even if they produce sexual products, remain united with the entire corm. In most of the Diphyidæ, on the contrary, the oldest cormidia separate from the parent stock before they arrive at sexual maturity, and either as Eudoxiæ or Ersææ lead an independent life. In this way a kind of alternation of generations is brought about, since the parent stock does not itself produce sexual products, but separates into secondary stocks, which do not reach sexual maturity until later on. Such a detached *Eudoxia group* (so the cormidia have usually been called) consists of a polypite with tentacles, a hydrophillium, and a gonophore which develops the sexual products in its manubrium, and at the same time by the rhythmical contractions of its swimming sack produces the locomotion of the detached Eudoxia. HAECKEL explains the hydrophillium, the polypite, and the tentacles as the constituent parts of a sterile person, in which the bilaterally symmetrical hydrophillium would represent the umbrella of the medusa. The Eudoxia cormidium would accordingly in the simplest case be composed of two persons: a sterile one and a fertile one (the gonophore or sexual bell). It is to be observed that the two persons named would represent two essentially heteromorphous medusæ of the same corm. Whereas the sterile person exhibits a bilaterally symmetrical structure and the above-mentioned dislocation of the parts, nothing of this kind can be recognized in the fertile person. The structure here is that of an ordinary quadriradial Anthomedusa, and the manubrium has retained its usual place.

LEUCKART and GEGENBAUR have shown that in various Eudoxiæ the gonophore, after the discharge of its sexual products, is replaced by the outgrowth of a new gonophore, and CHUN showed it to be probable that in all Eudoxiæ a quite regular replacement of the gonophores takes place, so that each Eudoxia has quite a number of gonophores developed one after another. Now let us imagine that the first one of these gonophores remains sterile, functioning merely as an organ of locomotion; that would lead to the form of the Ersææ (in HAECKEL's sense). As Ersææ are designated the cormidia which bud on the stem of Lilyopsis and Diphyopsis, and which, in addition to the parts described for the Eudoxiæ, possess a so-called special swimming bell, so that these cormidia, according to HAECKEL's interpretation, embrace at least three persons, two sterile and one fertile.

The different parts of the nectosome are also subject to a quite similar replacement by supervening buds. Even in the Diphyidæ the two nectocalyces are not retained throughout life. LEUCKART had already observed the presence of two to three bud-like supplementary bells in Epibulia, and CHUN showed that the nectocalyces of the Diphyidæ are subject to a con-

stant replacement by reserve nectocalyces of the same form. This
replacement also plays a considerable role, as we shall see directly,
in the metamorphosis of the Calycophoridæ.

The metamorphosis of the Calycophoridæ has been made
known chiefly through the investigations of CHUN (No. 54).
These refer principally to the development of the Mono-
phyidæ, *i.e.* those forms which are characterized by the
possession of a single nectocalyx on the nectosome. In a
small Monophyid called by CHUN Muggiæa Kochii, and
characterized by its tall pentagonal nectocalyx, CHUN was
able to prove that the larvæ arising from the eggs at first
possess a quite differently shaped, cap-like nectocalyx. By
the casting off of this primary provisional nectocalyx and
its replacement by the permanent heteromorphous one,
these larvæ, designated as Monophyes primordialis, pass into
the Muggiæa form, from the stem of which the groups of
individuals at sexual maturity detach themselves as Eudoxia
Eschscholtzii.

Since CHUN has recently been able to prove the presence
of these primary, heteromorphous, deciduous nectocalyces
in the case of the Polyphyidæ, it may be considered probable
that such nectocalyces also belong to the larval stages of all
Calycophoridæ. According to CHUN's theory, which HAECKEL
has adopted, the fundament of the pneumatophore in the
Physophoridæ would be homologous to the deciduous, pri-
mary nectocalyx of the Calycophoridæ.

General Considerations.—As regards the derivation of
the Siphonophora, there are at present two views, as yet
directly opposed to each other, underlying both of which is
the conception that the Siphonophore is a polymorphous
animal stock that has arisen by budding. But while some
authors (LEUCKART, CLAUS, CHUN) assume the starting-point
of this stock to be a floating hydroid-polyp stocklet, which
already had the power of producing medusæ (*hydroid theory*),
others (BALFOUR, HAECKEL) derive the Siphonophore from a
medusa, which, by the budding of its manubrium (like Sarsia
or Hybocodon), was able to produce new medusæ (*medusa
theory*). The former authors accordingly have two funda-
mental forms from which they are able to derive the mani-

fold parts of the Siphonophore body. They can consider certain parts (polypites, dactylozoöids, etc.) as metamorphosed polypoid individuals, other parts (nectocalyces, hydrophillia, gonophores) as metamorphosed medusoid individuals, which remain united with the colony. The adherents of the medusa theory, on the other hand, have at their disposal only the hydroïd medusa as a fundamental form for the derivation of all the numerous polymorphous parts of the Siphonophore organism, for only new medusæ can ever be produced from a medusa by budding. Since by this explanation the polypites are homologized with the manubria, and the tentacles with the marginal tentacles of a medusa, the adherents of this theory find it necessary to assume an ancestral form in which the medusa exhibited a bilaterally symmetrical structure, while a single tentacle was advanced to the base of the manubrium, and both these parts had emerged upon the ex-umbrellar side of the medusa-bell through a fissure in the umbrella—conditions which, as a matter of fact, do not exist in any Hydromedusa. As a further consequence the partisans of the medusa theory must assume the possibility of a considerable dislocation of these different primary organs and an extensive capacity of the individuals to multiply different organs. With all these assumptions, there arise certain difficulties which are not encountered in the hydroïd theory.[1]

Even if the ancestral form of the Siphonophora assumed by the medusa theory, and described above (which is re-capitulated in ontogeny by the Siphonula-stage and by the sterile person of the Eudoxiæ), were to be derived from bilaterally symmetrical Anthomedusæ with only one marginal tentacle (for example, from the Hybocodon belonging to Corymorpha), it would still be difficult to point out in any way the causes for the appearance of the fissure in the umbrella and the described dislocation of the organs. The difficulty is increased by the circumstance that these cha-racters are lacking in the sexual individuals of the Siphono-

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[1] It should be stated that recently HATSCHEK (*Lehrbuch der Zoologie*) has introduced modifications into HAECKEL's medusa theory, by means of which a part of these difficulties seem to be set aside.

phora, so that in pursuance of the medusa theory, we are
required to distinguish in the Siphonophora two highly
heteromorphous generations, the first, produced from the
egg, constructed upon the Siphonula type, and reproducing
by budding only, the second a generation of fertile indi-
viduals not bilaterally symmetrical, and without dislocation
of the primary organ. Still sharper, perhaps, is the contrast
between the Disconula of the Vellelidæ, which is referred
by HAECKEL to certain Trachomedusæ, and the structure of
the Chrysomitras.

On the other hand, for the hydroid theory there is the
difficulty of explaining how a firmly attached hydroid stocklet
could detach itself and become metamorphosed into a free-
moving, pelagic organism. If, however, we assume that a
hydroid stocklet attached itself by means of a broadened
basal plate to the surface of the water, instead of to a fixed
body, as may occasionally be observed in the Scyphistomas,
and acquired under favourable circumstances the power to live
on in this condition, then with this conception the transition
from the attached to the free mode of life is brought about
by a floating at the surface of the water, a form of locomotion
which has been retained in Physalia and Vellela. Nay, we
need only to conceive that the flattened basal part of the
stem, which attached itself to the under-surface of the water,
curved inwards like a canoe, and finally became, with its peri-
sarc-covered face, completely invaginated,[1] in order thus to
make the phylogenetic origin of the pneumatophore conceiv-
able, and to support this conception by the consideration
that such a course of development must have been constantly
accompanied by certain advantages to the entire colony.
Not until after the development of this hydrostatic apparatus
would a separation from the surface of the water and a
descent into greater depths become possible. The pneuma-
tophore would accordingly be the first, most primitive organ
by the development of which the characteristic peculiarities

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[1] It has actually been observed in the planula of various Cnidaria that
the future point of attachment, which has undergone glandular alteration,
is more or less invaginated, as in the Scyphomedusæ and in Eutima
(BROOKS).

of the Siphonophore organism were established. We might perhaps be led by such considerations to recognize in those forms with a persistent apical stigma (Rhizophysas, Physalias) the most primitive of the now existing Siphonophores.

In this proposed hypothesis of the derivation of the pneumatophore we are opposed to the conception, shared in by most investigators (comp. p. 72), that it is a modified medusa-bell. The latter view is founded partly on the structure of the fully developed pneumatophore and partly on its development. Even though the spaces of the gastrovascular system in the vicinity of the pneumatophore, divided as they are by septa, challenge a comparison with the radial canals of a medusa, and even though the bud-like fundament of the pneumatophore is uncommonly like a medusa bud, as has been stated by METSCHNIKOFF (pp. 62, 63), these resemblances do not appear to us to present proofs of a compulsory nature, the more so since the transition from a medusa into a hydrostatic organ involves a change of function that is somewhat difficult to comprehend. According to our way of looking at it, on the contrary, the apical position of the pneumatophore, sunk into the uppermost end of the stem, and its early appearance in the ontogeny of many forms, are most easily explained.

According to our notion, the pneumatophore would be the most primitive locomotor organ of the Siphonophora, to which a nectosome would be added only secondarily. Accordingly the Physophoridæ would represent the more primitive forms, and the Calycophoridæ derived forms, with divergent development caused by the loss of the pneumatophore and the in part higher differentiation of the nectocalyces. Among the Physonectæ (HAECKEL) the Apolemidæ, the nectosome of which is still provided with heteromorphous individuals, would perhaps represent the most primitive branch. Opposed to this theory, however, is the fact that histologically the Calycophoridæ exhibit the simplest conditions (KOROTNEFF); but these might have been simplified secondarily.

When with the above statements we adopt the hydroid theory founded by LEUCKART, it is hereby to be understood that, according to our point of view, the existing facts are most easily explained by this theory. Nevertheless we can as yet ascribe even to it only a certain degree of probability.

II. ANTHOZOA.

Alcyonaria.—The sexual products of the Anthozoa, which arise from the entoderm (HERTWIG, No. 9), undergo the process of ripening in sexual organs which belong to the

mesenterial septa. It is here also that the eggs in most
cases are fertilized, and frequently undergo the first stages
of development, viz., cleavage and the formation of a
spheroidal embryo consisting of two germ-layers. The
embryo is afterwards set free in the gastral cavity of the
parent, from which it is ejected through the mouth-opening,
usually in the stage of a ciliated planula. While thus many
Alcyonaria are viviparous, cases have also been observed in
which the eggs, either unfertilized or immediately after
fertilization has taken place, are extruded through the mouth-
opening of the parent, either singly or united into large
masses by means of a slimy substance (Alcyonium, Renilla,
Clavularia crassa).

The early development of the Alcyonaria has become
known chiefly through LACAZE-DUTHIERS (No. 88, Corallium),
KOWALEVSKY (No. 10, Alcyonium, Gorgonia), v. KOCH (No.
86, Gorgonia), E. B. WILSON (No. 98, Renilla), and KOWA-
LEVSKY ET MARION (No. 87, Clavularia, Sympodium).

The ripe egg of the Alcyonaria is usually rather rich in
granules of food-yolk, which, mixed with oil drops, is accu-
mulated especially in the inner parts, so that in certain cases
there is a sharp separation of a finely granular ectoplasm
from an endoplasm rich in food-yolk. Cleavage has been quite
variously described for the forms so far observed ; in fact, in
Renilla it exhibits remarkable individual variations. In
general it follows the total and equal type, and finally leads
to the development of a solid so-called *morula-stage*, consist-
ing of cells more or less uniform in size and exhibiting even at
an early stage a difference between the more finely granular
cells of the superficial layer and the coarsely granular
ones of the inner mass. An interesting modification of the
cleavage process is met with frequently in Renilla, and con-
stantly in Clavularia crassa. Here a multiplication of the
cleavage nuclei first takes place, corresponding to which
there is only an indentation of the surface, not a real cleav-
age of the egg. This does not take place until there are
sixteen cleavage nuclei, when it results in the formation of
the same number of separate blastomeres. We see that we
here have to do with a variation which forms a transition

to the type of superficial cleavage, which is wide-spread among the Arthropoda.

In general the cleavage stages of the Alcyonaria are characterized by the absence of the cleavage cavity. Monoxenia forms an exception. Here, according to HAECKEL (No. 78), there are produced in the course of a very regular cleavage a typical cœloblastula-stage and a gastrula invaginata.

In the morula a difference can early be recognized (Fig. 32 *A*) between a superficial cell-layer (ectoderm) and an inner cell-mass (entoderm). This difference becomes more marked in later stages (Fig. 32 *B*, *C*). The ectoderm cells by progressive division are metamorphosed into prismatic elements, which constitute a columnar epithelium (Fig. 32 *C*). Those of the inner cells lying next to the ectoderm also arrange themselves (Fig. 32 *C*, *en*) into an epithelial layer (the permanent entoderm), whereas the elements lying at the centre undergo a process of degeneration. The cell boundaries here become indistinct; vacuolar spaces make their appearance, and soon coalesce into a common internal cavity (the beginning of the gastral cavity, *h*); finally, this entire cell-mass is metamorphosed by fatty degeneration into a kind of detritus (*d*), which is gradually resorbed. At the same time a fine, structureless, hyaline membrane (the sustentative lamella) is secreted between the ectoderm and the permanent entoderm.

While these internal changes are taking place, the body elongates and gradually assumes an ovoid or, with increasing length, a vermiform shape, and its surface becomes covered with close-set cilia; thus the swarming *planula-stage* is developed (Fig. 32 *D*). The planula exhibits a somewhat broadened (aboral) end, which is directed forwards during motion, and a posterior (oral), more pointed pole. At the expiration of the swarming stage the larva attaches itself by means of its broadened anterior end to some convenient support. By a gradual shortening in the direction of the longitudinal axis the larva passes from the elongated into a low placentiform shape (Fig. 33).

At about the same time with the attachment, the in-

vagination of the *œsophageal tube* (*sl*) takes place, and also the
formation of the eight mesenterial septa. The œsophagus
arises in general as an ectodermal invagination (Fig. 33),
the bottom of which in later stages breaks through toward
the gastral cavity, thereby establishing the *inner opening
of the œsophagus*. The formation of the mesenterial septa
is referable to a folding of the entoderm, in which the
sustentative lamella also takes part. It seems that in the
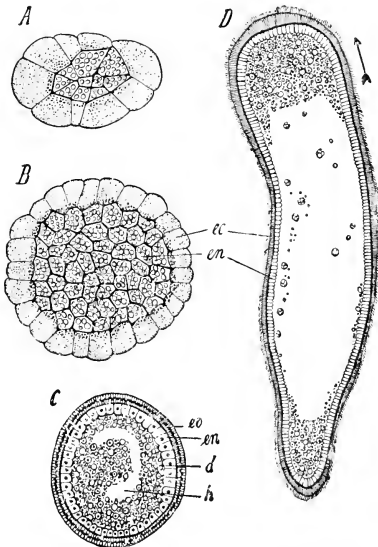
FIG. 32.—Stage in the development of *Sympodium coralloides* (after KOWALEVSKY
ET MARION). *A* and *B*, cleavage stages; *C*, embryo with permanent entoderm
(*en*) and inner mass of detritus (*d*), in which beginnings of the gastral cavity (*h*)
can be recognized; *D*, ciliated planula; *ec*, ectoderm; *en*, entoderm.

Alcyonaria all the eight mesenterial septa always make their
appearance at the same time. As regards the origin of
the musculature of the septa, especially the longitudinal
muscles, authors agree that they arise from epithelio-mus-
cular cells (myoblasts) of the *entoderm lamella*.

In Renilla the œsophagus is developed in the form of a solid ectodermal ingrowth, in which a fissure makes its appearance and opens to the exterior, whereas the development of the inner opening of the œsophagus does not take place until later.

FIG. 33.—Attached stage of *Sympodium coralloides* (after KOWALEVSKY ET MARION). *Ec*, ectoderm ; *en*, entoderm ; *sl*, œsophagus.

By the formation of the mesenterial septa the gastral space is separated into a central stomach cavity and eight peripheral gastral pouches. At the upper ends of the latter hollow, bud-like elevations now arise, in which we recognize the earliest fundaments of the eight (subsequently pinnate) tentacles, which accordingly owe their origin to simple evaginations of the body-wall.

The development of the septa, the formation of the œsophagus, and even the establishment of the tentacles may take place before attachment. In general, however, the attachment of the swarming larva precedes the formation of these organs. By means of the developmental processes mentioned the typical structure of the polyp is established. During these metamorphoses important changes in the structure of the ectoderm take place. By multiplication of the cells this layer becomes changed into a multi-layered epithelium. The secretion of a hyaline gelatinous substance [mesoglœa] now takes place between the cells of the deeper layers, which thus lose their connection with one another and assume more and more spindle or stellate shapes (Fig. 34). By these processes two different layers arise from the primary ectoderm : a superficial one, which from now on preserves the name of *ectoderm*, and the cells of which have retained the epithelial continuity, and a lower layer, which assumes more and more the character of a gelatinous connective tissue, and which will be called henceforth *mesoderm*. This layer accordingly is a product of the

ectoderm (Kowalevsky et Marion, No. 87). In it are
secreted the first *calcareous spicules* (*sclerites*) (v. Koch, Nos.
82 and 84, Kowalevsky). These arise as small, highly
refractive bodies (*sp*) within the mesodermal elements,
which resemble migratory cells, where they soon grow into
small needles having lateral outgrowths. The ectodermal
axial skeleton of the Gorgonidæ arises later than these
mesodermal parts of the skeleton. It must be regarded as
a cuticular secretion of the ectoderm of the basal foot-plate
(v. Koch), and at its first appearance consists of a thin
yellowish pellicle, which may be compared to the sheath
of Cornularia and Clavularia. There is soon noticeable on
this basal plate a small prominence, which grows up into
a process composed of concentrically arranged corneous
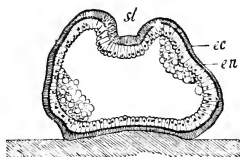lamellæ, and extends up between the mesenterial septa of the
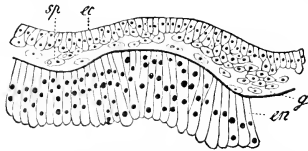
Fig. 34.—Section through the body-wall of a young attached stage of *Sympodium coralloides* (after Kowalevsky et Marion). *ec*, ectoderm; *en*, entoderm; *g*, mesoglœa; *sp*, earliest fundament of the calcareous spicules in cells of the developing mesoderm.

primary polyp. Thus the ectoderm of the foot-plate must
be correspondingly invaginated, and thus it comes about
that the axial process of the ectoskeleton contained within
the polyp is covered by a continuous ectodermal lamella
(the *axial epithelium*), from which the further development
of this part of the skeleton takes place. In the further
course of development, during the progressive growth in
length, the young polyp and the axial skeleton do not take
the same direction; the latter thereby acquires greater
independence, and represents the earliest fundament of the
whole axial skeleton which lies at the foundation of the
entire colony subsequently produced by budding (Fig. 36 *B*)
(v. Koch, No. 86 [1]).

[1] On the other hand, Studer (*Arch. f. Naturg. Jahrg.*, 1887) has

To explain the phylogenetic development of this axial skeleton of the Gorgonidæ, v. Koch (No. 85) has for comparison made use of the interesting discoveries on Gerardia (Antipatharia, Hexacorallia). These colonies of Gerardia form flat membranoid coverings over foreign bodies, and for this purpose commonly select the axial skeleton of dead Gorgonidæ as a support. A lamella of horn, which coats the support, is now secreted by the ectoderm of the lower surface of these colonies. The lamella surrounds the axis of the Gorgonia within it like a sheath. When at length the colony of the Gerardia by growth acquires an extent which stretches beyond the limits of the original support, then outgrowths covered with young polyps are produced, into which extend horny skeletal processes, produced by the common basal lamella, but no longer enclosing within them any foreign body. It is seen that here is produced the first trace of an independent free axial skeleton, while the basal plate of the skeleton, which in the higher forms is much reduced and attached to a foreign support, arises from the basal lamella.
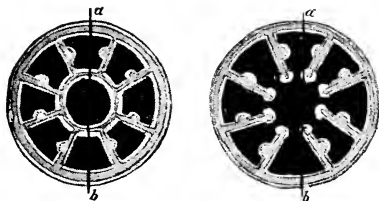
Fig. 35.—Two transverse sections through a polyp of the Alcyonarian type (diagram after v. Koch, from Lang's *Lehrbuch*); that at the left is at the level of the œsophagus, that at the right at the level of the gastral cavity. *ab*, plane of symmetry. The ventral side is directed upwards.

The polyps of the Alcyonaria present a typical bilaterally symmetrical structure, which is evident in the first place from the position of the longitudinal muscles in the mesenterial septa. Here the plane of symmetry (Fig. 35 *ab*) passes through two unpaired chambers (gastral pouches), which are distinguished from each other by the fact that the two septa which bound the *ventral* chamber exhibit the muscle ridges on the sides which are turned toward each other, whereas this condition is reversed in the *dorsal* chamber. On the remaining septa, in fact on all the septa, the longitudinal muscle ridges are so arranged that they face

recently defended the interpretation of the axis of the Gorgonidæ as a mesodermal growth.

K. H. E.   G

toward the ventral side of the polyp, whereas the surfaces of
the septa which are without longitudinal muscle bands face
toward the dorsal side. The bilateral symmetry can also be
recognized by the presence of a ventral ciliated groove
running along the laterally compressed œsophagus (*siphono-
glyphe*, Hickson), and above all by the condition of the
mesenterial filaments. Of these the pair belonging to the
dorsal septa differs from the others in structure, function,
and development. The filaments of the dorsal pair of
septa exhibit an epithelial band consisting of tall flagellate
cells, and produce a powerful upward ciliary current,
whereas the filaments of the other six septa are charac-
terized by their richness in gland cells, and they play an
important role in digestion. E. B. Wilson (No. 97) was
able to show that the latter take their origin as simple out-
growths of the entodermal epithelium of the septa, whereas
the dorsal filaments belong to the ectoderm, and are con-
tinued on to the margins of the septa as direct outgrowths
of the œsophageal epithelium.

An observation by Wilson is of general interest: that the develop-
ment of these dorsal filaments is retarded in the larvæ produced from
the egg, whereas in the bud they actually outstrip the other filaments in
development. Wilson explains this by the conditions of nutrition in
the bud, which requires a powerful upward stream of nutritive fluid for
its development.

Of the various kinds of non-sexual reproduction in the
Alcyonaria, *budding* is the most prevalent; by means of it
extensive colonies (*stocks, corms*) are developed, owing to
the fact that the newly arising individuals remain united
with the parent. In the simplest case a lateral "runner"
arises from the parent animal and grows out at its end into
a daughter individual. The portion remaining between the
two as a connective is called a *stolon* (Fig. 36 *A*). These
stolons, issuing from the base of the polyp, may form a net-
work (Cornularia), or fuse into a basal plate (Rhizoxenia).
We have seen above (p. 81) how, owing to the formation of
a basal skeletal plate upon which an axial skeleton arises,
the dendritic stocks of the Gorgonidæ can be derived from
such flatly extended colonies (Fig. 36 *B*). In other cases

the stolons do not belong exclusively to the basal part of the polyps, but arise at various levels. In this way the peculiar colony of Tubipora (Fig. 36 *C*) arises by the development of stolonic plates in higher positions, from which new buds grow out. In other forms, by the intimate fusion and irregular branching of the stolons, there is developed an intermediate tissue (cœnenchyma) traversed by numerous nutritive canals (Fig. 36 *D*), which unites the different individuals. In this way the antler-like colonies of Alcyonium are developed, and by the formation of a mesodermal axial
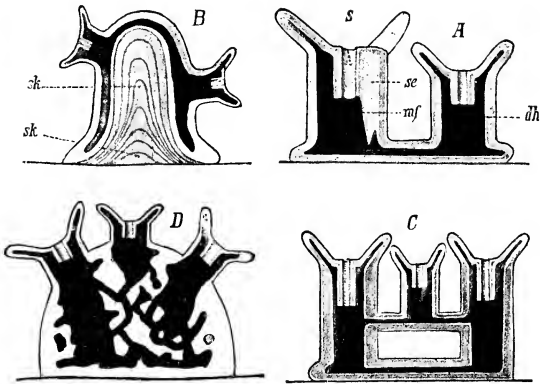
Fig. 36.—Diagrams of budding and stock-formation in the Alcyonaria (after v. Koch, from Lang's *Lehrbuch*). *A*, formation of the basal stolon; *B*, type of the Gorgonidæ; *C*, type of Tubipora; *D*, type of Alcyonarium; *s*, œsophagus; *se*, septa; *mf*, mesenterial ridges; *dh*, gastral cavity; *sk*, axial skeleton growing upwards by means of successive layers.

skeleton the more slender forms, such as Corallium, Scleorgorgia, Melithæa, etc. (v. Koch).

The development of colonies by budding is of special interest in those forms in which, owing to the regular orientation of the daughter individuals to the parent polyp, there is established a regular bilaterally symmetrical structure of the entire colony (Pennatula, Renilla). In these forms a well-marked polymorphism of the individuals is exhibited,

inasmuch as polyps which bear tentacles and become
sexually mature [autozoöids] can be distinguished from
sterile individuals lacking tentacles and having only two
septa, the so-called *zoöids* [siphonozoöids], which provide for
the inflowing of the water (WILSON).

The development of *Renilla* has been investigated by
E. B. WILSON (No. 98). Attachment is here suppressed, and
by the invagination of the œsophagus and the development
of the septa and tentacles there is produced from the planula-
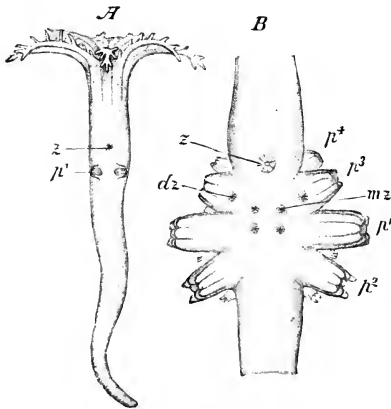
FIG. 37.—Two stages of development of *Renilla* (after E. B. WILSON). *A*, young
polyp with two polyp buds (p^1) and the terminal zoöid (z); *B*, central portion of a
somewhat older stage; p^1, p^2, p^3, p^4, polyp buds; z, terminal zoöid; mz, marginal
zoöid; dz, dorsal zoöid.

larva a free-moving polypoid form (Fig. 37 *A*), which, in
view of the development of the colony, can be called the *axial
individual*. The upper portion of this individual persists as
the *terminal polyp*, whereas the stem of the entire colony
(*rachis*) and its lower free part, the *stalk* (*peduncle*), arise
from its middle and lower portions. We may also retain for
Renilla these terms, which are borrowed from the Pennatu-
lidæ, because a striking similarity between these two forms
is established in their embryology. The eight septa of the

axial individual are developed in the anterior part of the polyp, and grow from in front backwards; nevertheless they are restricted, even in late stages, to the anterior parts of the individual, whereas in most Alcyonaria the septa extend as far as the posterior end of the body. On the other hand, another wall is developed in Renilla by a transverse infold-
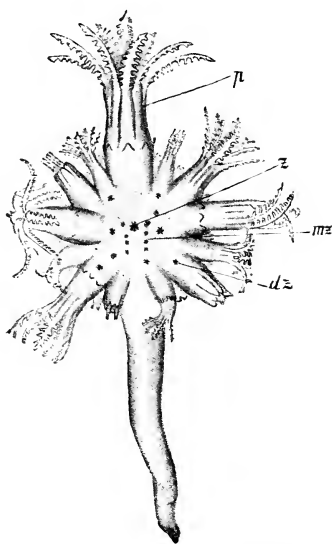
Fig. 38.—Older stage of development of the colony of *Renilla* (after E. B. WILSON). *p*, terminal polyp; *z*, terminal zoöid; *mz*, marginal zoöid; *dz*, dorsal zoöid.

ing of the entoderm from the posterior end of the body, the so-called *peduncular septum*, by means of which the gastral cavity is divided into a ventral and a dorsal half. The peduncular septum grows from behind forwards; and since it grows more actively at its lateral parts, its anterior margin assumes a curved form. Between the two entodermal layers of the peduncular septum is found a cell-mass which subsequently degenerates, and which is apparently homologous to

the skeletogenous layer of the Pennatulidæ, but which is
said by WILSON to arise from the entoderm.

At an early period the *budding of the daughter individuals*
begins; these are formed strictly in pairs on the dorsal side
of the axial individual (Fig. 37 *A*, p^1). The second pair of
polyp buds arises immediately behind the two first ones,
the third pair in front of and somewhat ventral from the
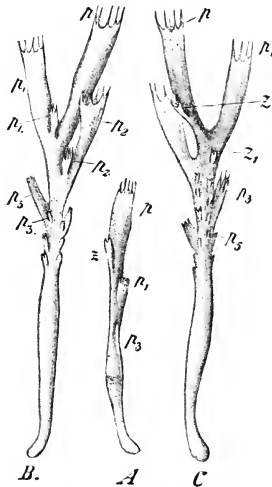
FIG. 39.—Young colony of Pennatula phosphorea (after JUNGERSEN). *A*, youngest
stage, seen from the right; *B*, older stage, from the ventral side; *C*, the same,
from the dorsal side; *p*, terminal polyp; *z*, terminal zoöid; p^1, p^1, polyps of the
first pinnate leaflet; p^2, p^2, polyps of the second pinnate leaflet, etc.

first pair, the fourth pair in the angles between the third
pair and the axial polyp (Fig. 37 *B*, p^1, p^2, p^3, p^1). The buds
arise separately at first, but subsequently their basal parts
fuse. The individuals that have arisen in this way very
soon assume a radial position; and since the buds that appear
later are formed in alternating positions and ventrad to
those first formed, and since in the further course of de-
velopment they grow so actively that they project beyond

these at the periphery, it follows that the oldest individuals are more and more crowded toward the dorsal side (Fig. 38). The terminal polyp also shares this fate. In this way is developed a discoid colony, the marginal individuals of which are the youngest.

The *zoöids* are formed at the same time as the sexual polyps. Even immediately after the appearance of the first pair of polyp buds, a large *terminal zoöid* (Fig. 37 *z*) can be recognized; this functions as an excurrent opening, and is soon followed by the so-called *marginal zoöids* (*mz*), arranged in two lateral dorsal rows, while *dorsal zoöids* (*dz*) make their appearance on the dorsal side of each of the individual polyps.

As far as the development of *Pennatula* is at present known, it is strikingly similar to that of Renilla. LACAZE-DUTHIERS (No. 90) has made some statements on the earliest stages of Pteroides (Pennatula) griseum; the later stages, relating to budding, have been described by JUNGERSEN (No. 81). Here also we find lying at the foundation of the colony an axial individual which is retained for a considerable time as the terminal polyp, and on the sides of which bud forth the daughter individuals, which appear in pairs, but alternating with one another. At the bases of these lateral polyps, that are the first to appear, and in positions corresponding to the ventral side of the axial individual, new buds continue to arise, thereby introducing the development of the pinnate leaflets, of which accordingly the dorsal individual exhibiting the greatest length is the oldest. On the dorsal side of the axis we find an unpaired terminal zoöid and other zoöids which are arranged in two rows. The *lateral zoöids*, which belong to the ventral surface, are not developed until later. In the young stages the terminal zoöid probably functions as the only excurrent opening. In the older stages, on the other hand, there is found at the upper end of the axis a group of *apical zoöids*, among which are probably to be found the terminal zoöid and the degenerated terminal polyp, as well as the adjoining polyps, these having assumed the function of the terminal zoöids.

In the *peduncular septum*, which here also divides the gas-

tric space of the axis into a dorsal and ventral canal, there is
found a calcareous axis (ectodermal according to v. KOCH's
conjecture), surrounded by an axial epithelium, and two
lateral canals lying at the sides of the former, which, as
nutritive or sap canals, belong to the gastrovascular system.

From the embryology it appears that the older authors
have employed the expressions " ventral " and " dorsal " for
the Pennatula colony in the opposite sense to that which
is admissible according to the orientation of the axial polyp
(JUNGERSEN).

Zoantharia.—In the majority of cases fertilization and
cleavage take place inside the mesenterial septa, and the
further development, as far as the complete formation of
the planula, in the gastral cavity of the parent. In this
stage the larvæ are cast out through the mouth-opening.
On the other hand, Cerianthus membranaceus and Actinia
parasitica (Adamsia Rondeletii), according to KOWALEVSKY,
eject the spawn in an unsegmented condition.

Considerable uncertainty still prevails regarding the
earliest developmental processes, the knowledge of which
we owe chiefly to KOWALEVSKY (No. 10), JOURDAN (No. 80),
and H. V. WILSON (No. 99). In many cases cleavage and
the differentiation of the entoderm seem to take place in
connection with the formation of a solid *morula*, therefore
in a manner similar to that which has been described for
the Alcyonaria. At least there is in support of this KOWA-
LEVSKY'S observation on Actinia parasitica (Adamsia Ronde-
letii), which is described in the following manner : "Cleav-
age is regular, but as the result of it there arises not a
blastodermic vesicle, but only an aggregation of cells, which
becomes covered with cilia, and swims about as a larva ;
subsequently a small depression is formed at one spot. The
opacity of the eggs made a further pursuit of the develop-
ment impossible." The author is convinced that the ento-
derm in this case is not formed by invagination, but by a
splitting off from the blastoderm, as in the Corallia. In
sections through ciliated larvæ of Astræa KOWALEVSKY found
the two layers, ectoderm and entoderm, composed of cylin-
drical cells, and an inner contained mass, which had obvi-

ously arisen from cells, but which now showed that it was
composed of nuclei and fat spherules only. A similar struc-
ture of the planula is also described for Actinia aurantiaca
and Balanophyllia regia; JOURDAN'S observations show, how-
ever, that from the presence of an inner mass filling up the
planula we are not at all justified in inferring the origin of
the mass from a solid morula. BALFOUR refers to observa-
tions of KLEINENBERG according to which the cleavage of the
Zoantharia is frequently unequal; this would allow one to
infer the formation of an epibolic gastrula. Accordingly
the formation of the entoderm by delamination from a solid
morula in this case still appears doubtful.

In another series of cases the development of a unilaminar
ciliated blastodermic vesicle has been observed, from which
the gastrula-stage is produced by invagination; thus in an
edible Actinian from Faro (Messina), closely related to
Actinia mesembryanthemum, observed by KOWALEVSKY.
Here the blastopore does not close completely, but is directly
converted into the inner opening of the œsophagus, while
the œsophagus, lined with ectoderm, is developed by the en-
folding of the margins of the mouth-opening. In Cerianthus
also the formation of a cœloblastula and an invaginate gas-
trula following total unequal cleavage was observed by
KOWALEVSKY. Probably Caryophyllia also belongs here.

In Actinia equina, according to JOURDAN, there is formed a typical in-
vaginate gastrula, whose gastral cavity is at first completely empty, and
whose entodermal cells contain but little food-yolk. Nevertheless the
stomach of the planula larva is filled with coarse yolk granules It still
remains uncertain whether these are produced by secretion or by the
partial disintegration of the cells of the entoderm.

According to the observations of H. V. WILSON on Manicina areolata,
first a cœloblastula is formed by total cleavage. Then, by the transverse
division of the tall cells of the blastosphere — consequently by delamina-
tion — coarsely granular cells are repeatedly constricted off, and finally
fill completely the cleavage cavity. While the ectoderm becomes some-
what more sharply marked off from the inner cell-mass, the œsophageal
invagination arises. The larva now becomes covered with cilia and
swims about. The permanent entoderm arises, as in the Alcyonaria,
from the inner cell-mass, the cells lying next to the ectoderm arranging
themselves into an epithelium, while the central mass is finally resorbed.

At any rate, through these various processes of develop-

ment there always arises the same larval form, with identical
structure : a bilaminar, thickly ciliated, oval, pyriform or
more elongated vermiform *planula*, which possesses an
ectoderm composed of prismatic or columnar cells, an
entodermic epithelium consisting of large cubical elements,
and a homogeneous membrane (sustentative lamella), which
is secreted between the two layers at an early period. The
internal cavity of this larva (gastral cavity) is in most cases
still filled with masses of food-yolk. In this swarming stage
there can be recognized a broader, anterior, aboral end of the
body, which subsequently serves for attachment, and is fre-
quently characterized by a long tuft of cilia and a narrower
posterior end ; here the œsophagus is formed by invagina-
tion, and at its deepest part a communication with the
gastral cavity is produced by resorption of the cells. The
further development takes place principally by the formation
of the mesenterial septa, the filaments, the tentacles, and,
finally, in the Corallia (Madreporaria), the calcareous
skeleton.

As regards the sequence in the development of the septa,
the views expressed by MILNE-EDWARDS ET HAIME, based
chiefly upon the condition of the tentacles and calcareous
septa of the adult animal, were formerly generally accepted.
According to them, first six primary septa are simultaneously
developed, then six of the second order in the interspaces
between these, then twelve septa of the third order, twenty-
four septa of the fourth order, and so on, the septa of each
newly appearing cycle being interpolated, as was maintained,
between those already present. On the other hand, we owe
to the investigations of LACAZE-DUTHIERS (No. 89) the know-
ledge that this regular arrangement, which is based on the
number 6, is a secondary one, and that the septa of a cycle
are formed at different times, becoming equalized only sub-
sequently. Most important of all in the earliest stages is a
well-marked bilaterally symmetrical condition, and the
stages with four and with eight septa are to a certain extent
well marked, whereas the intermediate stage, with six
primary septa, is a very transitory one. As regards details,
the statements of LACAZE-DUTHIERS on the sequence in the

development of the pairs of septa first to appear must be modified in accordance with the conjectures of O. UND R. HERTWIG (No. 9), which have been confirmed by the observations of H. V. WILSON (No. 99) and others. The sequence in the development of the different pairs of primary septa is consequently as follows. At first a pair of septa arises which is placed nearly at right angles to the elongated oral fissure which marks the plane of symmetry (Fig. 40 1). This pair of septa is formed as a longitudinal fold of the entoderm, inside of which there extends a process of the gelatinous sustentative lamella. By the development of this first pair of septa, which lies nearer to one oral angle than to the other, the peripheral part of the gastral cavity is separated into two gastral pouches, one of which is smaller than the other. By means of the second pair of septa (Fig. 40 2) the larger of the two pouches is separated into three parts. The third pair of septa is developed in the smaller of the two primary gastral pouches, and divides this in like manner into three parts, whereas the fourth pair of septa is developed in the unpaired pouch which is enclosed by the septa No. 2 (Fig. 40 3 and 4). This stage with four pairs of septa marks a kind of resting phase in the development. Up to this time the septa were always established in pairs, and in such a way that each new pair was developed in one and the same gastral chamber. For the pairs which now follow, Nos. 5 and 6, the statements of H. V. WILSON (No. 99) and A. C. HADDON (No. 77) agree with those of LACAZE-DUTHIERS to the effect that they take their origin in the two pairs of chambers which lie next to the pair of septa first formed. Accordingly the septa of these two pairs would make their appearance independently in four different gastral pouches (Fig. 40 B). On the other hand, the brothers HERTWIG (No. 9) have observed in Adamsia diaphana another mode of development of these two pairs of septa, both of which here arise in the chambers lying between septa 1 and 2 (Fig. 41). Accordingly even in the Hexactiniæ alone different conditions seem to prevail regarding the arrangement of the longitudinal muscles on the first eight septa and the development of the fifth and sixth pairs of septa.[1]

[1] [The recent investigations of BOVERI (No. III., Appendix to *Literature*

The twelve primary septa now arrange themselves in six
pairs, each of which encloses an *intraseptal chamber* (Fig. 42).
Two pairs of septa, called *directive septa*, lying opposite to
each other and corresponding in position to the angles of the
mouth (Fig. 42₃ and ₄), bear the longitudinal muscles on the
sides which are turned away from each other, all other pairs
of septa on the sides which face each other. The gastral
pouch lying between any two intraseptal chambers is called
an *interseptal chamber*. New septa are never developed in
the intraseptal chambers. They always appear in pairs, and
from now on in the interseptal chambers and in cycles based
on the number 6.
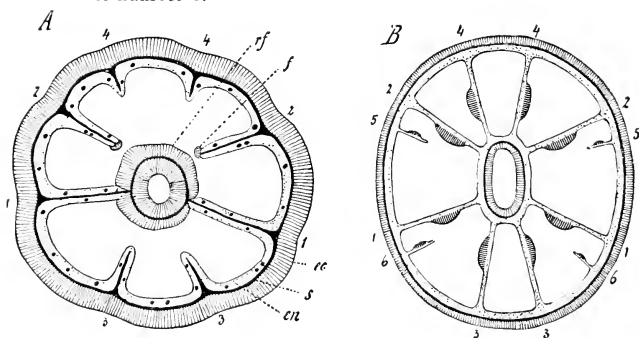
Fig. 40.—Diagram of the growth of the septa in Hexactinians. *A*, stage of
Manicina areolata with eight primary septa in cross-section (after H. V. Wilson) ; 1,
oldest pair of septa, which is in connection with the œsophagus; *ec*, ectoderm ;
en, entoderm ; *s*, sustentative lamella ; *f*, mesenterial filaments ; *rf*, part of the
ectoderm of the œsophageal tube that is bent outwards and backwards at the free
end of the tube ; *B*, stage of *Aulactinia stelloides* with twelve primary septa (after
McMurrich).

on Anthozoa) are especially important in this connection. Boveri confirms
the existence of both the above-mentioned types of septal growth in the
Hexactinia, of which the one was made known by Lacaze-Duthiers, the
other by Hertwig. In agreement with Haddon, McMurrich, and Dixon,
Boveri places special importance on the presence of an Edwardsia stage in
the ontogeny of the Hexactinia, and is inclined to regard the Edwardsia
type as the phylogenetic starting-point of all the groups of Actinia, an
opinion against which doubts have recently been raised, so far as re-
gards the Cerianthea and Zoanthea, by E. van Beneden (Nos. I. and II.,
Appendix) and Carlgren (No. IV., Appendix).—H.]

The condition described in regard to the growth of the septa applies to the Hexactinia and probably to all Hexacoralla. On the other hand, there are a number of groups among the Actiniaria in which other laws of septal growth prevail, which furnish characters of systematic importance (R. HERTWIG). In the *Paractiniæ* (Sicyonis, Polyopsis) there are found two pairs of directive septa, as in the type described above, and the rest of the septa also make their appearance in pairs. On the other hand, the number of the septa is not fixed by the numeral 6. The *Edwardsidæ* (Fig. 43 *A*), like the Hexactiniæ, exhibit two œsophageal grooves [siphonoglyphes] and two pairs of directive septa; nevertheless the arrangement of the longitudinal muscles on the septa indicates a bilaterally symmetrical structure, as opposed to the biradial condition of the adult Hexactiniæ. Of the

Fig. 41.—Transverse section of a young *Adamsia diaphana* (after O. UND R. HERTWIG), diagrammatic. The pairs of septa 5 and 6 are in process of development.

eight septa present, of which only the directive pair exhibits a paired grouping, six bear their longitudinal muscle bands on the side directed
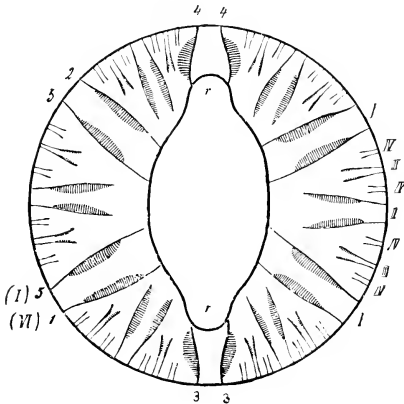
Fig. 42.—Diagram of the further growth of the septa in the Hexactiniæ. Of the numbers at the left 1 to 5 refer to the type of development of *Adamsia* (comp. Fig. 41), the numbers (*I.*) and (*VI.*) to the type of development of *Aulactinia* (comp. Fig. 40 *B*). At the right, *I.* to *IV.* indicate the pairs of septa of the first to the fourth cycle; *r*, *r*, œsophageal grooves [siphonoglyphes].

toward the ventral surface of the animal, whereas the ventral pair of
directives exhibits the longitudinal muscles on the opposite side. It
is worthy of consideration that, according to the coinciding observa-
tions of A. C. Haddon (No. 77) on Halcampa and Peachia and J. P.
McMurrich (No. 91) on Aulactinia, the position of the muscles on the first
four pairs of septa agrees with the arrangement in the Edwardsidæ
(comp. Fig. 40 B), so that accordingly in the ontogeny of some Hexactiniæ
an actual Edwardsia stage is passed through. A bilaterally symmetrical
type is also developed in the groups which now follow. In the *Monauleæ*
(Fig. 43 B) the dorsal pair of directive septa is lacking, whereas in the
paired arrangement of their septa they approach the Hexactiniæ. The
Zoantheæ (Fig. 43 C) also exhibit a paired arrangement of the septa, but
each pair consists of two unequal septa : a small microseptum, not reach-
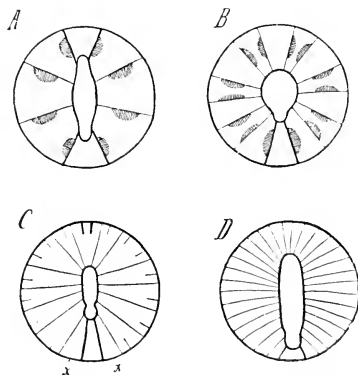
Fig. 43.—Diagram of the position of the septa—*A*, in the Edwardsidæ ; *B*, in the
Monauleæ ; *C*, in the Zoantheæ ; *D*, in the Cerianthææ.

ing to the œsophagus, and a larger macroseptum, extending to the
œsophagus. The two pairs of directive septa constitute the only excep-
tion to this, the dorsal pair exhibiting only microsepta, and the ventral
only macrosepta. The remaining mixed pairs of septa are so arranged
that they fall into a dorsal and a ventral group. In the dorsal group,
which always consists of only four pairs, each pair turns its macroseptum
toward the dorsal pair of directive septa. The number of pairs of the
ventral group is usually considerably greater, and is increased by the
appearance of new pairs next to the pair of ventral directive septa (at *x*
in the two adjoining interseptal chambers). Here, therefore, only two
interseptal chambers function as formative seats of new pairs of septa.

Each pair of these ventral groups turns its macroseptum toward the ventral pair of directive septa. Finally, in the *Cerianthea* (Fig. 43 *D*) only one œsophageal groove [siphonoglyphe] is found. Here the numerous septa are not arranged in pairs ; two particularly small septa attached to the base of the œsophageal groove (A. VON HEIDER) may be called directive septa. The septa lying at either side of them are the largest, and from here the septa continually decrease in size toward the dorsal side, so that it is probable that the zone of growth of new septa is situated at this place (HERTWIG). That the number of groups is possibly not concluded with the types described, is proved by *Gonactinia*, which represents a peculiar type allied to the Zoantheæ (BLOCHMANN UND HILGER, No. 74).

With respect to the development of the *mesenterial filaments*, H. V. WILSON (No. 99) has proved, at least as far as concerns the filaments of the twelve primary septa, that they take their origin as outgrowths from the ectodermal epithelium of the œsophagus. Even earlier A. VON HEIDER, on the basis of histological agreement, had argued for the ectodermal nature of the filaments in Cerianthus, and E. B. WILSON had conjectured that at least the lateral ciliate bands (*Flimmerstreifen*) belong to the ectoderm. A. ANDRES also believed that he had convinced himself that the filaments of the six principal septa take their origin by means of outgrowths from the ectoderm of the œsophagus. According to the observations of H. V. WILSON on Manicina areolata, it is to a certain extent probable that not only the lateral ciliate bands, but also the nettle- and gland-cell bands (*Nesseldrüsenstreifen*), arise from the ectoderm.

With respect to the more detailed processes of development, the mesenterial filaments of the first pair of septa differ from those appearing later. The establishment of the first pair of septa and the filaments belonging to it takes place in Manicina areolata at a time in which the space between the œsophagus and the body-wall is still filled throughout by a solid mass of entodermal cells. This cell-mass encircling the œsophagus is divided into two parts, corresponding to the two primary gastral pouches, which are subsequently hollowed out. This division is effected by the formation between the œsophagus and the body-wall of two partitions of the sustentative lamella, which constitute the foundation of the first pair of septa. It takes place in this way : the œsophagus approaches the body-wall until it comes in contact with it, then its sustentative lamella fuses with that of the body-wall ; when subsequently the œsophagus again separates from the body-wall, a bridge of the sustentative lamella is preserved between the two. While the fundament of the first

pair of septa is formed in this way, the development of the filaments takes place by simple downgrowth of the ectoderm of the œsophagus, in the direction of the two primary septa. The two gastral pouches first to appear are now completely hollowed out. The new pairs of septa next arise as foldings of the entodermal lamella of the body-wall, and their upper ends seem to be at some distance from the ectoderm of the œsophagus, so that no direct outgrowth of the latter can lead to the formation of the filaments. In order to establish the connection between the ectoderm of the œsophagus and the newly formed septa, the former must bend around at the inner opening of the œsophagus, and grow upward on the outer surface of the œsophagus, until it reaches the uppermost part of the newly formed septa, on to which it now advances to form the filament. This bent-over part of the ectoderm is seen in Fig. 40 *A*, *rf*. H. V. WILSON conjectures that the mesenterial filaments of all subsequently appearing septa are formed after this type.

In general the development of the mesenterial filaments takes place in the same sequence as that of the septa, so that the oldest pair of septa bears the most developed filaments.

The *tentacles* arise as simple evaginations of the body-wall over the different gastral pouches. The sequence of their origin has been described by LACAZE-DUTHIERS (No. 89), especially for Actinia mesembryanthemum. For the early stages it is closely connected with the sequence of the appearance of the different mesenteries and the formation of the chambers dependent on it. In this connection ought specially to be mentioned the fact that the tentacle which arises over the larger of the two first-formed gastral pouches considerably outstrips the others in development, so that for a long time the bilateral symmetry of the larva is marked externally by the presence of this one large tentacle (Fig. 44 *A*).

HAACKE (No. 76) has called attention to the fact that in attached stock-building forms, as in the blossoms of many Phanerogams, the bilaterally symmetrical fundamental form may be expressed by the position of the buds in relation to the parent animal, *i.e.*, to the axis of the entire colony, since the parts of the bud near to the axis undergo a different development from those remote from it. MOSELEY had already shown that in Saccophyton and Heliopora the polyps always have their dorsal sides turned towards the axis. We may conclude from such observations that the bilaterally symmetrical structure of the Anthozoa is caused by the formation of stocks. The solitary forms (Actinians) would then have to be derived from those forming colonies. Finally, we may assume that

the bilaterally symmetrical type, which at first is developed only in connection with budding, became so firmly established that it also found expression in the first stages of development from the egg (comp. above, p. 52).

After the formation of the first twelve tentacles, a rearrangement, according to the number 6, takes place, so that there are two cycles of six tentacles each. The larger ones, those of the first cycle, correspond to the six primary intraseptal chambers, whereas the smaller ones, those of the second cycle, alternate with them. Six large tentacles of the first cycle thus alternate regularly with six smaller ones of the second cycle. The appearance of new tentacles does not take place by the interpolation of one in each of the twelve intervals between the elements of the first and second cycles, but by the appearance of six pairs, which occupy only one half of these intervals, as is represented in Fig. 44 B. We
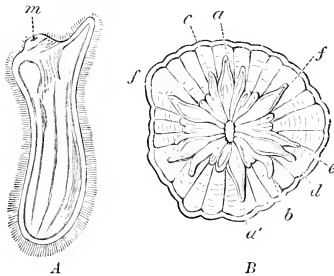
FIG. 44.—Two larvæ of *Actinia mesembryanthemum* (after LACAZE-DUTHIERS, from BALFOUR's *Comparative Embryology*). A, bilateral ciliated stage, with one large and several small tentacle buds ; *m*, mouth ; B, view of an older stage from above. There are twenty-four tentacles around the mouth. The sequence in the origin of the twelve primary tentacles is a', a, b, c, d, f, e.

here see that three tentacles lie in the intervals between every two tentacles of the first circle, one belonging to the second cycle and two being new ; but these are arranged in such a way that the middle one of the three everywhere belongs to the cycle of the youngest generation. This one now increases greatly in size, and outstrips the individuals of the former second cycle, which in this way lose their rank, and are classed in the third cycle. In later stages, cycles which differ in size (six tentacles of the first, six tentacles of the second, and twelve tentacles of the third cycle) actually alternate regularly with one another in position. It must be observed, however, that the present third cycle does not contain uniform elements, but six tentacles of the youngest stage of development and six which previously belonged to the second cycle. A rearrangement therefore has taken place. In the same way the number of the tentacles increases from twenty-four to forty-eight and to ninety-six by the appear-

ance of new pairs of tentacles, half of the intervals being left empty. Thus by rearrangement a fourth cycle of twenty-four and a fifth one of forty-eight tentacles are developed ; but these, like the third cycle before, consist of elements of heterogeneous origin.

Ordinarily the attachment of the hitherto free-swimming ciliated larva takes place in the stage in which the number of tentacles is increased from twelve to twenty-four.

It is to be expected that in those forms which exhibit a special law of septal growth the sequence of the appearance of the tentacles is correspondingly modified. In a larva called *Arachnactis* by SARS and A. AGASSIZ (No. 72), conditions of organization are found which, as has recently been shown by C. VOGT (No. 96), connect it with the *Ceriantheæ*.[1] The development of the tentacles also recalls the development of the Cerianthus larva, made known by HAIME. In Arachnactis the tentacles do not grow out in cycles between those already present, but there is a dorsal budding zone (as in the case of the septa; comp. p. 95), where the youngest tentacles are formed in pairs. The tentacles of the inner circle also are formed in the same manner. It follows from this that the tentacles of the ventral side must be the largest and oldest. The unpaired, perpetually dwarfed tentacle of the directive chamber, which is found between the longest paired tentacles, forms an exception.

The development of the *calcareous skeleton* of the Madreporaria has been studied by LACAZE-DUTHIERS (No. 88) and v. KOCH (Nos. 83 and 85) in Astroides calycularis. It takes place at the stage in which the first twelve tentacles of the larva have been developed, and in which attachment usually occurs.

The calcareous skeleton is formed as a secretion on the outer side of the ectoderm of the body-wall (Fig. 45). At first a delicate circular basal plate arises as a secretion from the ectodermal cells of the pedal disc. This *basal plate*, by means of which the larva attaches itself to some suitable

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[1] [In regard to the development of Arachnactis, the adult form of which has been found by HERTWIG and BOVERI, consult the recent statements of E. VAN BENEDEN (No. II., Appendix to *Literature* on Anthozoa) and BOVERI (No. III., Appendix to *Literature*).

A long time ago a very remarkable Actinia larva was described by SEMPER, and recently by E. VAN BENEDEN more in detail. This larva is characterized by the presence of a highly iridescent ciliate ridge running lengthwise of the body. VAN BENEDEN is inclined to refer it to the group of the Zoantheæ. Comp. SEMPER, "Ueber einige tropische Larvenformen," *Zeitschr. wiss. Zool.*, Bd. xvii., 1867, and VAN BENEDEN (No. I., Appendix to *Literature* on Anthozoa).—H.]

support, consists of roundish crystalline bodies, which subsequently fuse with one another. The earliest fundaments of the calcareous septa [sclerosepta] soon make their appearance. It was shown by MILNE-EDWARDS ET HAIME, and afterwards by LACAZE-DUTHIERS, that the calcareous septa correspond in position each to a gastral pouch, and therefore that they occur between every two mesenterial septa. The earliest fundaments of the twelve primary sclerosepta are called *radial ridges* (*Sternleisten*), and at first are **V**- or **Y**-shaped (Fig. 46). The fundament of the *theca* (*Mauerblatt*) arises by the peripheral ends of the radial ridges soon becoming fused with one another. All of these are structures which are secreted by the ectoderm of the pedal disc,
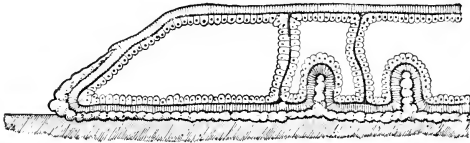
FIG. 45.—Development of the calcareous skeleton of *Astroides calycularis* (after v. KOCH), diagrammatic. The section is made perpendicular to the pedal disc in the direction of a secant. At the bottom the fundament of the basal plate; to the left the epitheca; to the right two radial ridges [sclerosepta] growing upwards from below, alternating with two mesenterial septa [sarcosepta].

and naturally the more these skeletal parts rise upwards the more the ectodermal layer of the pedal disc must undergo a kind of invagination. It follows from this that in later stages also those parts of the skeleton which apparently lie inside the body of the polyp are covered by an epithelial lamella belonging to the ectoderm of the pedal disc (*calycoblast layer*, v. HEIDER). But the lateral walls of the body in its lower portions also deposit externally a calcareous layer, which constitutes the fundament of the so-called *epitheca* (Fig. 45). The so-called *columella* is formed by the fusion of the radial ridges [sclerosepta] with one another at their inner, central ends. Six of the twelve radial ridges soon become more prominent, so that there is established an arrangement in two cycles. Subsequently other cycles make their appear-

ance by the interpolation of new small septa in regular order
between the existing ones.

Non-sexual reproduction in the form of *fission* and *budding*
is found widely distributed in the Zoantharia ; by this means
extensive colonies are developed
in the skeleton-forming Corals
(Sclerodermata), whereas in
the group of non-skeletal Ac-
tiniaria (Malacodermata) the
individuals produced by fission
or budding usually separate
entirely, so that, with few ex-
ceptions (Zoantheæ), the forms
in this case remain solitary.
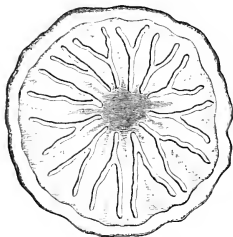
FIG. 46.— Basal plate of a larva of
Astroides calycularis, soon after at-
tachment, with twelve radial ridges
(after LACAZE-DUTHIERS, from BAL-
FOUR's *Comparative Embryology*).

Budding in the Actiniaria has been
observed more rarely — Epiactis
(VERRILL, ?), Gonactinia (BLOCHMANN
UND HILGER), Zoanthus. More fre-
quently reproduction takes place by
fission. This may divide the parent
animal into two nearly equal parts : either as *longitudinal fission,* which
begins at the oral disc and progresses toward the base, or takes the oppo-
site direction, or as *transverse division,* a kind of reproduction which has
been described in detail for Zonactinia prolifera by M. SARS and by
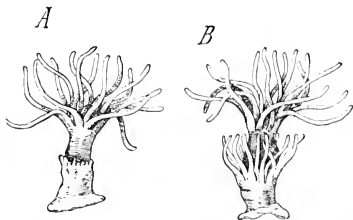
FIG. 47.—Two stages of transverse fission of *Gonactinia prolifera,* SARS (after
BLOCHMANN UND HILGER).

BLOCHMANN UND HILGER (No. 74), and which in its outcome presents strik-
ing resemblances to the divisions in *Flabellum* and *Fungia* described by
SEMPER, and to the process of strobilization in the Scyphozoa. In Go-
nactinia it is always young animals that undergo transverse division.

Somewhat below the middle of the parent animal is formed a circle of bud-like projections, out of which is developed the circle of tentacles of the lower individual. While the upper part is being constricted off, the oral disc and the œsophagus of the lower offspring of the division are developed. Finally, the upper part detaches itself. It appears that both parts have the power to divide again.

Another remarkable, more widely distributed kind of division, which had already been observed by DICQUEMARE and by DALYELL (No. 4), has recently been studied in detail by A. ANDRES (No. 73), and has been called *laceration* (Fig. 48). This consists in the abstriction of fragments of a basal expansion. At the margin of the base of an Actinian a small part is characterized by the opacity of its entoderm and by its firm adherence to the support, the latter being caused by a secretion of the ectoderm. By the contraction of the parent animal, the modified marginal part is torn away from it. This can now be metamorphosed either directly into a small Actinian, or after further separation into smaller fragments.

Both kinds of non-sexual reproduction, fission and budding, are widely distributed among the Corallia. They here lead to the formation of extensive stocks of various shapes. In many cases (Oculinacea and Astræacea) in which it was formerly believed that lateral budding occurred, STUDER (Nos. 94 and 95) was able to show, upon closer investigation, that there exists a reproduction by fission, one of the resultants of division coming with further growth to occupy a position on the lateral wall of the other part. A similar kind of reproduction has been observed among the Fungiaceæ in Herpetolitha limax.

Genuine basal budding is found, for example, in Turbinaria, where the base of the colony exists as a common plate of cœnenchyma, at the margin of which new individuals bud; likewise in Galaxea.

Fig. 48.—Reproduction in *Aiptasia lacerata* by means of abstriction of a basal part (after A. ANDRES). *A* to *C*, advancing abstriction; *D*, *E*, metamorphosis of the fragment into a small Actinian.

The form of longitudinal fission occurring in the Corallia, which usually begins with a constriction of the oral disc, may remain more or less incomplete, so that the individuals remain united with one another in series. This arrangement can be recognized even in the skeleton, since
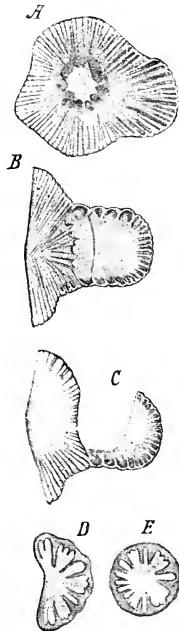
a whole series of individuals remains enclosed by a common theca, whereas the septa are placed perpendicular to the direction of the tortuous valleys extending between the thecæ (Meandrina).

In the stone corals also, budding and fission may lead to the formation of individuals which separate from the parent and live independently. In Blastotrochus there are lateral buds that separate, whereas in Flabellum a kind of transverse division occurs. The young stages of the Fungidæ form small coral stocks from which the solitary forms, which become sexually mature, are abstricted by transverse division. Since one and the same branch may undergo this process of transverse division several times, the resemblance to the strobilization of the Scyphozoa is very striking. Here also there is a true alternation of generations (SEMPER, No. 93).

III. SCYPHOMEDUSÆ.

Of the forms belonging here the *Lucernaridæ* and *Charybdeidæ* are contrasted with the *Discophora* proper. While the embryology of the latter has been repeatedly investigated, we have as yet only a fragmentary knowledge of the two groups first named.

Lucernaridæ.—FOL and KOROTNEFF have given accounts of the larvæ of the Lucernarians. The development from the egg has been more thoroughly investigated by KOWALEVSKY (No. 108), whose results have recently been confirmed by R. S. BERGH (No. 101). After the egg and sperm have been discharged into the water fertilization takes place, at the completion of which the egg retracts somewhat from the vitelline membrane. Two polar globules are formed, and then the first cleavage furrow arises. By means of total and equal cleavage a multicellular stage is formed, which presents no cleavage cavity. The pointed ends of the prismatic cells meet at the centre. An accumulation of entoderm cells now takes place inside this so-called morula ; this is accomplished by a contribution of elements from a definite region of the egg, so that the production of the entoderm here seems to approach the type of polar ingression. KOWALEVSKY believes that it is chiefly a transverse division of the prismatic cells in this region that leads to the contribution of entodermal elements ; however, simple ingression is not wholly excluded. The bilaminar stage resulting from this is at first completely spherical (Fig. 49 *A*), but soon elongates in the direction of the future chief axis (Fig. 49 *B*). The entoderm cells meantime become vacuolated, and arrange themselves more and more in a single row, so that there results from this a rod-like planula, which, like that mentioned for Æginopsis (p. 57), resembles a detached hydroid tentacle (Fig. 49 *C*). This planula of the Lucernaridæ is not ciliated, but creeps slowly about with worm-like movements. The first nettling cells are developed a its posterior end. Preparatory to assuming the polypoid form, it eventually attaches itself

by means of its anterior end. The further development could not be
followed. R. S. Bergh, however, mentions a young stage in which the
tentacles were not yet united into groups, but were distributed along the
margin of the bell, while the arms were not yet developed. Eight ten-
tacles lying in definite radii could be recognized as fundaments of
marginal papillæ.

Charybdeidæ.—W. Haacke (No. 106) has given a description of some
young forms of the Australian Charybdæa Rastonii, which already con-
siderably resembled the adult animal. These accounts are thus far the
only ones on the embryology of this genus. As contrasted with the
cubical form of the adult animal, the young Acalephs showed an
approach to a pyramidal shape, and the apex of the umbrella was more
strongly arched than in the adult. The youngest stage that was observed
exhibited a canal somewhat excentrically situated, and extending from
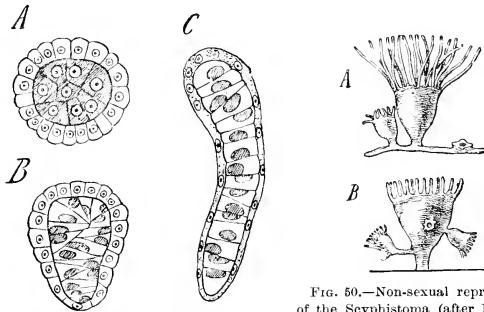
Fig. 49.—Three stages in the develop-
ment of Lucernaria (after R. S. Bergh).

Fig. 50.—Non-sexual reproduction
of the Scyphistoma (after M. Sars)
—A, by the formation of stolons; B,
by lateral budding.

the central stomach to the dome of the umbrella, where it ended blindly.
Haacke regards it as the remains of a communication with a Scyphis-
toma nurse, and therefore maintains the probability of an alternation of
generations in the Charybdeidæ.

From the egg of most *Discophora* (*Discomedusæ*) a fixed
polypoid creature is first developed, which is attached by
one pole, and has the mouth at the opposite end, at some
distance from which a circle of tentacles is developed (Fig.
51, 3, 4). The Lucernaridæ are essentially a more highly
developed form of these *scyphopolyps*, which become sexually
mature. In all other Scyphomedusæ the polypoid form

(*Scyphistoma*) appears to lack the power of generating sexual products, exhibiting only non-sexual reproduction, which occurs in two modifications : (1) as budding (lateral budding and formation of root-runners or stolons) (Fig. 50), by means of which a scyphopolyp is always produced again — this either separates from the parent and attaches itself independently, or may remain united with the parent, thus temporarily producing small colonies (scyphopolyp stocks)—(2)
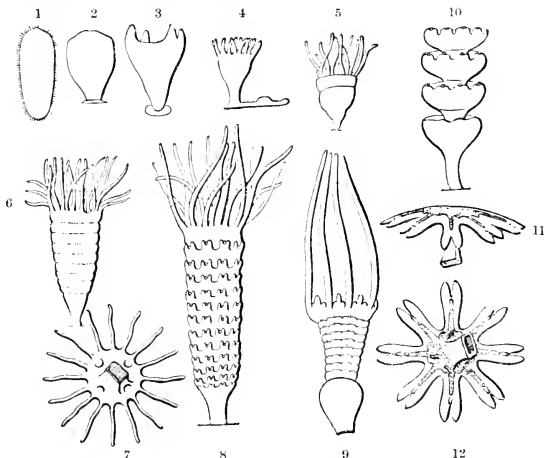
Fig. 51.—Cycle of development of *Aurelia aurita* (from Hatschek's *Lehrbuch*). 1, planula ; 2, attached larva ; 3, young Scyphistoma with four tentacular buds ; 4, Scyphistoma with stolonic growth ; 5, beginning of the strobilization, indicated by a circular furrow ; 6, 8, 9, 10, various strobilæ polydiscæ ; 7, Scyphistoma from above ; 11, Ephyra from the side ; 12, Ephyra from below.

as strobilization, in reality a transverse division with subsequent regeneration. By means of transverse constrictions the scyphopolyp (Fig. 51, 6) separates into superposed discoid parts (*strobila stage*, Fig. 51, 5—10), each one of which, by the production of marginal lobes and corresponding internal metamorphoses, is changed into a young medusa, which at first shows the characteristic form of the *Ephyra stage* (Fig. 51, 11, 12), and is not converted into the permanent

form of the sexually mature medusa until after a metamorphosis, which in most cases is rather complicated.

In most of the Discophora hitherto studied development takes place in the form of an alternation of generations already described. This is wanting in the Lucernaridæ only, they representing a sexually mature scyphopolyp stage, from the eggs of which individuals of the same form arise. On the other hand, among the free-swiming acraspedote medusæ cases (Pelagia) of direct development are known, in which a larva developed from the egg of the medusa changes directly into the Ephyra stage. This is looked upon as a case of cœnogenetically abbreviated development, since the formation of a non-sexually reproducing nurse-form (Scyphistoma) is suppressed.

Development of the Scyphistoma.—The development of Aurelia (A. aurita and A. flavidula) is that of which we have the most complete knowledge; it has been made known through numerous investigations—those of M. Sars (No. 112), v. Siebold (No. 114), L. Agassiz (No. 2), Claus (Nos. 102 and 103), Haeckel (No. 107), and Goette (No. 105). In the following we adhere chiefly to the description of Goette, by whose investigations a number of new points of view have been gained.

The eggs of Aurelia aurita pass from the ovary into the gastral cavity of the parent, and from there through the mouth into the folds of the oral arms, where, enveloped by a slimy secretion from the entoderm, they undergo embryonic development as far as the stage of the swarming planula. They are enveloped by a delicate vitelline membrane, which is lost in the later stages of cleavage.

By total and equal cleavage (Claus) the egg divides into a number of equal-sized blastomeres, which arrange themselves in a single layer about a comparatively small cleavage cavity (cœloblastula). While, according to Claus (in harmony with the statements of Kowalevsky), the gastrula-stage is reached by means of a process of invagination,[1] in which

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[1] [The observations of Claus have been fully corroborated by the recent investigations of Frank Smith (No. VII., Appendix to *Literature* on Scyphomedusæ) on *Aurelia flavidula*. In this species the entoderm is pro-

the lumen of the archenteron can be recognized only as a linear fissure in the plug-like ingrowth, another method of formation of the lower germ-layer, that may be called polar ingression, has been maintained by GOETTE. According to GOETTE, the cells of the blastula have not the same form in the entire circumference, but are somewhat shorter and broader in one hemisphere. From this region there is a migration of individual cells into the blastocoele, until finally this cavity is completely filled with a solid cell-mass (entoderm). The archenteron arises in this in the form of a fissure, which soon breaks through to the exterior at the region from which the immigration of entoderm cells took place, thereby forming the primitive mouth (prostoma).

Even during this process the embryo, originally spherical, elongates, so that the longitudinal axis passes through the primitive mouth and the apical pole lying opposite to it. But the primitive mouth very soon closes completely. At the same time the larva becomes narrowed at this end, so that it is pyriform. The swarming out of the ciliated embryo (planula, Fig. 52 A) now takes place; the broader apical pole is directed forwards in swimming, whereas the narrower pole, at which the closure of the primitive mouth took place, comes to lie behind. Nettling capsules very soon make their appearance on the swarming larva; these arise in great numbers at the posterior pole, whereas they are almost wanting at the anterior end.

Even during the swarming stage a shallow depression is developed at the anterior (apical) pole of the larva, and at this point the epithelium acquires a glandular nature. The larva now attaches itself by the apical pole to some support,

duced by the formation of a distinct invagination gastrula. A migration of cells into the blastocoele, as described by GOETTE, was also occasionally observed in A. flavidula. However, these cells appear to disintegrate without taking any part in the formation of the entoderm.

On the other hand, the entoderm is formed in *Cyanea arctica*, according to McMURRICH (Appendix to *Literature* on Scyphomedusae, No. V., p. 314, and No. VI., p. 90), by an inward migration of certain cells of the blasto- sphere, and in *Cyanea capillata*, according to HAMANN (No. IV., Appendix to *Literature*), by the ingrowth from one pole of the embryo of a solid rod, which subsequently becomes hollowed out to form the gastral cavity.—H.]

and thus the former anterior end becomes the foot of the scyphopolyp; this soon contracts a little, whereas the posterior end widens, so that in this way the body acquires the goblet shape characteristic of polyps (Fig. 52 *B*). During the attachment a cement, which soon hardens into a plate with upturned margins (Figs. 54 and 55 *k*), is secreted from the foot. The secretion of a mesogloea begins early between the two layers of the larva (Fig. 52 *B*, *g*).

The next change is the formation of the permanent mouth, which arises by a process of invagination. The ectodermal layer of the prostomal pole invaginates into a gradually deepening ectodermal pocket (Fig. 52 *B*, *s*), at the bottom of which a perforation, leading into the gastral cavity, soon arises. In this way an *oesophagus*, lined with ectoderm, is produced (Fig. 52 *C*); the outer opening is known as the *mouth*, the inner, communicating with the gastral cavity, as the *inner opening of the oesophagus* (Fig. 52 *C*, *sp*). By means of this process of invagination the entodermal sac becomes crowded downwards, but not throughout its entire extent. Since the larva is compressed laterally, two glove-like entodermal processes, corresponding in position to the longer of the secondary axes, are preserved. These project upward, and are the *first two gastral pouches* (Fig. 52 *C m* and *D m*). Very soon, however, in a plane at right angles to this, *a second pair* of gastral pouches grows upward as diverticulæ of the central stomach (Fig. 52 *E*), so that now the radiate type with four rays is reached. We now have an oesophagus invaginated from the ectoderm, in the circumference of which, at the four radii, lie gastral pouches in connection with the gastral cavity.[1] At these places, where two neighbouring gastral pouches come in contact, a *partition*, or

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[1] [Our knowledge of the first processes of development in the Scyphistoma stage has been materially increased by recent investigations, which have advanced information in several directions. Nevertheless it is not possible as yet to pronounce final decision concerning these developmental processes. The observations of GOETTE have been only partially confirmed by CLAUS (Nos. I. and II., Appendix to *Literature* on Scyphomedusæ). As the result of his most recent observations, CLAUS (No. II.) denies totally the presence of an ectodermal pharynx. Of special importance are the statements of CLAUS (No. II.) concerning the formation of

septum (Fig. 52 *E*, *st*), is produced by their contiguous lateral walls. These four septa lie in the *interradii*, whereas the *four*
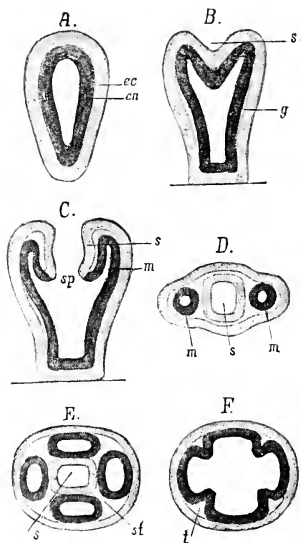

FIG. 52.—Diagrammatic sections through various successive stages of *Aurelia* (after GOETTE). *A*, planula; *ec*, ectoderm; *en*, entoderm; *B*, attached larva with forming œsophageal invagination, *s*; *g*, mesoglœa; *C*, completed rupture of the œsophageal invagination; *sp*, inner opening of the œsophagus; *m*, gastral pouches; *D*, transverse section through the stage represented in *C* at the level of the œsophagus; *E*, transverse section through an older stage at the level of the œsophagus; *F*, transverse section through the same stage at a part nearer to the stalk; *s*, œsophagus; *st*, septa; *t*, tæniolæ.

primary gastral pouches lie in the four *chief radii* (*perradii*).

the proboscis in the developing Ephyra of the strobila stage, a point which had not hitherto received any careful attention.

Recent observations by GOETTE (No. III.) on *Cotylorhiza tuberculata* and *Pelagia noctiluca* have led to the astonishing result, that of the four primary gastral pouches,—although the first pair is of entodermal origin, being produced from diverticula of the archenteron,—the second pair is ectodermal in origin, since it arises by evagination from the ectodermal pharynx.—H.] Consult also IDA H. HYDE, No. VII. *b*.—TRANSLATORS.

The structures occurring between these [eight] radii are designated as *adradial*.

The lower free margins of the four septa soon become continuous with the wall of the central stomach in the form of four longitudinal folds, which ultimately extend through the entire length of the scyphopolyp, even into the foot. These folds are known as the *longitudinal folds*, or *tæniolæ* (Fig. 52 *F, t*), and the sinuses of the central stomach limited by them as *gastral furrows*.

In the further metamorphosis of the larva the form changes, approaching more and more the shape of a goblet (Fig. 53).
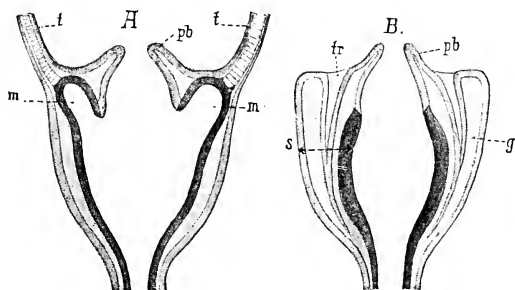
Fig. 53.—Diagrammatic longitudinal section through a Scyphistoma (based on GOETTE). *A*, perradial longitudinal section; *B*, interradial longitudinal section; *pb*, proboscis; *t*, tentacle; *tr*, septal funnel; *m*, gastral pouches; *g*, mesoglœa; *s*, septum. The entoderm is represented as a dark layer.

The lower narrow portion is called the *stalk* or *peduncle* (Fig. 55 *st*), the prolongation of the central stomach extending into it the *peduncular canal*. The upper part of the body becomes flattened, and thus forms the *oral disc* or *peristome*, in the middle of which rises the cone-shaped *proboscis* (Fig. 53 *pb*) with its central four-sided mouth-opening. The four corners of the mouth are placed perradially (Figs. 54 *C* and 55).

The first four *tentacles* now arise over the four gastral pouches, and, in keeping with the successive appearance of the pouches, those over the first pair of pouches arise first, and then those over the second pair. A cylindrical ento-

dermal cord grows from the apex of each gastral pouch diagonally upwards and outwards, pushing before it the ectoderm of the outer margin of the peristome. The ento- derm cells in the tentacular buds soon arrange themselves in a single row (Fig. 53 *t*).

Other important fundaments of organs are represented by the septal funnels which are now established. Four funnel- like invaginations arise from the ectoderm of the peristome in the interradii; these sink into the septa, and extend down- wards as solid cords of cells, which are continued along the tæniolæ and even beyond these into the stalk (Fig. 53 *B*; Fig. 54 *A* and *C*, *tr*). In this solid portion, the cells appear to be fused with one another, and on their surface longi- tudinal muscle fibrillæ are differentiated, so that the four [septal] *longitudinal muscles* extending in the tæniolæ arise in this way (Fig. 54 *A*, *B*, *sm*).

The young Scyphistoma thus produced is characterized therefore as a goblet-shaped polyp, with four longitudinal folds (tæniolæ) of the entodermal sac extending upwards as four septa, which are stretched between the body-wall and the invaginated ectodermal œsophagus. The stomach is accordingly divided into a central cavity and four gastral pouches (peripheral intestine [*Kranzdarm*]), which lie be- tween the septa and are directly continuous with the gas- tral furrows. Four perradial tentacles are attached to the margin of the peristome, while four interradial septal fun- nels extend from the peristome into the septa and tæniolæ (Fig. 53).

The metamorphosis into older Scyphistomæ (Figs. 54 and 55) takes place by an increase in the number of the ten- tacles and other changes, which efface more and more the original characters, and lead by a gradual transition to the structural plan of the Ephyra.

The budding of the tentacles presents many irregularities. Heretofore it has been believed that normally after the formation of the first four tentacles, radial in position, the development of four interradial ones (*i.e.*, placed over the septa) took place, and then, after all these eight tentacles had reached the same length, ensued the development of eight others, lying between them (therefore adradial), and so on. According to GOETTE,

however, the four tentacles that immediately succeed the four primary ones are not placed over the septa, but bud out from the corners of the gastral pouches of the second pair, which lie next to the septa, and only gradually move into positions over the septa. In this way, their axial, entodermal cords acquire connections with the gastral pouches of the second pair. Since the gastral pouches of the first pair soon follow with the formation of four new tentacles, the equivalence of the first four
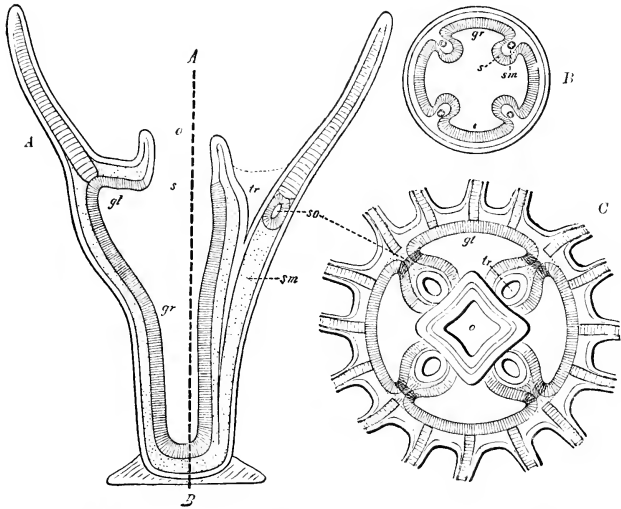

FIG. 54.—Diagrammatic representation of the structure of an older Scyphistoma (based upon GOETTE, from HATSCHEK's *Lehrbuch*). *A*, longitudinal section : at the left, perradial ; at the right, interradial ; *AB*, chief axis ; *o*, mouth ; *s*, inner opening of the œsophagus ; *gt*, gastral pouches ; *gr*, gastral furrow ; *so*, septal ostium ; *tr*, septal funnel ; *sm*, septal muscle (the dotted line does not quite reach to it) ; *B*, transverse section through the lower part of the body ; *gr*, gastral furrow ; *s*, septum ; *sm*, septal muscle ; *C*, view of the oral side (references as in *A*).

primary gastral pouches is established for the first time in the stage with twelve arms. GOETTE, therefore, maintains that the numerical series, 4, 12, 20, 28, etc., is the primitive one for the budding of the tentacles, whereas the actually observed series, 4, 8, 16, 24, 32, etc., corresponds to a cœnogenetically modified condition. It should be mentioned that the formation of each new tentacle takes place by an outfolding of the corresponding part of the gastral pouch, so that in reality a small secondary gastral pouch is produced with every tentacle.

The further metamorphosis of the developing Scyphistoma consists in a widening of the central stomach, whereby the œsophagus gradually moves into the proboscis (Fig. 54 A), and the gastral pouches tend to become obliterated. At the same time the entrances to the four funnels, which are widely open toward the peristome, produce a circular, groove-like depression, involving the entire circumference of the originally flat peristome, which thereby approaches the bell shape of the sub-umbrella of the medusa ; the proboscis, which has become more elevated, corresponds to the oral tube [man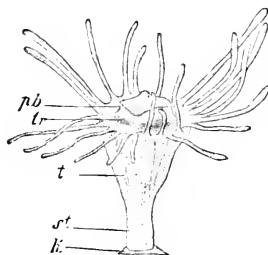ubrium], while the gastral pouches, separated by the septa, represent the peripheral intestine (*Kranzdarm*) of the medusa. *The Scyphistoma, by gradual metamorphoses, has approached in the most essential features the structure of the medusa* (comp. Figs. 54 A and 57).

FIG. 55. — Scyphistoma of *Aurelia aurita*. *pb*, proboscis ; *tr*, entrance into the septal infundibulum ; *t*, tæniolæ; *st*, stalk ; *k*, adhesive mass.

In most of the other Discophora, the development of the Scyphistoma seems to take place in quite the same way, especially in *Cotylorhiza borbonica* (KOWALEVSKY, GOETTE) and *Cyanea capillata* (SARS, VAN BENEDEN, AGASSIZ), where the eggs likewise undergo the first stages of development attached to the oral arms, and enveloped in a slimy jelly. On the other hand, the early development in *Chrysaora*, a form which is also striking on account of its hermaphroditism, presents notable deviations (CLAUS, No. 102 and No. 3). Here fertilization and the entire embryonic development take place within the ovary, so that the larvæ are not born until they reach the planula stage. The very small membraneless eggs are surrounded in the ovary by a pedunculated follicle, which owes its origin to the cells of the germinal epithelium. Fertilization and cleavage are transferred to an early stage in the development, so that at the same time with the embryonic development there is a considerable growth of the embryo as the result of a continual supply of food material on the part of the parent. This food supply is provided by the follicular cells. In these particulars the development of the egg and embryo of Chrysaora recalls that of the viviparous Aphidæ and the Polyphemidæ among the Cladocera. In other

respects the phenomena of the embryonic development are essentially the same as those we have described for Aurelia. By means of total and equal cleavage, a cœloblastula arises, out of which by infolding an invaginate gastrula develops, whose prostoma remains open for a considerable time, but finally closes completely. From observations by BUSCH, it appears as if reproduction of the embryo, by means of longitudinal division, frequently took place at this stage. This recalls the occurrence of fission in the blastula of Oceania armata, according to METSCHNIKOFF (p. 49). In the stage of the ciliated planula the larvæ of Chrysaora pass from the ovary into the gastral cavity of the parent, and thence to the outside world through its mouth. A glandular modification of the ectoderm of the anterior pole of the larva, by means of which the attachment subsequently takes place, can be recognized, whereas the posterior (oral) pole is characterized by the appearance of nettle capsules (CLAUS).

The opaque whitish or yellowish eggs of *Nausithoë* are laid singly, and are characterized by a gelatinous envelope, provided with nettle capsules (O. HERTWIG). Cleavage is here total, and in the first stages unequal, though finally a cœloblastula with walls of nearly uniform condition is produced by the gradual obliteration of the great differences in size between the blastomeres. The blastula changes into an oval, ciliated swarming larva, the cells of which are thickened at the posterior pole, where the gastrula invagination takes place. After invagination the blastopore becomes completely closed. METSCHNIKOFF (No. 12), to whom we owe the knowledge of these processes, was able to observe the attachment of the planula, which is accompanied by the development of a discoid basal expansion, and its metamorphosis into a small scyphopolyp provided with four tentacles and covered with a thin layer of periderm, so that metagenesis has been proved for this form also. METSCHNIKOFF believed that he was justified in assuming that the Spongicola fistularis of F. E. SCHULZE (Stephanoscyphus mirabilis, ALLMAN), which is parasitic in sponges, and in which KOWALEVSKY seems to have observed a kind of strobilization, is the Scyphistoma form of Nausithoë.

Strobilization.—The simplest form of reproduction of young medusæ is represented by the *monodisc strobila* (Fig. 59 *A*), occasionally observed even in Aurelia. In this case only one young medusa (*Ephyra*) separates from the Scyphistoma. While the adoral tentacle-bearing portion of the scyphopolyp is by gradual changes converted into the form of the Ephyra, it becomes separated by means of a circular, transverse furrow from the basal portion of the body, and finally detaches itself completely. The basal remnant can, by regeneration of the oral portion, grow again into a complete

scyphopolyp, and subsequently go through the process of
strobilization again, and so on.

In most cases, however, new transverse furrows make
their appearance on the basal part before the detachment of
the first Ephyra, so that on the elongated cup of the scypho-
polyp a whole set of Ephyræ (ten to thirty) are developed at
approximately the same time; but of these any one that is
nearer to the base of the polyp is younger than those distal
to it (*polydisc strobila*) (Figs. 56 and 51 6—10). In this case
also the basal portion finally reproduces both a circle of
tentacles and the oral part of a scyphopolyp, and is thus
enabled to continue its existence as a scyphopolyp when
the production of Ephyræ ceases. A polydisc strobila can
be derived from a monodisc. In the former new transverse
divisions follow one another so rapidly that a large number
of Ephyræ are in process of development at the same time.

The oral portion of a scyphopolyp, in metamorphosing
into an Ephyra, must undergo certain changes, part of
which make their appearance before the first indication of an
abstriction is produced by the circular furrow. The most
important internal change is introduced by the disappearance
of the septa and the peripheral communication between the
four gastral pouches which is thus brought about. Since
the entodermal columns of the four septal tentacles are con-
tinuous with the walls of both the gastral pouches adjoining
the septum (p. 111), there is produced at this place a con-
nection between the neighbouring gastral pouches. At this
point a small perforation now arises in the septum (Fig. 54
so), but this very soon widens to such an extent that only
the thickened inner margin of the septum, which is tra-
versed by the septal infundibulum, is preserved (Fig. 57
so). By the formation of these *septal ostia*, the four gastral
pouches coalesce into a common peripheral gastral chamber
(*peripheral intestine*) [*Kranzdarm*]. The four septal infundi-
bula, clothed by an entodermal covering (remains of the
septa), now traverse the gastral space in the form of four
columns (*columellæ*), which are not attached to the wall of
the central stomach except at its bottom.

A further change is brought about by the disappearance

of the Scyphistoma tentacles and the growing out of the
margin of the peristome into a lobed crown consisting of
eight (four perradial and four interradial) marginal lobes
(Fig. 56). Since the marginal lobes are not formed by the
outer body-wall alone, but contain a corresponding diverti-
culum of the entodermal sac, the peripheral gastral chamber
in this way acquires eight blind sacs: the *lobe-pouches* (Fig.
58 *l*). The marginal or *primary lobes* [*Stammlappen*] soon
develop three processes at their ends, of which the middle
one buds forth from the sub-umbrellar part of the
lobe at some distance from the margin,
and becomes the *sensory body* [*Sinneskolbe*]
(*sk*), while the two lateral processes bud
forth from the margin and become the *alar
lobes*. Inside of these are found the *alar
pouches* (Fig. 58 *f*) as prolongations of the
lobe-pouches; in the sensory body also
there is found a prolongation of the gastral
entodermal layer, which is destined to pro-
duce the otolith crystals.

The peripheral gastral chamber up to
this time was simple and undivided, and at
its periphery ran out into the eight lobe-
pouches. Since the disc of the developing
Ephyra is always flat, the upper and lower
(ex-umbrellar and sub-umbrellar) walls of
the peripheral gastral chamber are very
close to each other, and these two walls

FIG. 56.— Strobila
polydisca of *Aurelia
aurita*. On the up-
permost Ephyra the
Scyphistoma ten-
tacles in process of
degenerating.

now grow together from the margin inwards from sixteen regions
of the circumference [the shaded areas in Fig. 58], and thus
form sixteen radial fusions or concrescence-bands, which are
situated *sub-radially* (*i.e.* between the per-, inter-, and adradii).
In this way the marginal part of the peripheral intestine is
separated into sixteen *marginal pouches* (radial peripheral
pouches, Fig. 58 *m*), which are separated from one another
by the concrescence-bands (cathammata). Eight of these
marginal pouches are situated in the per- and interradii, and
are continuous with the lobe-pouches, while eight others
are adradial and interpolated between the former. In later

stages the marginal pouches become narrower and move
apart; the sixteen regions of fusion [cathammata] thus
spread out into a bilaminar plate, which connects all of the
marginal pouches with one another: the *medusoid, vascular,*
or *cathammal plate.*

The detachment of the Ephyra now takes place, and from
this time on it moves about freely by rhythmical contractions
of its discoid body, the former point of attachment being
directed upwards, and the manubrium downwards (Fig. 51,
11). The columellæ, which are frequently the means of the
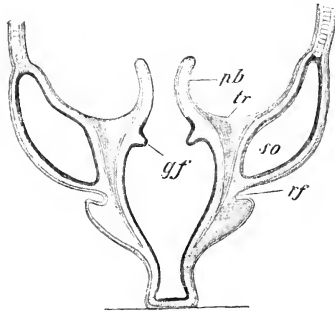final connection with the nurse form, now degenerate. It

Fig. 57.—Interradial longitudinal section through an Ephyra monodisca, with
the Scyphistoma tentacles still retained (diagram modified from GOETTE). *pb*,
proboscis; *tr*, septal funnel; *gf*, gastral filament; *so*, septal ostium; *rf*, constrict-
ing annular groove.

is probable that the last metamorphosed remnant of the
septal infundibula can be recognized in the four sub-genital
cavities (p. 122) lying on the sub-umbrellar side below the
gonads of the medusa. With the degeneration of the
columellæ the boundary between the central stomach and the
peripheral intestine entirely disappears, and the boundary
at which the ectoderm of the œsophagus is continuous with
the entodermal lining of the peripheral intestine is indicated
only by means of four tentaculoid gastral filaments (Figs.
57, 58 *gf*), which have budded forth at the bases [oral ends]
of the columellæ.

The Ephyra (Fig. 51, $_{11}$ and $_{12}$, and Fig. 58), accordingly, possesses a flat, discoid body, from the under-side of which the manubrium hangs down. The margin is prolonged into bifid *marginal lobes*, each one of which bears a sensory body between its alar lobes. Four of these are perradial, and correspond to the radii of the oral cross, whereas the four interradial ones fall in the radii of the gastral filaments. The
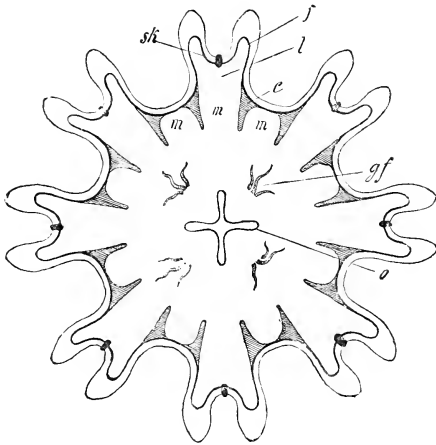

Fig. 58.—Diagrammatic figure of an embryo of an Ephyra. *o*, cruciform mouth-opening; *gf*, gastral filaments; *l*, lobe-pouches; *f*, alar pouches; *c*, cathammata, or regions of fusion of the peripheral intestine; *sk*, sensory bodies.

broad, flat gastral space is prolonged into sixteen peripheral marginal pouches, which are connected by means of the vascular plate. Of these pouches the eight perradial and interradial ones are directly continuous with the lobe-pouches and alar pouches. The ectoderm on the oral side of the disc (sub-umbrella) forms a broad, band-like circular muscle, while paired longitudinal muscle-bands stretch along the marginal lobes and into the alar lobes.

Hypogenetic Development of the Larvæ of Pelagia.
—Schneider (No. 113) and Haeckel (No. 107) have already

observed that the scyphopolyps of Aurelia aurita, when they are placed in unfavourable conditions (for example, in aquaria), show little inclination to form polydiscous strobilæ, but frequently develop only monodiscous strobilæ (Fig. 59 *A*). In fact, HAECKEL observed in certain cases that the transverse division of the scyphopolyp metamorphosing into an Ephyra is altogether sup-

pressed, so that the entire body of the larva is converted into the adult animal. This is HAECKEL's so-called *Ephyra pedunculata* (Fig. 59 *B*), which was observed in the attached as well as in the free-swimming condition. Here therefore the alternation of generations is omitted, and a simple metamorphosis (hypogenesis) has taken its place.

The latter condition is the normal and only one in *Pelagia noctiluca*, the development of which has been made known through KROHN (No. 109), KOWALEVSKY, and METSCHNIKOFF (No. 12). In this case there is first formed a blastula which has a large cleavage cavity, and soon becomes covered on the surface with flagella. At the same time an invagination from the posterior pole is formed, which leads to the development of a gastral cavity
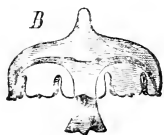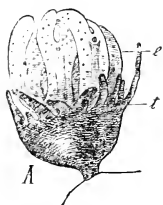
FIG. 59.—*A*, Strobila monodisca of *Cyanea capillata* (after P. J. VAN BENEDEN); *e*, lobes of the Ephyra; *t*, newly formed circle of Scyphistoma tentacles on the basal portion.

B, Ephyra pedunculata of *Aurelia aurita* (after HAECKEL).

which does not by any means completely fill the space of the primitive cleavage cavity (Fig. 60 *A*). The blastopore does not close, but becomes the mouth of the larva. A shallow depression is very soon noticeable at the posterior end of the free-swimming larva, in the middle of which the part surrounding the mouth projects in the form of a cone (Fig. 60 *B*). This projection becomes the oral cone of the Ephyra (Fig. 60 *C*, *m*), and the circular depression surrounding it the umbrellar cavity, while on the peripheral margin a division into eight marginal lobes is soon noticeable, into which

the gastral cavity is continued in the form of lobe-pouches (Fig. 60 C). After the Ephyra shape has thus found expression in the region of the oral pole, the larva shortens in the direction of the chief axis, and gradually assumes the flat, discoid form of the Ephyra. Meantime the larva loses the covering of flagella, and from now on moves like a medusa by the regular contractions of the margin of the disc. In Pelagia accordingly the larva coming from the egg passes directly into the Ephyra, although GOETTE has pointed out that, owing to its structure, we must regard the first stages of this metamorphosis as free-swimming Scyphistoma stages.
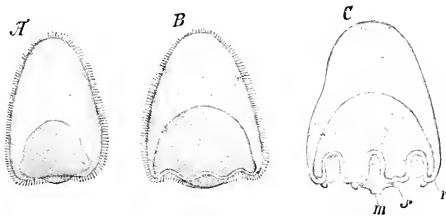

FIG. 60.—Three stages of development of the free-swimming larva of *Pelagia noctiluca* (after KROHN). *r*, marginal lobes; *s*, sensory bodies; *m*, mouth-opening.

Metamorphosis of the Ephyra.—The metamorphosis of the Ephyra is accompanied by a constant increase in the size of the body. The sensory bodies of the Ephyra become the eight marginal bodies [rhopalia] of the medusa. Since the adjacent alar lobes, from which the *ocellar lobes* arise, do not continue to grow with the same rapidity as the rest of the body, new structures, corresponding in position to the adradial regions, are developed in the margin (adradial or intermediate marginal lobes).

The simplest conditions directly referable to the Ephyra are found in the Ephyropsidæ (Nausithoë), in which the sixteen alar lobes of the Ephyra are retained comparatively well developed, while eight adradial (intermediate) tentacles alternate with these. The pocket-like marginal pouches separated by narrow concrescence-bands (CLAUS) and the absence of arm-like prolongations of the angles of the mouth are so many characters derived directly from the Ephyra. In the families of the

Pelagidæ and Cyanidæ also the original character of the gastrovascular system is preserved, the sixteen marginal (radial) pouches being retained as broad spaces separated by only narrow concrescence-bands, and not communicating by any circular sinus. More complicated conditions are found in the Aureliidæ, the metamorphosis of which from the Ephyra has been accurately described by CLAUS (No. 102 and No. 3) for Aurelia and Discomedusa (Umbrosa). In Aurelia the enlargement of the disc is accompanied by the development of eight intermediate (adradial) marginal lobes, on the ex-umbrellar surface of which numerous short tentacles, arranged in a single series, are developed (Fig. 61 i). While
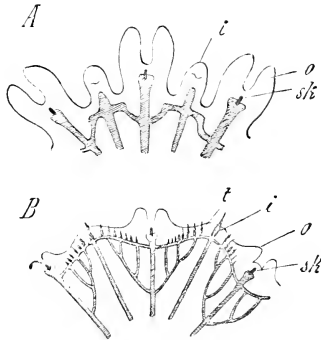

Fig. 61.—Development of the margin of the disc and the canal system of *Aurelia aurita* (after CLAUS). *A*, quadrant of an Ephyra disc 3 mm. in breadth; *B*, quadrant of a young Aurelia with a disc 9 mm. in diameter; *i*, intermediate (adradial) marginal lobes; *o*, ocellar lobes; *sk*, sensory bodies; *t*, tentacles (somewhat removed to the ex-umbrellar side).

the disc thus gradually enlarges, the sixteen marginal pouches grow out into elongated, narrow radial vessels, between which the concrescence-bands extend as broad areas of the vascular plate. By the separation in places of the two lamellæ of this plate, secondary canals are developed, by means of which there is formed first a zigzag, and subsequently a peripheral circular communication between the different radial vessels (*ring sinus*), besides numerous lateral branches of the radial vessels (Fig. 61). The four oral arms, beset with papillæ, arise as outgrowths from the four angles of the mouth. That which especially interests us in the metamorphosis of the Ephyra of Rhizostoma, made known by CLAUS (Nos. 3 and 103), is the metamorphosis of the oral stalk (manubrium). The broadened ends of the four oral arms grow out into bifurcate lobes, thus producing the fundaments of the eight oral arms, while by a similar process of growth at the ends of these the fundaments of the

dorsal tufts [*Dorsalcrispen*] of the lower part of the arm arise. The fundaments of the shoulder tufts [*Schulterkrausen*], or scapulettes, arise in pairs as papillary elevations in the eight radii, and only subsequently assume an adradial position (CLAUS). The lateral margins of the arms, which are bent under, now grow together, so that there arise from the brachial furrows closed canals, which open to the outside world by means of the so-called funnels, rhizostomes or oscula suctoria (originally lateral folds of the margins of the arms). As the last trace of the mouth, closed by concrescence, we find the central cruciform oral raphe.
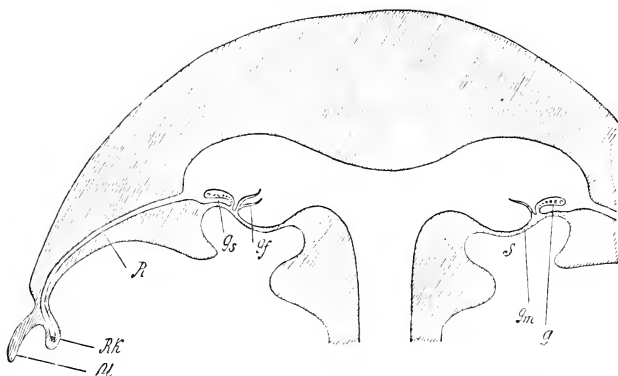

FIG. 62.—Diagram of an interradial longitudinal section through a Scyphomedusa (based on a figure by CLAUS). *R*, radial vessel; *Rk*, marginal bodies [rhopalia]; *ol*, ocellar lobes; *Gs*, genital sinus; *G*, genital band; *Gf*, gastral filaments; *Gm*, gastro-genital membrane; *S*, sub-genital sinus.

An account of the metamorphosis of one of the Versuridæ (Stylorhiza punctata) has been given by v. LENDENFELD (No. 110).

We have still to mention certain organs which are developed at the places originally marked by the four degenerating columellæ, *i.e.* in the interradii. These are, first of all, the *gastral filaments* and the *genital band*. In the youngest Ephyræ only one of the gastral filaments, which originally budded forth as tentacle-like growths at the base of the columellæ (Fig. 57 *gf*), is found in each interradius. However, their number is soon increased (Fig. 58 *gf*), and finally numerous filaments occur, usually arranged in a curved line corresponding to the inner side of the

genital band (Fig. 62 *G*), which is now developing as a fold
of the gastral wall. The sexual products arise from elements
of the wall of this fold, are ripened (Fig. 62) between its
two lamellæ, and by the dehiscence of the wall pass into the
gastral cavity, whence they reach the outside world through
the mouth. The space underlying this fold and communi-
cating with the gastral cavity is called the *genital sinus*
(Fig. 62 *Gs*). The genital band, which is usually horse-
shoe-shaped, is often interrupted at the interradius, so that
we then find in the four interradii eight paired *gonads*,
which are often more or less adradially placed, a condition
which probably must be looked upon as the primitive one.
With the progressive increase in the thickness of
the mesogloea, which grows, principally at the four corners of
the mouth, into massive pillars, there is in the interradial
region a more and more marked development of an invagina-
tion of the outer surface of the body, which is called the
sub-genital cavity (Fig. 62 *S*), and in its earliest beginnings
is perhaps to be referred to the cavity of the septal infundi-
bula. While, accordingly, the body-wall of the medusa is
thickened by an increase of the mesogloea all around this
place, it here remains as a very thin *gastro-genital membrane*
(Fig. 62 *Gm*), which in many forms (*e.g.* Pelagia) shows a
tendency to protrude outwards like a hernial sac, so that
in this way a *genital sac* (*gastro-genital pouch*) projecting into
the sub-genital sinus is developed.

While one might conclude from the structure of the adult genital band
that it was developed by a simple folding of the sub-umbrellar wall of
the stomach, the investigations of v. LENDENFELD and HAMANN show
that the earliest fundament of the genital band is merely a thickening
of this wall, and that an elevation of this thickening in the form of a
fold does not take place until later, when an invagination pushes forward
more and more from the distal side, thus producing the genital sinus.

General Considerations.—The fact that in the eggs
of most Scyphomedusæ a Scyphistoma stage is first de-
veloped, and that this stage is also indicated in the modified
development of Pelagia (GOETTE), shows that we must
imagine the ancestral form of the Scyphozoa as an attached
Anthozoa-like polyp, which originally possessed, in addition

to the power of sexual reproduction, that of non-sexual reproduction by budding and division. In reproduction by means of transverse division, the basal peduncular end of the divided polyp must have reproduced a new oral part, whereas the detached oral portion had to move away from the place of its origin and seek a new place of attachment. Before it could attach itself, however, it must by growing have reproduced the apical part of the goblet-shaped body and the stalk, so that in this way there arose two individuals of the same form as the parent. In this migration of one of the offspring of the division was furnished the motive for its metamorphosis in the direction of an increased power of locomotion, whereby a difference between the form of the attached *polyp* and that of the free-swimming *medusa* was initiated. From what has been said it is not to be wondered at, that the two forms are connected by gradual transitions; nevertheless we shall have to adhere theoretically to the differences of these two morphological conditions. The medusa is therefore a morphological phase of the Scyphozoa which has proceeded from the scyphopolyp; but, owing to the assumption of free locomotion, it is more highly developed, the presence of sensory bodies and marginal lobes and the more highly organized musculature of the sub-umbrella, with concomitant increase of the elastic mesogloea of the umbrella, being characteristic of it.

In the Calycozoa the scyphopolyp reaches its highest phase of development, whereas the Peromedusæ are to be looked upon as the most primitive medusa forms. The latter still reproduce the elongate bell-shaped form of the umbrella, with its apical, stalk-like process, derived from the attached polypoid ancestral forms, and in the possession of large septal funnels resemble the scyphopolyps, whereas the development of the margin of the umbrella marks them as medusæ. In contrast to them, the Ephyropsidæ and the corresponding larval Ephyra form appear as a further stage in the developmental series, in which the apical, elongate bell-shaped part of the umbrella and the peduncular rudiment have been lost, and in which the septal funnels have degenerated. We must explain the four interradial points

of adhesion (septal nodes, HAECKEL), which are present in the Ephyropsidæ on the external side of the row of gastral filaments, as the remains of the columellæ corresponding to these funnels. The Semæostomæ and the Rhizostomæ are derived by further metamorphosis from the Ephyra form.

If we imagine that in the above-supposed attached ancestral form a division of labour made its appearance of such a nature that the power of non-sexual reproduction was retained by the attached scyphopolyp form, while the generation of the sexual products was confined to the free-swimming (medusa) forms, resulting from the transverse division, the origin of the kind of alternation of generations characteristic of the Scyphomedusæ would in this way be explained.

Whereas the tendency formerly was to unite the Hydrozoa and Scyphomedusæ into a common group, in more recent times our conception has led to a complete separation of these two divisions. O. UND R. HERTWIG's (No. 9) doctrine of the diphyletic origin of the medusa form and their distinguishing between Ectocarps and Entocarps first prepared the way for this separation. Although various persons, especially CLAUS (No. 102), had previously placed importance upon the presence or absence of the tæniolæ, which are also possessed by the polyps, as characteristic differences, nevertheless the sharp separation between the scyphopolyps and the hydropolyps was first established by GOETTE (No. 105). On the other hand, the observations of GOETTE, especially the discovery of the ectodermal nature of the œsophagus in the Scyphistomæ, have led to approximating this group to the Anthozoa, so that recently various authors (LANG, HATSCHEK), in accord with GOETTE, have united the two groups as *Scyphozoa*. It must be mentioned, however, that the scyphopolyps are separated from the Anthozoa by the possession of septal infundibula, and by the ectodermal origin of the longitudinal muscles, to which are to be added as distinctive characters differences in the origin of the first four gastral pouches and many differences in general histological character—greater development of the mesodermal tissue in the Anthozoa. Even though we

assume, then, that Scyphomedusæ and Anthozoa are descended from a common polypoid ancestral form which was already characterized by the possession of an ectodermal œsophagus, still the direct union of the two groups does not seem to be as yet sufficiently established.

General Considerations on the Cnidaria.—The Cnidaria constitute a very homogeneous, well-defined branch of the animal kingdom. We assume that the fundamental and ancestral form from which they are derived was a polyp similar to Hydra, the chief axis of which was the same as in the preceding free-swimming ancestral form. A free oral pole and a pole of attachment can be distinguished. The latter corresponds to the anterior pole of the free-swimming ancestral form. The radial type in the structure of the Cnidaria has arisen in connection with the attached mode of life, whereas in many Cnidaria, as the result of stock-formation, a bilaterally symmetrical type is secondarily developed. It appears that even the ancestral form of the Cnidaria had developed the quadriradial structure, so that those forms in which, on account of the arrangement of the tentacles, no definite secondary axes can be recognized, like the *Corynidæ* and *Clavidæ*, would represent a secondary modification. The growth of the Cnidaria frequently takes place by the typical intercalation of new radii between those already present (HATSCHEK).

The Hydrozoa are derived directly from this Hydra-like ancestral form (*Archihydra*), whereas the common ancestral form of the Anthozoa and Acraspeda is developed from it by the formation of an ectodermal œsophagus and radial septa. The presence of the longitudinal muscles in these septa indicates that they were developed in connection with the attached mode of life. In the ontogenetic series, it is true, the septa often make their appearance before the attachment and before the development of the tentacles, from which GOETTE concluded that there was an ancestral form, called a *Scyphula*, common to the Anthozoa, Acraspeda, and Ctenophora, which was characterized by a free-swimming mode of locomotion and by the possession of an œsophagus and radial septa. It is possible, however, that

ontogeny does not represent the primitive condition in this regard.

The attached polyp form recurs in the ontogeny of most Cnidaria. In the Anthozoa and Lucernaridæ it constitutes the adult animal; in the Hydrozoa it is co-ordinate with the Hydromedusa; whereas in the Acraspeda, in comparison with the highly developed medusa form, it must instead be considered as the young stage. Many medusæ (Tracheomedusæ, Pelagia) develop directly from the free-swimming larvæ into the medusa (comp. pp. 53 and 118). But here also certain conditions of development can be interpreted as modified polypoid stages.

The development of free-swimming sexual forms (medusæ) did not take place until after the separation into hydropolyps and scyphopolyps, and therefore occurred in the two groups independently. The differences in organization between the hydroid- and scyphopolyps are explained by the different structure of their polyp forms and by their independent development. The hydroidmedusa is developed as a lateral bud, whereas the strobilation of the Scyphomedusæ is to be explained as a process of transverse division. The medusa must be explained as a polyp which acquired powers of free movement, and as a result of this underwent certain changes in form. The first cause for the evolution of such locomotion we have recognized in the migration which in non-sexual reproduction (division, budding) the detached portion must undertake before attaching itself.

An opposite explanation, which is based chiefly on the occurrence of hypogenetic forms, and which sees in these the more primitive conditions, starts from a free-swimming medusoid ancestral form, the larvæ of which, also at first leading a pelagic life, had secondarily acquired the attached mode of life and reproduction by budding or division. The polypoid forms would then have to be considered as cœnogenetically interpolated larval conditions (C. VOGT, No. 115 ; BROOKS, No. 17). However, the entire structure of the medusæ points to a primitive attached ancestral form too clearly for us to grant this interpretation.

In the search after those hypothetical free-swimming ancestral forms which preceded the attached Hydra-like form, we must first think of such creatures as are repre-

sented in the ontogeny of Pelagia, for example, by the stage of the gastrula invaginata, *i.e.*, a ciliated, ovoid, free-swimming form, in which an archenteron opening to the outside world by means of the prostoma was developed by an invagination at the posterior end.

It can easily be explained how an ovoid blastula-like heteropolar ancestral form happened to develop the earliest beginnings of the archenteric invagination at the posterior pole of its body. In the case of monaxial, heteropolar blastular larvæ which are allowed to swim through water containing particles of carmine, it can be seen that these particles are repulsed at the anterior and lateral parts of the body by the movements of the larvæ, whereas they are crowded together at the posterior pole. Here accordingly was a favourable place for the reception of particles of food, and by a flattening or shallow invagination of the posterior pole these favourable conditions were increased. The archenteron therefore in its earliest beginnings was a pit in which to catch particles of food.

If we incline to the view that the hypothetical ancestral form of the Cnidaria was similar to the gastrula invaginata, then in most Cnidaria we must assume a secondary change in the ontogeny, for *the typical larval form of the Cnidaria is the planula*, a form in which we can recognize a ciliated ectoderm and a more or less compact entodermal mass within. The taking of food is here suppressed. This form serves exclusively for locomotion and the consequent dissemination of the species over a larger territory. In attached forms such larval conditions are of great importance for the preservation and distribution of the species. In the interest of this function, the archenteric cavity appears to have degenerated in the planula.

It is probable that the transition from the free-swimming gastrula-like ancestral form to the attached polypoid form was brought about by means of an interpolated creeping stage, which would be recalled by the creeping planula of many existing forms (*e.g* Lucernaria).

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CHAPTER III.

CTENOPHORA.

Tectonic.—The body of the Ctenophore exhibits a *chief* axis, the poles of which are marked, one by the position of the mouth, the other by the sensory organ located at the apex. Perpendicular to this chief axis two mutually perpendicular *secondary axes* can be distinguished; they are of unequal length, and are further distinguished from each other by the dissimilar organs occurring in their course. The plane determined by one of these two secondary axes and the chief axis we designate with CLAUS (No. 4) as the *lateral or transverse plane* (Fig. 63 *aa*), for the tentacles are situated in it, and thus a comparison with the lateral parts of the body of the Bilateria is permitted. This plane is also called by CHUN (No. 3) the infundibular plane, since the part of the gastro-canal system known as the infundibulum attains its greatest dimensions in this direction. In accordance with the comparison with the Bilateria above mentioned, the plane corresponding to the other secondary axis is called the *sagittal plane* (Fig. 63 *bb*), or, according to CHUN, on account of the extensions of the stomach occurring in this direction, the *gastral plane*. The body of the Ctenophore is divided by these planes into four quadrants, all of which, however, are not congruent with one another, as is the case in quadriradial animals, but only the diagonally opposite ones, each quadrant being like a reflected image of the neighbouring ones. Since in radiate animals each radial part (antimere) is divided into two symmetrical halves by the plane of its radius, it follows that in the Ctenophora each quadrant corresponds to only the half of such a radial part, and that it becomes an entire antimere only after the

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addition of a second adjacent quadrant. *Accordingly the Ctenophora are radiate animals with two rays* (FR. MÜLLER, CLAUS). In this case it is impossible, though of no consequence, to determine whether we ought to designate the radii of the sagittal plane as perradii and those in the transverse plane as interradii, or *vice versâ*. By the unequal development of organs lying in the plane of a secondary axis the biradial structure may be converted into the bilaterally symmetrical (for example, in the larval form known as *Thoë paradoxa* by the development of a single tentacle).
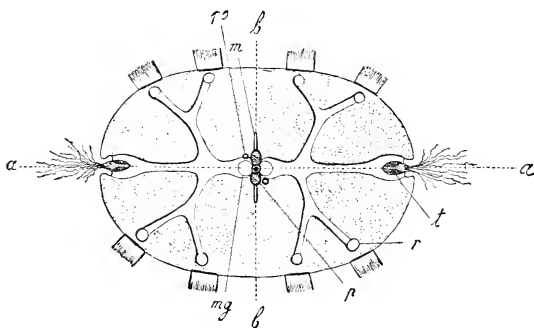
FIG. 63.—Mertensia stage of *Eucharis multicornis* seen from the sensory pole (after CHUN), diagrammatic. *aa*, transverse axis; *bb*, sagittal axis; *m*, stomach; *po*, excretory pores; *p*, polar plates of the apical sensory organ; *t*, tentacular apparatus; *mg*, gastral vessels and *r*, meridional vessels in cross-section.

The bilateral symmetry of two neighbouring quadrants of the Ctenophore suffers a certain derangement by the position of the two excretory pores. For the infundibulum communicates with the exterior by means of two openings situated in the vicinity of the apical pole (Fig. 63 *po*), which lie in two diagonally opposite quadrants. This derangement is, of course, to be explained as the result of the suppression of two pores, for probably there was originally one pore present in each quadrant, consequently four in all, a condition which, according to R. HERTWIG (No. 12, p. 318), is retained in Callianira bialata. There is no essential change in the biradiate structural plan of the Ctenophora owing to this asymmetrical development of the excretory pores, just as in the Bilateria, for instance, an organ is frequently seen to develop asymmetrically without the bilateral type being thereby destroyed (CLAUS).

If we regard one of the cross-axes as the *perradius*, and the other as the *interradius*, we must, in accordance with the terminology employed above (pp. 108, 115) for the medusæ, designate as *adradii* those falling between perradii and interradii, by means of which each quadrant is halved, whereas the eight radii lying between the adradii and the cross-axes should be interpolated as *subradii*. The latter would nearly correspond in position to the eight ribs, and, following the suggestion of CLAUS (No. 4), we shall designate those lying next to the sagittal plane as *subsagittal*, those lying nearer to the transverse plane as *subtransverse*.

Embryonic Development.

The embryonic development of the Ctenophora has been described principally by ALLMAN (No. 2), KOWALEVSKY (No. 14), FOL (No. 7), A. AGASSIZ (No. 1), CHUN (No. 3), and METSCHNIKOFF (No. 16). It takes place in the different species in a nearly similar manner.

The Ctenophora are hermaphroditic. The generation of sexual products takes place either intermittently throughout the entire year, as at Naples, or it is confined to the summer months, as in Northern seas (Trieste, North American coast). The eggs in most cases are deposited singly and fertilized in the sea-water; however, the laying of eggs in strings of about ten each has been maintained for some forms (Pleurobrachia Flem. according to KOWALEVSKY, Bolina according to A. AGASSIZ).

The eggs of the Ctenophora (Fig. 64) are enveloped by a

FIG. 64.—Egg of *Lampetia pancerina* (after CHUN). *ek*, ectoplasm; *en*, endoplasm; *d*, vitelline membrane.

delicate structureless pellicle (vitelline membrane), which (Fig. 64 *d*) is rather widely separated from the surface of the egg. The space thus resulting is filled with a transparent jelly, in which the egg proper is so embedded that it always lies at about the middle. The structure of the latter recalls the eggs of the Siphonophora, Geryonidæ, etc. We can distinguish a superficial layer consisting of formative yolk (ectoplasm, *ek*) and

an endoplasm (*en*) filling the inside. The latter is foamy, owing to the existence of a large number of spherical vacuoles, between which only a scant reticulation and mesh-work of protoplasm (formative yolk) is left. It is very probable that these spherical vacuoles are all filled with a homogeneous, slightly refractive mass, which has sub-stantially the characters of food-yolk. Therefore in what follows we shall occasionally designate the entire endoplasm merely as food-yolk mass. The germinative vesicle is found in the superficial cortex of ectoplasm (Fig. 64).

Even though the cleavage in the Ctenophora, as we shall see, exhibits its peculiarities, yet we can on the whole desig-nate it as total, unequal cleavage, which leads to the forma-tion of an epibolic or circumcrescence gastrula. However, this latter type of gastrulation is not preserved in its purity, for eventually an invagination process participates in the sinking of the entoderm into the embryo.

The first furrows that make their appearance are to be designated as meridional, inasmuch as they cut through from the animal to the vegetative pole in the direction of the subsequent longitudinal axis. By means of the first of these furrows the egg is divided into two equal parts (Fig. 65 *A*); by means of the second furrow, likewise extending in a meridional direction and perpendicular to the first, there are formed four cleavage spheres, arranged crosswise (Fig. 65 *B*, *F*); these are oriented in such a manner as re-gards the embryo resulting from them that each cleavage sphere corresponds to one quadrant of the embryo (FOL, No. 7). The third act of cleavage leads to the appearance of additional meridional furrows, which, as the dotted lines in Fig. 65 *F* indicate, make an angle of 45 degrees with those already present. If this cleavage were to take place regu-larly in the way indicated, eight large cleavage spheres of equal size lying in one plane would result. On the con-trary, the eight-cell stage presents a variation from this regularity which recurs in all Ctenophora, and is import-ant for the subsequent formation of the embryo. For the furrows that now make their appearance are shifted in such a manner that, as is indicated by the dotted lines in

Fig. 65 *G*, each cleavage sphere is divided into a larger and a smaller part. The most striking thing in this is that by the regular paired arrangement of the four smaller cleavage spheres a difference between the cross-axes (secondary axes) of the embryo can already be recognized, so that even as early as this stage the biradiate structure is clearly expressed; and, according to Fol (No. 7), the longer of the two diameters corresponds to the transverse, and the shorter to the sagittal, axis. The transverse plane (infundibular or tentacular plane) therefore separates the embryo into two
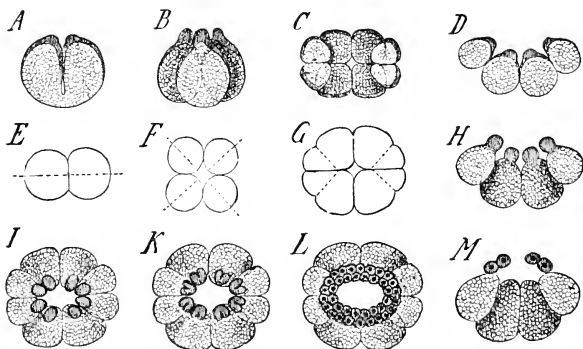
Fig. 65.—Diagrammatic representation of the cleavage of the Ctenophora, based on the figures of A. Agassiz. *A*, stage of division into two cells; *B*, four-cell stage from the side; *C*, eight-cell stage seen from above; *D*, the same in transverse section; *E*, two-cell stage from above; *F*, four-cell stage from above; *G*, plan of the next succeeding division; *H*, transition to sixteen-cell stage; *I*, the same from above; *K*, *L*, succeeding stages with multiplication of the micromeres; *M*, such a stage in cross-section.

rows of four cells each, as is represented in Fig. 65 *C*. Another peculiarity of this stage consists in the fact that its eight cells no longer lie in one plane; the smaller lateral cells move to a higher level, whereby, as can be seen in Fig. 65 *C* and *D*, the entire fundament becomes somewhat basket-shaped. In this way a difference between the two poles of the chief axis is also indicated even now, and the concavity of the basket-like fundament

corresponds, according to METSCHNIKOFF (No. 16), to the so-called upper or future sensory pole. Furthermore a histological difference between the smaller and larger blastomeres of this stage is said to be noticeable, inasmuch as a larger amount of ectoplasm is involved in the formation of the smaller cleavage spheres.

We have designated the furrows appearing up to this time as meridional, because they had the same direction as the chief axis. The next one to appear is, on the contrary, perpendicular to the chief axis (Fig. 65 *H*), and must therefore be called an equatorial furrow. The formative yolk collects in the upper part of the eight cleavage spheres, and is constricted off in the form of small cells (Fig. 65 *H*), so that in this way we obtain a stage composed of eight macromeres, consisting almost exclusively of food-yolk, and eight micromeres (Fig. 65 *I*). Since in many instances the cells of the embryo in this stage separate from one another, leaving a space at the centre, the fundament becomes annular, a ring of eight micromeres resting upon a larger one of eight macromeres. The cavity formed at the centre, which is open above and below, as in the eight-cell and sixteen-cell stages of Sycandra raphanus, we must designate as a cleavage cavity (blastocœle).

Subsequently a rapid multiplication of the micromeres takes place, on the one hand by division of those already
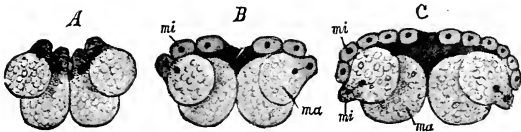
FIG. 66.—Three cleavage stages of a Ctenophore egg (diagrammatic). *mi*, micromeres; *ma*, macromeres (from LANG'S *Lehrbuch*).

present (Fig. 65 *K*) and on the other hand by the abstriction of new micromeres from the underlying macromeres (Fig. 66 *B* and *C*). In this way the annular cell-mass of micromeres continues to spread out, and finally rests like a

cap upon the mass of macromeres, which it covers over (Fig. 65 M, Fig. 66 B and C).

We may from now on consider this cap-like fundament of micromeres, in accordance with its destiny, as ectoderm. It spreads out more and more, especially by the progressive growth of its marginal parts, so that it soon envelops not only the upper portions, but also the lateral parts, of the mass of macromeres (Fig. 66 C and 67 A).

In this way the latter moves more and more into the interior of the embryo, so that we here see a two-layer embryonic form (gastrula) produced by means of circumcrescence or epiboly. Frequently the forward growth of the margin of the ectoderm does not proceed uniformly at all points, but a more active marginal growth is shown at points corresponding to the four radii. Finally the macromeres are seen to be covered by ectoderm on all sides except the lower surface, where the ectoderm still presents a large circular gap (Fig. 67 A), which we may designate as the gastrula-mouth or blastopore. Up to this time the dominant activity of the embryo consisted in the production of ectodermal elements. The macromeres were involved in this only in so far as they constantly budded off new ectodermal elements from their upper surfaces. When the stage last mentioned has been reached, this kind of increase of the ectoderm ceases, and the macromeres from now on become active in another direction. It is noteworthy, in contrast with the considerable multiplication of the ectoderm cells, that up to this time the eight macromeres have undergone no increase in numbers. But now they begin to divide, so that stages with twelve and then with sixteen macromeres can be observed. Afterwards the division of the macromeres becomes irregular. Meanwhile the basket-like arrangement of the macromeres has vanished, and they now form a more placentiform mass (Fig. 67 A).

We have designated the micromeres as ectoderm; we could not, however, employ the term "entoderm" for the macromeres, because, on the one hand, they still contained parts which were to be constricted off by budding and added to the ectoderm, and because, on the other hand, as we know

through METSCHNIKOFF (No. 16), they are also destined to
supply the elements of the mesoderm. For in the present
stage (Fig. 67 A) there is effected a new abstriction from
the macromeres of small elements (me), which we may
designate as mesoderm cells. At first these form a cell-plate,
which lies at the lower, free surface of the macromeres,
when the latter are not yet covered by ectoderm. But in
the stages which now follow (Fig. 67 B and C) certain im-
portant changes are accomplished by means of which this
fundament soon reaches the inside of the embryo. In this
connection we must first glance at the upper pole of the
embryo (Fig. 67 A). Here the embryo still exhibits a small
opening, which in earlier stages (Fig. 66 B and C) was
larger and is to be referred to the inner circumference of
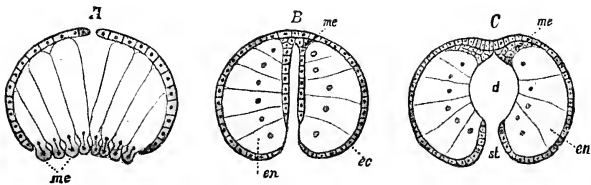
FIG. 67.—Three embryos of *Callianira bialata* in transverse section, diagram-
matic (after METSCHNIKOFF, from LANG'S *Lehrbuch*). *ec*, ectoderm; *en*, entoderm;
me, mesoderm; *d*, intestinal cavity; *st*, œsophagus (fundament of stomach).

the ring of micromeres (Fig. 65 I, K, L). This opening in
the stage of Fig. 67 A is still in connection with a cavity
existing between the macromeres, which we recognize as
the remains of the cleavage cavity. Both the cleavage
cavity and the upper opening in the ectoderm, which has
been erroneously assumed by many authors to be the blasto-
pore, now disappear by the neighbouring cells closing tightly
together. At the same time an invagination of the lower
surface of the macromeres and of the adjacent mesodermal
plate (me) is effected; by means of this a cavity (gastrula
cavity) is formed opening downwards, the lower portion of
which is lined with entoderm cells, the upper portion with
mesodermal elements (Fig. 67 B). In the further course of

development this cavity enlarges (Fig. 67 *C*, *d*), while the
mesodermal elements move upward more and more, and
finally spread out in the form of a plate on the inner surface
of the ectoderm (Fig. 67 *C*, *me*). Meanwhile the circum-
erescence on the part of the ectoderm has made further pro-
gress. Even now it not only covers the under-side of the
embryo, but also grows up into the interior of the gastral
cavity, so that an invagination of the ectoderm (Fig. 67 *C*,
st) arises, which is comparable with the œsophagus of the
Anthozoa, and from which the so-called stomach of the
Ctenophora is subsequently developed.

The statements of the different authors regarding the first stages of
cleavage are essentially in agreement with one another, but in regard to
the later stages, and more especially concerning the orientation of the
embryo, they differ somewhat, the point in question being the determina-
tion of the poles of the chief axis. If in the earlier stages we call that
pole which in our figures is the upper one the micromere pole, and the
opposite one the macromere pole, the disputed point is whether or not
subsequently the micromere pole becomes the sensory pole, and the macro-
mere pole the oral pole. We have adhered to METSCHNIKOFF's descrip-
tion (No. 16), which agrees with KOWALEVSKY's later memoir (*Literature* on
Cnidaria in General, No. 10), because such an orientation seems probable
through comparison with the eggs of mollusca and worms having
unequal cleavage and subsequent epibolic development, and because a
homology of the sensory body of the Ctenophora with the apical plate
of these forms appears thus to be provided for.

The development of all Ctenophora in the stages thus far described
appears to take place in very much the same way. Lampetia pancerina
alone appears, according to CHUN (No. 3), to possess peculiarities,
especially, among others, the existence of a sixteen-cell stage, formed
on a strictly quadriradiate plan, etc.

The embryo has now assumed a nearly spherical form
(Fig. 67 *C*). But the two ends of the chief axis are dis-
tinguished by shallow depressions. In viewing the embryo
from above, one recognizes that the transverse axis still
exceeds the sagittal in length. From now on a growth in
the direction of the chief axis is especially noticeable
(Fig. 68). The embryo thereby becomes more elongated.
Since at the same time the upper end of the body increases
in size, principally by the development of the tentacular

apparatus, a pear-shaped or heart-shaped form is evolved (Fig. 70 *A*).

Hand in hand with these changes goes the differentiation of the ectodermal structures which are characteristic of the Ctenophora : the tentacular apparatus, the ciliary plates, and the apical sensory organ. At an early period are to be noticed in the upper half of the body two ectodermal thickenings (Fig. 68 *t*) lying opposite to each other in the transverse plane; such an abundant multiplication of ectoderm cells occurs in these places, that they become many layers deep. These two thickened areas form each the fundament of a so-called *tentacle base* (Fig. 69 *B*, *tb*). Within the territory of these a ridge, known as the *tentacle stalk* (Fig 69 *B*, *ts*), soon makes its appearance, and out of it arises the fundament of the *tentacle* (*t*). At the same time with the earliest formation of the tentacular apparatus, four rows of cells situated adradially become conspicuous by their active proliferation. These cells are covered with cilia, which at first are short and fine; they begin to beat slowly backwards and forwards, and soon fuse together in such a way as to form the *swimming plates* (Fig. 68 *r*). In this way two rows of swimming plates arise on each of the four fundaments, so that in these first stages the eight ciliated ribs appear grouped in pairs. Originally each rib exhibits only a very few (usually four to six) swimming plates, and, as a rule, their number is not increased until after the abandonment of the egg-membranes. The swimming plates, as has been shown, are to be regarded as fused cilia; they are higher differentiations of a continuous coat of cilia attributable to the ancestors of the Ctenophora. In this connection it is interesting to know that Chun (No. 3) was able to demonstrate on the embryo of Eucharis multicornis a fine ciliation covering the whole surface. Of this ciliation there are retained throughout life only eight fine meridional rows, which extend from the rows of swimming plates to the upper pole of the body, and establish the connection with the sensory body located there. This *apical sensory organ*, which is perhaps to be considered as the centre of the nervous system, is also de-

veloped from a thickening of the ectoderm (Fig. 68). The
otoliths, which are at first small and then increase in size,
are formed in certain of these cells; they are finally
extruded upwards, to constitute the otolithic mass sus-
tained on the four S-
shaped springs (cilia).
In many cases the first
otoliths are formed in
the epithelium in four
groups, corresponding
to the different quad-
rants of the body of
the Ctenophore (A.
AGASSIZ, FOL). The bell-
shaped case developed
over the sensory organ
arises, like the swim-
ming plates, from four
groups of long cilia
fused with one another
(Figs. 68, 70, 72). The
ciliated *polar plates*
(Fig. 63 *p*) are formed
in connection with this
sensory body as thick-

FIG. 68.—Diagram of a Ctenophore embryo
at the time of the formation of the entodermal
sacs, all organs in transverse section, except
the fundaments of the ciliary plates, *r*, which
correspond to the outer surface. *ot*, otoliths;
t, fundament of the tentacular apparatus; *ms*,
mesoderm; *en*, entoderm; *ec*, ectoderm; *g*,
mesoglœa; *m*, stomach; *c*, central intestinal
cavity; *d*, diverticula of the same (fundaments
of the entodermal sacs).

ened regions of the ectoderm, which at first are rounded, but
subsequently much elongated.

We have seen that two parts can be distinguished in the
fundament of the gastrovascular system (Fig. 67 *C*): a
lower, which arose as an ectodermal invagination, the
inner surface of which is soon covered with a coat of
cilia, and out of which the so-called *stomach* subsequently
arises; and an upper (*d*), bounded by entodermal cells, which
represents the fundament of the *infundibulum* and the
ressels. The differentiation of this upper, entodermal
portion into its individual parts can be considered as essenti-
ally a kind of formation of diverticula. As can be seen
in Fig. 67 *C*, the entoderm cells, as the macromeres after
giving off the ectodermal and mesodermal elements may

now be called, exhibit a tendency to orient themselves radially about the central cavity d. Designating the point of transition of the fundament of the stomach into that of the infundibulum as the *inner opening of the œsophagus* or *infundibular fissure*, the increase in the length of the stomach causes this fissure to move into the central cavity, a wall being formed by means of which a central portion of the cavity is separated from a lateral part (Fig. 68). This lateral portion is not retained as a single space, but divides into four diverticula, which, in accordance with their mode
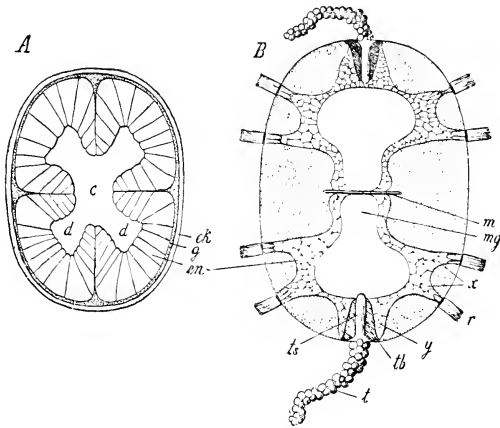
FIG. 69.—Further formation of the gastrovascular system after CHUN). *A*, embryo of *Beroe*, in optical transverse section at the time of formation of the four entodermal sacs; *ek*, ectoderm; *en*, entoderm; *g*, mesogloea. *B*, development of the permanent canal system in an embryo of *Eucharis multicornis*. View from below: *m*, stomach; *mg*, fundament of the gastral vessels; *x*, fundament of the meridional vessels; *r*, ciliary plates; *y*, fundament of the tentacular vessels; *tb* tentacle base [*Tentakelboden*]; *ts*, tentacle stalk; *t*, tentacle.

of origin, communicate at their upper parts with the central infundibular fundament, and have their blind ends directed orally (Fig. 68 *d* and Fig. 69 *A*). Inasmuch as the greater portion of the entodermal cells is grouped about these four blind sacs, it is divided from now on into the four so-called

entodermal sacs, each one of which corresponds to a quadrant of the Ctenophore body. The distinct separation of these four entodermal sacs is materially promoted by the simultaneous appearance of the *mesoglœa* (Fig. 69 *A*, *g*). This transparent secreted mass accumulates between the stomach, the entoderm, and the surface ectoderm (Fig. 68 *g*), and forms septa-like processes, which extend especially between the entodermal sacs. The rapid increase of the mesoglœa, into which cells soon migrate, occasions the considerable increase in the size of the embryo during this stage. By the formation of the mesoglœa in the further course of development, the fundament of the gastrovascular system is forced farther and farther away from the outer surface of the body. An intimate contact is retained only at the points corresponding to the eight ribs and the fundaments of the tentacles (Fig. 69 *B*); by a large accumulation of entodermal cells the places are here indicated at which, by the formation of additional diverticula, the eight rib-vessels (meridional canals) and tentacular vessels are developed. The origin of the two gastral vessels is to be attributed to a similar formation of diverticula (Fig. 69 *B*, *mg*).

The mode of formation of the four entodermal sacs by the deeper penetration of the inner opening of the œsophagus, which has been described by Chun (No. 3) and represented in his Fig. 18, Taf. vii., recalls the quite similar mode of formation of the two primary gastral pouches of the Scyphistoma according to Goette. (Comp. p. 107.)

During these changes the characteristic lateral compression of the stomach has already been effected (Fig. 69 *B*, *m*). On the contrary, the central part of the vascular system, which is metamorphosed into the infundibulum, exhibits a compression, more or less distinct in all Ctenophora, in the direction of the other (sagittal) secondary axis, so that these conditions could be utilized by Chun (No. 3) in designating the cross-axes. The more the vascular system is developed, the more do the entodermal cells acquire the histological characters of the permanent walls of the vessels.

We have traced the fundament of the *mesoderm* until, in the progressing invagination of the gastral cavity, it arrives

at its top, finally to spread out flat on the inner surface of the ectoderm at the apex of the embryo. The plate thus formed, which frees itself more and more from the entoderm, at first elongates only in the direction of the transverse plane; later, however, by a new mesodermal growth from the original centre, a cruciform mesodermal fundament (Fig. 71 *m*) is formed, on which we can distinguish two longer (lateral) and two shorter (sagittal) mesodermal bands. The former are closely applied to the funda-ments of the tentacles (Fig. 70 *A* and *B*), and supply the meso-dermal axes, especially the musculature, of the tentacles, whereas the median (sagittal) bands become the seat of the formation of migratory cells (Fig. 71 *g*), which wander into the mesoglœa and give rise to the cellular elements of the gelatinous tissue by becoming metamorphosed there into stel-late connective-tissue cells and branched muscle fibres.

In regard to the development of the mesodermal structures we have followed exclusively METSCHNIKOFF'S (No. 16) description. Formerly the origin of the elements of the gelatinous tissue was attributed by KOWALEVSKY (No. 14) and CHUN (No. 3) to an im-migration of ectodermal cells (the superficial as well as the gastral epi-thelium). According to CHUN, this immigration does not cease with the embryonal stage, but throughout life adds new muscle elements to the gela-tinous tissue. The immigration of ectodermal elements into the mesoglœa during embryonic life is directly denied

FIG. 70.—Two stages of the de-velopment of *Callianira bialata* (after METSCHNIKOFF, from LANG's *Lehr-buch*). *en*, entoderm; *me*, meso-derm; *me*[1], mesenchyma; *t*, tentacle; *sk*, sensory body; *d*, intestinal cavity; *st*, œsophagus (fundament of the stomach); *g*, mesoglœa.

by METSCHNIKOFF. Accordingly the gelatinous tissue would be essentially a mesodermal formation; and even though in later stages ectodermal

muscle fibres were secondarily to sink into the mesoderm, nothing in the real nature of the gelatinous tissue would be changed by this.
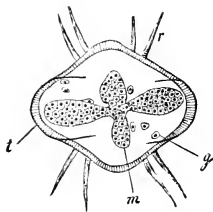
FIG. 71. — Embryo of *Callianira bialata* viewed from above (after METSCHNIKOFF). *r*, ciliary plates; *t*, fundament of the tentacular apparatus; *m*, cruciform mesodermal fundament; *g*, migratory cells in the mesoglœa.

In order to explain the presence of four mesodermal bands, KLEINENBERG (*Literature* Annelida, i., No. 26, p. 13) perceives in them an indication of the existence of four tentacles (two lateral and two sagittal) in the ancestral forms of the Ctenophora, of which those in the sagittal plane have become degenerated. It is interesting to know that in the Beroidæ, which are without tentacles, there exists an entirely similar mesodermal fundament, which extends in the transverse direction at the apical pole, and there comes to lie under two ectodermal thickenings (rudiments of tentacles) (METSCHNIKOFF). The further fate of this mesodermal fundament could not be followed.
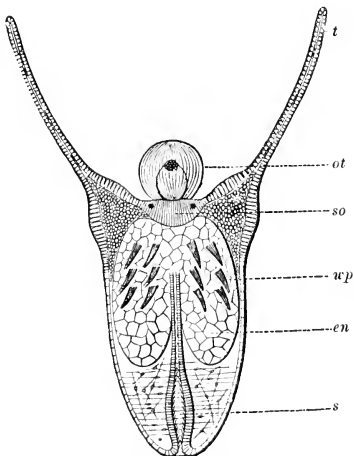
FIG. 72. — Young larva of *Callianira bialata* (after KOWALEVSKY, from HATSCHEK's *Lehrbuch*). *t*, tentacles; *ot*, auditory organ; *so*, apical organ; *wp*, the rows of ciliary plates; *en*, the four entodermal sacs; *s*, œsophagus.

As regards the formation of the sexual organs, which does not fall within the period of embryonic development, but occurs in later stages, R. HERTWIG has shown by his observations on Callianira that it is probable that they are of ectodermal origin. The sexual products, to be sure, ripen directly under the epithelium

of the meridional vessels, but a cord of cells which unites the ectoderm to the sexual organs points to their ectodermal origin. Sac-like invaginations of the superficial epithelium have also been observed, which perhaps represent the original fundaments of genital sacs.

Metamorphosis.—After the proof had been produced by the observations of J. PRICE and JOH. MÜLLER that the young forms of the Ctenophores resemble to a certain extent the adult animals, and that consequently no alternation of generations was interpolated in their life-history, one was inclined to assume for them a direct development. MCCRADY was the first to show the existence of a rather marked metamorphosis by his observation that the young Bolinæ just hatching from the egg were formed after the type of the Cydippidæ. Since then the details of the metamorphosis have become known through the researches of A. AGASSIZ, J. W. FEWKES, and especially of C. CHUN.

Since the *Cydippidæ*, by the absence of anastomoses of the meridional vessels and the blind termination of the gastral vessels, retain throughout life the most primitive type of distribution of the vessels, the metamorphosis in them is simple. Nevertheless it should be mentioned that the Pleurobrachiæ, which are round in cross-section, are compressed in young stages by the shortening of the sagittal diameter, and in this regard recall the Mertensiæ (CHUN). If CHUN's hypothesis is confirmed, according to which the remarkable Thoë paradoxa (which is characterized by the possession of a single extensible tentacle projecting from a tentacle-sheath resembling a chimney-pot near the sensory body) belongs in the life-history of Lampetia pancerina, then a much more elaborate metamorphosis will have to be ascribed to some of the Cydippidæ.

The metamorphosis of the *Lobatæ* has been described by MCCRADY, A. AGASSIZ (No. 1, Bolina), FOL (No. 7, Euramphæa), and FEWKES (Nos. 5 and 6, Ocyrrhoë, Mnemiopsis), and especially in CHUN's (No. 3) extensive presentation of the course of development in Eucharis multicornis. The latter form in particular exhibits a series of larval stages differing from the adult in habit as well as in the course of the vessels. Here again the point of departure is a Mertensia stage having the structure of the Cydippidæ (Fig. 63), with distinctly shortened sagittal and elongated transverse diameters, which is all the more striking since in the adult form the opposite condition in the length of the cross-axes exists. In the *first stage with the fundaments of lobes*, which now follows, a considerable increase in the length of the meridional vessels is noticeable. At the same time the subsagittal vessels become longer than the sub-

transverse ones, and correspondingly the subsagittal ribs exhibit a larger number of swimming plates. In the further course of development the meridional vessels pass into the oral lobes, and their lower ends become bent; in this way the subtransverse vessels come to be the longer. Whereas in the *adult* the lower ends of the vessels in each lobe are united in such a way that the two subtransverse vessels communicate with each other, and the two subsagittal vessels with each other, at *this stage* the subtransverse vessel forms with the subsagittal vessel of the same quadrant a closed system of tubes (Fig. 73).
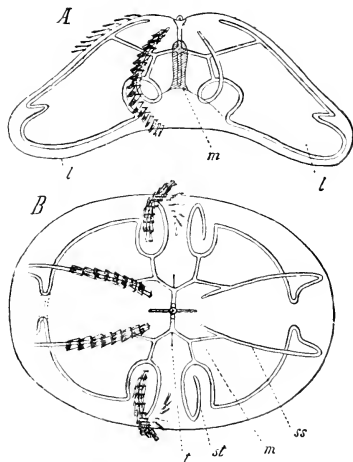
Fig. 73.—Medusiform stage of *Eucharis multicornis* (after Chun). *A*, view of the sagittal plane. *B*, view from above : on the right-hand side the ribs are omitted ; *m*, stomach ; *l*, oral lobes ; *t*, rudimentary tentacular apparatus ; *st*, subtransverse, *ss*, subsagittal, meridional vessel. At *x* the subsequent connection of the vessels is indicated by dotted lines.

There now follows a *stage of medusiform habit*, the course of the vessels remaining about the same (Fig. 73), in which, as in the adult, the sagittal diameter already exceeds the transverse. In this larva, which, like a Medusa, moves through the water by the pulsating action of its oral lobes, a complete degeneration of the tentacular apparatus (*t*) occurs; this is replaced in the succeeding *Bolina stage* by a new tentacular fundament. In this stage is reached the form of body and distribution of vessels typical of the Lobatæ, for, on the one hand, the connection of the subtransverse with the subsagittal vessels is

broken, whereas the vessels of each lobe having the same name come into communication with each other at their lower ends (Fig. 73 *B*, at *x*), and, on the other hand, each gastral vessel, which up to this time ended blindly, sends out two transverse processes at its oral end, which open into the subtransverse vessels of the same side. With the development of (1) the cæcal pouches (characteristic of Eucharis) above the base of the tentacles (metamorphosed tentacle-sheath) and (2) the dermal papillæ the form of the adult animal is reached.

CHUN was able to establish the fact that under certain conditions the Mertensia stage attains sexual maturity, so that the existence of a remarkable *heterogeny* is established for the Ctenophora.

The metamorphosis of the Cestidæ, as CHUN's observations on Cestus show, proceeds from a Mertensia stage quite similar to that of Eucharis. Here also the sagittal diameter is at first shorter than the transverse, although subsequently it so vastly predominates in the ribbon-like body. That which especially characterizes the Cydippidoid early stage of Cestus is the presence of a single swimming plate on each rib, corresponding to
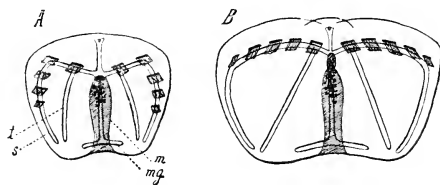
FIG. 74.—Two stages of development of *Cestus veneris* (after CHUN). *A* resembles the Cydippidæ in form : *m*, stomach ; *mg*, gastral vessel, with its processes; *s*, subsagittal *t*, subtransverse meridional vessel ; *B*, somewhat older stage with the ciliary plates in their permanent position.

the uppermost of the four embryonic swimming plates, the lower ones of which become degenerated. The further course of the metamorphosis is tolerably simple. At first the larva is round in cross-section ; then it is flattened in the transverse direction (Fig. 74 *A*), so that the flat ribbon-like shape is more and more expressed. At the same time the short meridional vessels and the gastral vessel grow downward. The latter soon puts forth two transverse processes (Fig. 74 *mg*), which extend parallel to the lower margin of the larva. Of the meridional vessels the subsagittal (Fig. 74 *s*) continue to grow out and become arched, while on their upper parts new swimming plates are formed, which at first are placed at right angles to the meridional vessels, but later (corresponding to the conditions of the adult) are placed with their bases in the direction of the meridional vessel (Fig. 74 *A* and *B*). The ends of the meridional vessels and of the processes of the gastral vessels come together in the lower corners of the now trapezoidal, flattened larva (Fig. 74 *B*) and

there fuse; thus the arrangement of the vessels of the adult animal is reached.

The metamorphosis of the *Beroidæ* described by ALLMAN (No. 2) and A. AGASSIZ (No. 1) takes place in an unusually simple manner. The larva is at first round in cross-section, and later is flattened transversely. Of the meridional vessels the subsagittal first grow the more vigorously, and reach the edge of the mouth, where they meet two processes from the gastral vessel of the same side, which extend along the edge of the mouth, and fuse with them. The subtransverse vessels meet these transverse processes only later, and then the ramifications of the vessels begin to grow forth.

General Considerations.

—The Ctenophora exhibit in their organization a whole series of features by means of which a closer relationship with the Cnidaria—Cœlenterata in the narrowest sense—appears to be established. To this series belong, if we ignore the more superficial resemblances of the gelatinous transparent body, first of all the possession of a very similar gastrovascular system, the presence of tentacles, the bases of which exhibit relations to the canals of this system, the position of the ripening sexual products in these canals, and the similar character of the eggs. In fact, up to the present time the Ctenophora have usually been incorporated with the Cœlenterata; HAECKEL (No. 11), indeed, with whom CHUN (No. 3) concurred, conjectured that the group of the Cladonemidæ, and particularly Ctenaria, which belongs to this group, constituted the intermediate link between the Anthomedusæ and Ctenophora. Even though this genus presents a remarkable resemblance to the Ctenophora in the possession of only two marginal tentacles and corresponding cæcal pouches, in the mesoglœa of the umbrella (tentacle-sheaths), and in the eight exumbrellar nettling ridges corresponding to the ribs, still the view that these resemblances were based upon true homology has been somewhat shaken by HARTLAUB (Nos. 10 and 11), who was able to produce evidence that in the closely allied Eleutheria the brood-cavity lying over the stomach arises as an ectodermal invagination from the cavity of the umbrella, and therefore could not be homologized, as HAECKEL maintained, with the infundibulum of the Ctenophora. Even earlier than this R. HERTWIG (No. 12, p. 444) had produced

important evidence which militates against the derivation of the Ctenophora from the comparatively highly organized and specialized Cladonemidæ.

It appears to us, however, as if it were not these difficulties alone, but rather grounds of a more general nature, that have been influential recently in causing several writers (R. HERTWIG, LANG, and HATSCHEK) to concede a more independent position to the Ctenophora. We have learned to consider the attached polyp, a Hydra-like creature, as the ancestral form and archetype of the Cnidaria, and believe it probable that in this instance the radial structure has been developed in connection with the attached mode of life, as is so frequently the case. Wherever among the Cnidaria pelagic species occur, we can easily refer them to attached forms, from which they have descended. The medusa must therefore be looked upon as a modified polyp that has attained the power of free locomotion. All these pelagic Cnidaria have, however, as evidence that they are organisms secondarily derived from an attached form, the following characteristics: () the loss of the general coat of cilia and the development of new locomotor organs depending upon muscular action; (2) little tendency on the part of the ex-umbrellar portion of the bell to produce any organs whatever. This latter feature of the Cnidarian medusa is connected with the original function of its apical pole as a point of attachment and the former comparatively unexposed and unimportant position of the ex-umbrellar side, which corresponds to the lower surface of the cup of the polyp.

The Ctenophora do not exhibit any polypoid stage in their ontogeny. We would not ascribe too great an importance to the absence of this, for the ontogeny of Geryonia and Pelagia furnishes us with an example of how quickly in an abbreviated development just this stage is blotted out past identification; it is therefore not the circumstance that the ontogeny of the Ctenophora contains no indication of an attached stage, but rather the existence of certain prominent features of organization in the Ctenophora, which makes it seem to us probable that an attached stage has never been interpolated in their series of ancestors. A system depend-

ing upon ciliary motion here functions as the principal
locomotor apparatus. This primitive form of motion ac-
quires in this case an importance and a development such
as exists nowhere else in the animal kingdom, whereas in
the Cnidaria it is not so prominent. The presence of the
sensory organ at the apical pole, which is, perhaps, to be
explained as the central point of the nervous system, makes
it seem unlikely that in any ancestral form there existed
at this point a region of separation, a cicatrized place of
attachment. Furthermore the abundance of organs on the
outer surface of the body (which would correspond to the
ex-umbrella) argues against direct relationships between
Medusæ and Ctenophora.

From what precedes we must conclude as most probable
that the Ctenophora represent an independent stem of the
animal kingdom, which is connected with the Cnidaria
(Cœlenterata in the restricted sense) only at its roots, and
has in common with them only those ancestral forms which
preceded the passage and metamorphosis into the polyp
form. The Ctenophora have most probably always retained
the original pelagic mode of life, and have brought to the
highest state of development the likewise primitive form of
motion by means of cilia, without exchanging it for the
secondary kind of movement by means of muscular action.
If we were to form a picture of the hypothetical pelagic
ancestral form of the Ctenophora, it would probably corre-
spond most nearly to certain Actinian larvæ, which exhibit a
tuft of cilia at the anterior end and the mouth-opening at
the posterior pole, while within, the development of the
gastral pouches has already begun by the formation of
septa. The tuft of cilia at the anterior end of the body
would furnish the starting-point for the development of the
apical sensory organ, while the development of the ribs
would have advanced hand in hand with the further develop-
ment of the gastral pouches.

If, then, we admit that the Ctenophora and Cnidaria have
a common stem only at their very beginnings, the question
arises how far the Ctenophora exhibit relationships to the
hypothetical ancestral form of the Bilateria. Apparently

the assumption of such relations cannot be altogether rejected. The similar position of the central nervous system at the anterior pole of the body in the Ctenophora and many worm larvæ, the production of the mesoderm as a separate germ-layer in the form of four mesodermal bands arranged crosswise, and the high state of development of the mesenchymatous tissue, appear to argue for such an assumption. First of all, there are, as we shall see, many features agreeing with the development of the Turbellaria. Accordingly there do seem to exist certain relationships between the Ctenophora and the hypothetical ancestral form of the Bilateria. Nevertheless we hesitate for many reasons to imagine the latter to be precisely a Ctenophore. In contrast to the Turbellaria, which by the retention of a uniform coat of cilia recall primitive conditions, the Ctenophora represent a side branch of the phylogenetic tree, which has developed independently along one line, but which scarcely furnished the basis for the direct development of higher animal forms.

In the remarkable forms *Cœloplana Metschnikowii* and *Ctenoplana Kowalevskii*, forms directly intermediate between the Ctenophora and Turbellaria were thought to have been recognized (Nos. 13 and 15). However, to us they appear to present only peculiarities that can readily be explained from the typical structure of a Ctenophore as the result of adaptation to a creeping mode of life. The similarity to the Turbellaria would then rest upon mere analogy. Such an explanation is admissible, for even among the true Ctenophora some forms have the power of adhering to firm surfaces and of creeping about by means of the broadened foot-like margins of the mouth (Lampetia), so that the starting-point is here given for development in this direction. The fact that with the degeneration of the ribs (ciliate bands) the general ciliation secondarily came again into prominence ought not to be very surprising, for CHUN and R. HERTWIG have shown that remnants of a general ciliation are retained in the adult condition of the Ctenophora also.

It should be mentioned that in the origin of the four entodermal sacs, in the presence of the four mesodermal bands, in the development of the ribs on four adradially placed ectodermal thickenings, etc., there is manifested a distinct tendency to express its quadriradial structure. Probably the biradial structure of the Ctenophora has been developed from the quadriradial by the different development of each pair of opposite radii, so that the biradial structure does not represent the simplest condition of the radial type, but corresponds to a derived condition.

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CHAPTER IV.

PLATHELMINTHES.

I. TURBELLARIA.

SYSTEMATIC : A. DENDROCŒLIDÆ, with branched intestine.
    (a) *Polycladida*, with a median chief intestine, which gives off numerous branches.
    (b) *Tricladida*, without chief intestine; three intestinal branches are directly attached to the pharynx.

B. RHABDOCŒLIDÆ, with straight unbranched intestine or without intestine.
    (a) *Rhabdocœla*, with a spacious cavity in the region of the intestine.
    (b) *Alloiocœla*, the cavity in the intestinal region reduced by the great development of the parenchymatous tissue.
    (c) *Acœla*, without distinct intestine.

THE Turbellaria which inhabit the land and fresh water (*Tricladida* and *Rhabdocœla*) as well as many marine forms (*Polycladida*) have a direct development, whereas other Polyclads undergo a metamorphosis in which there is a free-swimming ciliated larva. The development best known is that of the Polyclads, and of these we will first consider the forms which develop directly. Closely related to these Polyclads are those with a metamorphosis, for in the latter the embryonic development proceeds in much the same way as in the former. The embryonic development of the Triclads, on the contrary, is different, while that of the

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Rhabdocœles in turn resembles that of the Polyclads; the
Rhabdocœles are, however, like the Triclads in the produc-
tion of yolk cells.

I. Polycladida.

A. Direct Development.

The development of the Polyclads has been described,
chiefly in the works of Goette (No. 3), Hallez (No. 6),
Selenka (No. 20), and Lang (No. 13).

The eggs, united by means of a slimy secretion, are usually
laid in the form of a unilaminar plate, in which they lie
more or less regularly side by side. In the *Euryleptidæ* they
are attached to some support by means of a stalk (Selenka,
Lang). Ordinarily each egg is surrounded by a thin shell,
which in some cases (*Pseudoceridæ*) is provided with an
operculum. Fertilization, which sometimes takes place after
oviposition, is usually preceded by the formation of the two
polar globules. These do not separate at once from the egg,
but remain united to it by means of yolk-substance. The
spermatozoön then passes between them in penetrating into
the egg. Such is the process in *Thysanozoön*, according to
Selenka's observations. Since only *one* spermatozoön is
bestowed upon each egg, the act of fertilization in this
instance seems always to be accomplished with great cer-
tainty.

Cleavage is unequal. Even the first two blastomeres are
of different sizes. Each of them divides into two, and
these four blastomeres also differ in size. Owing to their
differences in position and size, the various regions of the
body of the embryo, it is said, are already indicated. At
first the two smallest blastomeres lie crosswise over the
larger ones (Fig. 75 *A*). They indicate the upper, aboral
pole, a conclusion which is confirmed by the polar globules,
since these lie above them, whereas the two large blasto-
meres correspond to the lower, oral pole. Furthermore it
is shown that even thus early the anterior end of the animal
is indicated by the smaller of the two large blastomeres,
the posterior end by the larger one, and that the two
smallest blastomeres correspond to its sides.

After the four blastomeres have arranged themselves in one plane, a small cell buds forth at the upper [aboral] part of each cell. In this manner four cells arise, from which subsequently the entire ectoderm takes its origin (Fig. 75 *B*). As soon as the four primitive ectoderm cells have come close together, again four cells, the primitive mesoderm cells, are budded off at the aboral pole of the large blastomeres. These cells lie in such a position that they are not covered by the ectoderm cells (Fig. 75 *C*). The ectoderm cells then increase to the number of eight. Four additional mesoderm cells have meantime been constricted off from the large blastomeres, and the four already present have divided into eight. Ectoderm and mesoderm in the form of a cap overlie the four large blastomeres, which from now on must be considered as entoderm (Fig. 75 *D*). At the lower pole of these four primitive entoderm cells four smaller entoderm cells are constricted off, a process which is repeated, and in the same manner, at the upper pole (Fig. 75 *E*). We will state at this point that it is the upper and lower entoderm cells which supply the intestinal epithelium, whereas the large middle ones constitute a kind of food-yolk and soon disintegrate (Fig. 76 *A* and *B*). Even before the division of the primitive entoderm cells has taken place, the cells of the ectoderm have considerably increased in number. They move downward and begin to grow over the mesoderm cells. Fig. 75 *E* and *F* show these conditions in a diagrammatic way. The further growth of the ectoderm now proceeds rapidly, and the entoderm and mesoderm are soon entirely covered by it. The formation of the epibolic gastrula is herewith completed. The ectoderm becomes covered with a dense coat of short cilia, and the embryo begins to rotate in the egg-shell.

We have represented the cleavage as LANG figures it for *Liscocelis tigrina*. Although differing in details, it still agrees on the whole with the processes as they have been described for other *Polyclads* (*Leptoplana, Eurylepta*) by HALLEZ and SELENKA. The differences relate to the formation of the mesoderm and entoderm. As regards the former, four mesoderm cells are constricted off only once from the large blastomeres ; and these by division then give rise to the mesoderm. According to

SELENKA, entoderm cells are formed at the lower pole only of the large blastomeres. According to GOETTE (in *Stylochus*), such a differentiation of the mesoderm as is described by other authors does not take place. The cells, which in his figures seem to correspond to the mesoderm cells, he considers as ectoderm. According to GOETTE, *Stylochus*, in which the development of a mesoderm has not yet taken place, represents a
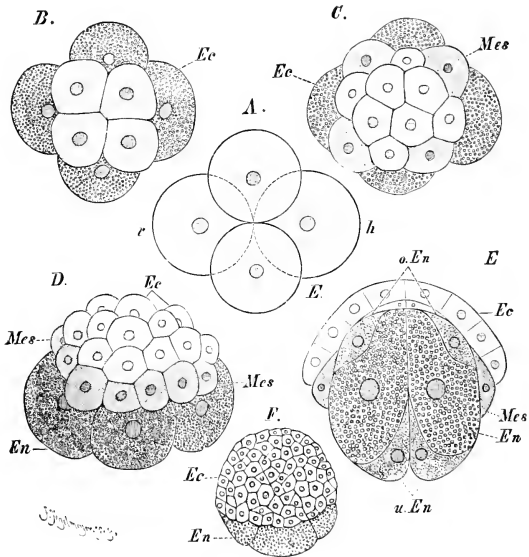
FIG. 75.— *A* to *F*, cleavage stages of the eggs of Polyclads (after LANG). *A*, diagram of a stage of four blastomeres, of which the two larger ones correspond to the anterior (*v*) and posterior (*h*) parts of the body, the smaller ones, lying above them, to the sides of the body; *B* to *D*, more advanced stages of *Discocelis tigrina*, *B* and *C* seen from above, *D* from the side; *F*, later stage of the epibolic gastrula of *Thysanozoön Brochii*, seen from the side. *Ec*, ectoderm; *En*, entoderm; *o. En* and *u. En*, upper and lower entoderm; *Mes*, mesoderm.

more primitive condition than the rest of the *Polycladida*. This condition follows as a result of the shape of the entoderm. The central entoderm cells do not in this case become food-substance, but with the others form the wall of the intestine (Fig. 76 *C*). Everything enclosed by ectoderm GOETTE looks upon as entoderm. Only after a part of the

intestine had become useless, owing to the metamorphosis of a portion of
the entoderm cells into food-substance, and another part had been com-
pelled to move into its place, could this process give rise to a distinct
mesoderm.

The further development of the embryo of *Discocelis* con-
sists first of a complete overgrowth on the part of the
ectoderm and the resulting closure of the blastopore. The
elements of the ectoderm become more like an epithelium,
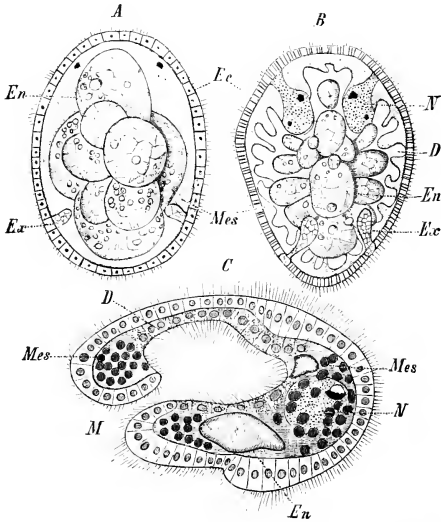
Fig. 76.—*A* to *C* (after A. LANG). *A* and *B*, embryos of *Discocelis' tigrina*, seen
from the ventral side; *C*, median longitudinal section through GOETTE's larva of
Stylochus pilidium. *Ec*, ectoderm; *En*, remains of the entodermal cells in process
of disintegration; *Ex*, fundament of the excretory organ (?); *D*, branches of the
intestine and (in *C*) intestinal epithelium; *Mes*, mesoderm; *N*, fundament of the
central nervous system.

their cilia stronger and more dense. A change in the outer
form now takes place, the aboral pole being pushed forward,
the oral backward. The anterior end is distinguished by
the appearance of the first pair of eyes, which here arise as

small pigment spots (Fig. 76 *A*). Under them the brain is established somewhat later in the form of two club-shaped bodies (Fig. 76 *B*). These bodies develop as ectodermal thickenings, which afterwards sink deeper and by means of a broad commissure unite into the common mass which they constitute in the adult. The two longitudinal nerve-trunks arise from them by means of a backward growth. Two cell-growths, which perhaps are to be explained as parts of the water-vascular system, make their appearance as ectodermal structures in the posterior portion of the ellipsoidal embryo (Fig. 76 *A* and *B*, *Ex*).

The development of the intestine takes place by the abundant multiplication of the upper and lower entodermal cells. In Fig. 76 *A* the embryo appears filled with the mass of central entoderm cells which have been metamorphosed into food-yolk. The small entoderm cells are distributed over the surface of these; they penetrate between the yolk-spheres, the substance of which they dissolve, and are finally converted into intestinal epithelium. This takes place in the following manner: scattered entoderm cells surround a mass of yolk which has become reduced in size by disintegration, and, as they begin to absorb this, form a short tube, which unites with other intestinal cavities that have arisen in the same way (SELENKA). When, finally, the intestine, with its branches, has arisen in this manner, the embryo acquires the general appearance of the adult worm (Fig. 76 *B*). The mouth arises at the place of the pre-existing blastopore from an invagination of the ectoderm, which fuses with the wall of the intestine. Fig. 76 *C* shows this condition in *Stylochus*. The ectoderm supplies the epithelial lining of the pharynx and pharyngeal pocket, the musculature of which arises from the mesodermal elements that are found massed in large numbers in the region of the invagination (Fig. 76 *C*).

According to HALLEZ, as well as SELENKA, the mesoderm continues its development from its earliest beginnings by the outgrowth of the primitive mesoderm cells into four mesodermal bands placed crosswise; these fuse with one another as soon as their cells become more numerous, and

then lie under the ectoderm like a calotte. According to LANG's description also, there is formed from the four groups of mesoderm cells a continuous layer, which attains to a greater extension on the ventral side than on the dorsal (Fig. 76 *C*). Only later does the mesoderm give rise to the musculature of the body-wall and the connective-tissue reticulum. By the formation of vertical mesodermal septa, which advance from the periphery towards the median plane, the branches of the intestine increase in length at the expense of the central yolk-mass. New septa, which encroach on these branches from the margin of the body, split them up into secondary branches, so that the intestine increases the number of its ramifications.

When, finally, the greater part of the food-yolk has been consumed, and the previously ellipsoidal embryo has undergone a flattening in the dorso-ventral direction, it breaks through the egg-membrane and reaches the outside world as a young Turbellarian.

B. *Indirect Development.*

The embryonic development takes place in a manner similar to that of the forms without metamorphosis. Therefore even in what has preceded we might, in a number of instances, have considered forms with indirect development. But, instead of developing into turbellarian-like forms, the ovate embryo of this type acquires lobe-like processes (Fig. 77). They arise first by an elongation of the ectodermal cells at the points affected, and then by an evagination of the ectoderm. The typical larval form of the Turbellaria, which arises in this way, is represented by MÜLLER's larva, as it has been named after its discoverer (Nos. 17 and 18). This larva (Fig. 77) possesses eight processes, three of which are situated in the region of the mouth, two others laterally, and three dorsally. They are provided at their margins with a border of longer cilia. If these ciliated appendages are to be compared to the ciliated bands of other larvæ, they would have to be designated as the preoral ciliated band, by means of which an oral area is separated

from an aboral one. The eyes, as well as the fundament
of the nervous system lying under them, are present in the
anterior, dorsal part of the body. Behind the middle, ven-
tral appendage, the pharynx is already seen (Fig. 77).
The intestine also is already established, and appears
branched; in short, the internal organization of the larva
corresponds nearly to that with which we became acquainted
in the recently hatched embryo of Discocelis.

The larvæ circle around in the water by the aid of their
cilia, revolving upon themselves in various directions. The
older, more elongated larvæ, on the
contrary, are always seen swim-
ming with the anterior part of the
body directed upwards. They ro-
tate around the long axis only.

After the larvæ have swarmed
for a considerable time, they ex-
change their primitive ovate form
for a more and more elongated one.
Fig. 77 (probably a larva of *Thysa-
nozoön*) represents a stage older
than the embryos just hatched
from the egg, which are more com-
pact. The elongation of the body
is accompanied by a broadening
of the anterior and a narrowing of

FIG. 77.—MÜLLER's larva seen
from the ventral side (after JOH.
MÜLLER, from BALFOUR's *Com-
parative Embryology*). The heavy
line indicates the ciliated band.
m, mouth; *u.l*, the so-called
upper lip.

the posterior end (Fig. 78 *A*). It can be recognized from
Fig. 78 *A* that, in spite of the presence of the larval appen-
dages, the form of the worm is already expressed. This is
still more the case in the stage represented by Fig. 78 *B*, in
which the larval appendages are rapidly degenerating.
These finally disappear altogether, and the form which
characterizes the adult animal is reached by the gradual
completion of the internal organization, the increase in the
number of eyes, the outgrowth of the nervous system into
the longitudinal nerve-trunks, the differentiation of the
pharyngeal apparatus and the rest of the muscular system
from the mesoderm, and the development of the intestine,
with its branches.

Somewhat different from MÜLLER's larva, though still derivable from
it, is that of *Oligocladus auritus* (Fig. 79), which has been carefully
studied by HALLEZ. Like MÜLLER's larva, it also possesses eight lobe-
like processes, two of which, however, the median ventral and dorsal
ones, have moved far forward. The first one, situated in front of the
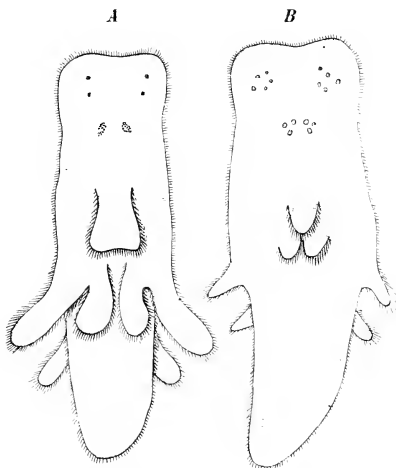
FIG. 78.—*A* and *B*, larvæ of *Fungia aurantiaca* (after A. LANG) about to change
into the worm, seen from the ventral surface. The eyes are indicated for the
sake of better orientation.

mouth, attains a considerable size, so that the anterior end appears
spread out like an umbrella. Behind, as in MÜLLER's larva, there are
two ventral, two lateral, and two dorsal appendages surrounding the
larva. Rigid cilia at the anterior and posterior ends of the body give a
characteristic appearance to the larva.

GOETTE's larva of *Stylochus pilidium* resembles MÜLLER's larva less.
In it (if we make use of the expressions employed for MÜLLER's larva)
the two lobes situated at the sides of the mouth-opening are especially
well developed (Fig. 80). The lobe lying in front of the mouth, on the
contrary, is less developed, as is also the middle dorsal one. Other
appendages are wanting. Inasmuch as the back is arched, this part
assumes a bell-shaped appearance, and the larva acquires a resemblance
to a *Nemertean pilidium*, which is increased by the occurrence of rigid
cilia. The apex is marked by the dorsal lobe (Fig. 80). The larva in

this figure (Fig. 80) has a different orientation from that of the other turbellarian larvæ, in order to bring out better its resemblance to the pilidium larva. Its discoverer, GOETTE, also compares it directly to the

pilidium. If we consider that *Stylochus* has a simpler course of development (see *supra*, the absence of nutritive yolk), then it appears not impossible that the larva of *Stylochus* represents a primitive condition, a lower larval form, which perhaps still has relationships to the larval forms of the *Nemerteans*. The fact that MÜLLER's larva also presents a similar form at a certain stage is an argument in support of this view. MÜLLER's larva itself would then represent a more highly developed form. LANG, to be sure, believes that *Stylochus* simply leaves the egg at an earlier stage, arriving at the condition of MÜLLER's larva only during its free existence, whereas GOETTE maintains that it is developed directly into the

FIG. 79.—Larva of *Oligocladus auritus*, Lang (*Eurylepta auriculata, Clap.*), seen from the side (after HALLEZ, from BALFOUR'S *Comparative Embryology*).

adult animal by an increase in length.

The larva of *Stylochopsis ponticus* described by METSCHNIKOFF [1] also
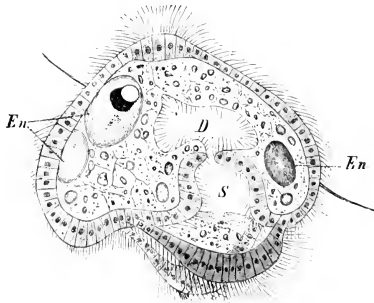
FIG. 80.—Larva of *Stylochus pilidium* seen from the side (after GOETTE). *D*, intestine; *En*, remains of the entoderm cells; *S*, pharynx.

[1] This work by METSCHNIKOFF, published in a Russian periodical,— "Studies on the Development of the Planariæ," *Memoirs of the Neo-*

seems to resemble GOETTE's larva. It is said also to resemble the pilidium in form.

Quite different from the larval forms hitherto considered is a planarian larva found by A. AGASSIZ, which he ascribes to *Planaria angulata*. This larva, in which a branched intestine is already present, shows a distinct external segmentation corresponding to the lateral branches of the intestine (Fig. 81). At first the body is cylindrical; it is only in the course of further development that it becomes flattened and takes on the form of a turbellarian. Unfortunately a confirmation of AGASSIZ's short communication has not yet appeared.

FIG. 81.—Larva of *Planaria angulata* (?) (after A. AGASSIZ, from BALFOUR's *Comparative Embryology*).

II. TRICLADIDA.

The difference between the development of the freshwater *Dendrocœlida* (Triclads) and that of the *Polycladida* is to be explained by the fact that it takes place under altogether different conditions. In the cocoons laid by freshwater Dendrocœles, which are disproportionately large as compared with the size of the animal, there is found, in addition to the egg-cell, a large number of yolk-cells. According to METSCHNIKOFF (No. 15), the proportion of the two kinds of cells in *Planaria polychroa* is such that there are four to six egg-cells to about ten thousand yolk-cells. In *Dendrocœlum lacteum*, on the other hand, twenty to forty egg-cells are present in one cocoon (IIJIMA, No. 8; HALLEZ, No. 7). The yolk-cells surround the egg-cells in a radial arrangement, and fill the remaining space of the cocoon. They are able to move like amœbæ by sending out pseudopodia.

As soon as the first stages of cleavage have taken place in the egg-shell (Figs. 82 and 83), this remarkable phenomenon occurs: the blastomeres do not remain united, but move far

apart (Figs. 83 and 84). They lie quite isolated, as if they had no sort of relation to one another, as is seen, for example, in the thirteen-cell stage of *Dendrocœlum* (Fig. 84). One would be inclined to think of this as an abnormality if the observations of METSCHNIKOFF, IIJIMA, and HALLEZ did not entirely agree on this point. The subsequent development likewise proceeds in a manner altogether original, its peculiarities being evidently a result of the large amount of yolk-substance which must be taken up by the embryo.
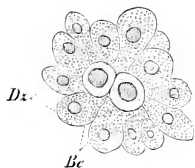
FIG. 82.—Cleavage stage of two blastomeres (*Be*), with the surrounding yolk-cells (*Dz*), of *Dendrocœlum lacteum* (after IIJIMA).

In the further course of development some of the yolk-cells are dissolved, so that the embryo now lies in a finely granular protoplasmic mass, in which some of the nuclei of the yolk-cells can still be recognized (Fig. 84). The division of the blastomeres continues, and as a result of it there is produced a spherical heap of from seventy to eighty irregu-
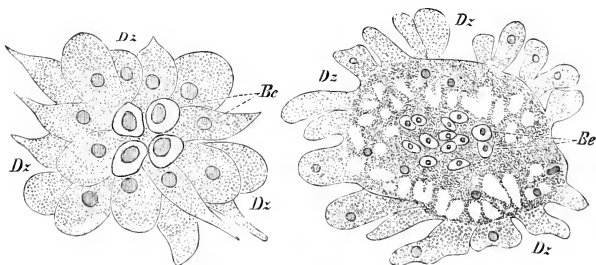
FIGS. 83 and 84.—Cleavage stages of *Dendrocœlum lacteum* (after HALLEZ). In one stage four blastomeres (*Be*), in the other thirteen, with surrounding yolk-cells (*Dz*), which in the later stage are partly fused into a common mass. Their nuclei (shaded dark) are still visible in this mass.

larly arranged cells. Changes are soon manifested in this, which result in the establishment of the germ-layers. Some of the peripheral embryonic cells move to the edge of the

surrounding homogeneous food-mass, and by becoming flat-
tened out and uniting with one another form there a thin
membrane [ectoderm]. Later a small group of cells in the
mass of loosely associated embryonic elements becomes dis-
tinguishable by its presenting a more compact arrangement.
This spherical group of cells at first lies in the middle of the
embryonic mass, but later moves to the periphery. Here it
unites with the ectoderm. It then becomes hollow, and its
cells are differentiated into various layers, thus forming the
provisional organ known as the embryonal pharynx (Fig.
85 A). Four cells, which enclose a small space, are applied
to the inner end of this pharynx. According to HALLEZ, these
constitute the earliest fundament of the intestine (Fig. 85 A).
The fundaments of the pharynx and intestine would be
looked upon, then, as entodermal, but the migratory cells
which remain between ectoderm and entoderm could not be
designated as mesoderm, for later, according to HALLEZ,
ectodermal as well as entodermal elements arise from them.
These migratory cells contribute at first to the formation of
the musculature of the embryonal pharynx, becoming elon-
gated and spindle-like, and being applied to its outer side.

The significance of the pharynx, which now begins to
execute swallowing movements, consists merely in its trans-
porting the yolk-cells into the embryo (Fig. 85 B). As soon
as the pharynx begins to function, the intestine becomes
rapidly filled with yolk-cells, which cause a great distension
of the intestine and the entire embryo. The inconsiderable
entoderm and likewise the ectoderm become stretched to
an extraordinary degree, so that they can be recognized only
with difficulty. In order to prevent a bursting of these thin
layers, cells derived from the migratory elements unite with
them. METSCHNIKOFF's statement that yolk-cells which have
migrated in from the outside are converted into the epithe-
lium of the intestine is not corroborated by HALLEZ. Accord-
ing to this observer, the primitive entoderm always forms a
wall, although a very delicate one, bounding the parenchy-
matous tissue of the embryo. This entoderm, to be sure, is
said to be of a provisional nature only. It disappears sub-
sequently, and the adjoining migratory cells unite to form

the intestinal wall. Immediately before the secondary for-
mation of the intestine takes place, the embryo would be to
a certain extent in the condition of the acœlous Turbellaria,
in which the food-bodies pass directly into the body paren-
chyma. To be sure, an intestinal cavity would exist in the
embryos, but it would be limited by the body parenchyma.
Should these observations be confirmed, they might perhaps
throw some light on the establishment of the conditions
which exist in the *Acœla*.
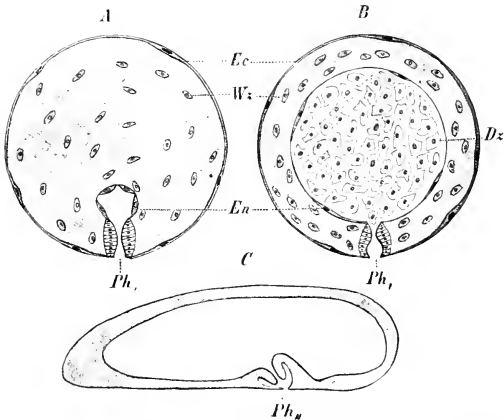
Fig. 85.—Sections through embryos of *Dendrocœlum lacteum* (somewhat diagram-
matic, after HALLEZ). *Ec*, ectoderm; *En*, entoderm; *Dz*, yolk-cells; *Ph'*, provisional
embryonal pharynx and (in Fig. C, *Ph''*) permanent pharynx; *Wz*, migratory
cells.

The branched form of the intestine of Triclads arises in a
similar way to that of the Polyclads, *i.e.*, by the ingrowth of
connective-tissue septa from the periphery toward the middle
line. This tissue, like the body musculature, owes its origin
to the migratory cells, from which the sexual organs likewise
arise (IIJIMA).

The fundament of the nervous system was found by the three authors
mentioned lying deep in the body tissues, and they could not discover
that it had any connection with the ectoderm. If the statement of

HALLEZ proves to be true, that portions of the migratory cells are employed even after this in the formation of the ectodermal layer, then such a mode of formation of the nervous system could be more readily referred to the ectodermal method of origin, which was met with in the *Polycladida*. However, it is not to be denied that the earliest appearance of the nervous system in the *Tricladida* points to a mesodermal mode of origin, such as was attributed to it by the brothers HERTWIG (*Cœlomtheorie*) even at the time they wrote. Recently, too, in the related *Nemerteans*, the nervous system has been derived from the mesoderm (HUBRECHT).

When the embryonal pharynx has fulfilled its function, the provisional mouth-opening closes, the pharynx degenerates, and an irregular heap of cells lies in its place. In this a cavity then arises, the cellular lining of which represents the internal epithelium of the pharyngeal pocket, for the permanent pharynx is formed at the same spot. This therefore arises, as it seems, from the entoderm (or mesoderm), whereas in the *Polyclads* an invagination of the ectoderm gives rise to its formation. The cylindrical form of the pharynx is due to the fact that the surrounding cells take part in its formation. Before the pharynx attains its final shape, the union with the lumen of the intestine takes place, and later the mouth-opening also breaks through to the exterior.

During the developmental processes described, the embryo has frequently changed its form. At first ovate, it becomes spherical after the introduction of the yolk-cells ; then at the time of the formation of the permanent pharynx it again elongates and becomes flattened on the ventral side (Fig. 85 *C*). The pointed portion corresponds to the anterior part of the body.

III. RHABDOCŒLIDÆ.

The development of the rhabdocœlous Turbellaria is still the least known. Various forms belonging to the genera *Prorhynchus*, *Prostomum*, *Mesostomum*, *Schizostomum*, and *Macrostomum* were studied by HALLEZ (No. 6) in some stages of development, but he studied only the winter eggs. These eggs, which are surrounded by a firm capsule, are attached to aquatic plants by means of a mucilaginous secretion. In many forms (*Prostomum lineare* and *P. Steenstrupii*) the cap-

sule is drawn out into a stalk, by means of which it adheres
to fixed objects (Fig. 86), in much the same way as in
the fresh-water Dendrocœles. In each capsule there is
usually found only one egg-cell, in rare cases (*Prostomum
Steenstrupii*) two of them. As in the fresh-water Dendro-
cœles, the egg-cells occupy only a small part of the capsule,
the remaining space being filled with yolk-cells (Fig. 86).

In spite of the presence of the yolk-
cells, development proceeds in a manner
similar to that of the *Polycladida*. Per-
haps when the development of the
Rhabdocœlidæ becomes more accurately
known intermediate conditions will be
found here, which will explain the
aberrant condition of the *Tricladida*.

After the expulsion of the polar
globules and fertilization, the egg di-
vides first into two, then into four,
blastomeres of equal size. Four
smaller ones are constricted off from
these (SALENSKY). The further cleav-
age processes could not be observed
by HALLEZ; their result, however, is
an epibolic gastrula, which entirely
resembles that of the *Polycladida*. The

FIG. 86.—Stalked egg
capsule of *Prostomum
Steenstrupii* with two egg-
cells (*Ez*) and surrounding
yolk-cells (after HALLEZ).

ectoderm becomes covered with cilia, and the embryo floats
in the mass of yolk-cells. It is therefore equivalent to
a larva, which, however, does not attain to a wholly free
life, just as the larvæ of the *Gnathobdellidæ* and *Oligochœtæ*
live within the cocoon, and are nourished by the albumen
occurring in it.

In a later stage of the embryo the entoderm is seen to be
arranged in a continuous layer. Its cavity becomes connected
with the outer world by means of the pharynx. It appears
as if it were, as in the *Tricladida*, of entodermal nature. The
yolk-cells are conveyed by means of it into the intestine.
Yet the pharynx of the *Rhabdocœlidæ*, contrary to that of the
Tricladida, at once reaches its permanent form. The
primitively spherical embryo by becoming elongated and

flattened assumes the form of a flatworm. In *Prostomum lineare* an invagination of the ectoderm at the anterior end of the body gives rise to the pharyngeal sheath and the pharynx.[1]

[1] [The development of the Rhabdocœla and Acœla has recently been studied by PEREYASLAWZEWA (see Appendix to *Literature* on Turbellaria, Nos. I. and II.).

According to this author, the development is the same in all the *Acœla* studied by her—Convoluta paradoxa, Aphanostoma diversicolor, Aph. pulchella, and Darwinia variabilis—so that one description, that of Aph. diversicolor, answers for all. The formation of polar cells and fecundation occur before the eggs are laid. The first cleavage results in two cells of equal size. Preparatory to the second cleavage the nuclei elongate, and approach the side opposite that where the polar cells have taken refuge. With the second cleavage each of the two cells is divided into two, one of which is four times as large as the other. The four cells finally assume a symmetrical arrangement around the chief axis, the two planes of cleavage becoming mutually perpendicular. The two small cells now divide, producing four of equal size arranged in a cross at the upper pole. Then the two large cells divide into unequal parts, a larger basal cell and a smaller one, lying nearer the plane of the four micromeres. This eight-cell stage is a true blastula with cleavage cavity, and is quickly followed by the division of the two basal cells, from which result four basal cells of equal size (ten-cell stage), arranged not in a cross, but in a row, which determines the long secondary axis. Two of the four basal cells, the middle ones, are so crowded at their superficial ends by their mates that they become wedge-shaped and finally forced into the cleavage cavity. Thus gastrulation begins as a true emboly, but it is completed by a process of epiboly. During invagination nearly all the pigment granules are accumulated in the lower ends of the four basal cells, which are then abstricted as four small dark cells. Somewhat prior to this, however, the two cells lying a little below the plane of the four micromeres divide, and their products are arranged symmetrically (on either side of the plane determined by the chief axis and the long secondary axis). The eight cells of the upper half of the egg now divide, producing sixteen. With this (twenty-four-cell) stage gastrulation is well advanced, but it is completed in the following stages by the overgrowth of the products of the sixteen micromeres. "The two lateral cells, having given rise to the two small (?) primitive-entoderm cells, represent the third layer: the mesoderm." We understand the author to mean by "the two lateral cells" the two cells which constitute the end of the row of four basal cells, but the account is not satisfactory. A small but well-marked archenteron, communicating with the outside by means of a blastopore, exists from the stage when the entoderm consists of only two cells, which assume a concavo-

General Considerations.

In considering the development of the Turbellaria, the first thing to attract attention is the radial structure of the embryonic fundament: the four large blastomeres from which, above and below, the entoderm cells have separated, the radially arranged ectoderm cells, but especially the four groups of mesoderm cells. This condition points to the affiliation of the Turbellaria with radially constructed animals, a relationship which, in fact, has been advocated, either on anatomical or embryological grounds, by numerous writers (KOWALEVSKY, SELENKA, LANG, CHUN, GOETTE). An attempt has been made to trace the Turbellaria back to the Ctenophora.

convex shape and enclose the archenteric fissure between them. Before the overgrowth of ectoderm is completed the two entoderm cells and the two mesoderm cells have each divided into two. The blastopore shifts (about ninety degrees) from the basal side to one end of the *short* secondary axis, and becomes the permanent mouth. Thus the pole of the blastopore, which is also that of the polar cells (?), becomes the caudal end of the worm. At the opposite pole, which protrudes somewhat, a bundle of clear cells represents the first trace of the frontal organ, while two slight depressions, symmetrically placed and of short duration, are accompanied by permanent thickenings of the ectoderm, which constitute the fundament of the nervous system. A marked feature of the early stages is the bilateral symmetry, which is noticeable from near the beginning of cleavage up to the time the young become ciliated. "There is no hint of a radial appearance in either blastula or gastrula."

The only representative of the *Rhabdocœla* studied by PEREYASLAWZEWA was Macrostoma histrix, in which the eggs are so opaque that it is difficult to trace the early stages. After the egg is laid it undergoes contractions which result in elevations and deep excavations of all parts of its surface. Several (four to eight) polar cells are formed at different points on the periphery; these have the appearance of very hard and compact fusiform bodies (!). The first cleavage furrow divides the egg into two unequal cells; the second furrow, perpendicular to the first, divides each of these into two equal parts, so that there are now two large and two small blastomeres. The subsequent cleavage stages were not followed accurately, but "it is certain that the two small segments representing the ectoderm arise from two large segments." Gastrulation is by epiboly. It is uncertain whether the blastopore becomes the permanent mouthopening, or is closed, and a new mouth formed at the cephalic pole. In later stages the embryo is more transparent. The mesoderm then exists, it is maintained, in the form of two longitudinal bands, each of which is separated into two layers by a fissure: the body cavity. The outer layer, uniting with the ectoderm, forms the subcutaneous muscular layer; the inner, uniting with the entoderm, forms the muscular layer of the intestinal wall. Other organs are formed as in Aphanostoma.—THE TRANSLATORS.]

According to the recent investigations of METSCHNIKOFF (No. 16) on Ctenophores, the embryonic development of this group offers some resemblances to that of the Polyclads. The ectoderm cells are constricted off from the four blastomeres originally present, and grow over them from above. As in the Polyclads, four mesodermal groups are present here, and likewise take their origin, although in a somewhat different way, from the large blastomeres. The subsequent deportment of the mesodermal tissue is similar in the two groups in so far as it fills the entire space between ectoderm and entoderm. Since among the lower forms the Ctenophora are the only ones which present mesodermal tissue of this kind, there is in that fact an argument for placing the Turbellaria in relation with them.

The often-attempted comparison of the systems of organs in Ctenophora and Turbellaria, especially that of the gastrovascular apparatus, is, however, less satisfactory. On the contrary, LANG's suggestion concerning the position of the cilia and the manner of their motion in the Turbellarian larvæ appears to us to be of some importance. The cilia are arranged in regular transverse rows on the ciliated band, and all the cilia of a transverse row move at the same time in a manner which quite recalls the strokes of the swimming plates of the Ctenophora. If the cilia of a row were to fuse with one another, says LANG, then the structure arising in this way could not be distinguished from such a swimming plate. But how far LANG's attempted homology of the eight ciliated lobes with the ribs of the Ctenophora has claim to validity is very doubtful.

Possibly also the brain of the Turbellaria can be referred to the apical plate of the Ctenophora. It has been determined embryologically by LANG that the originally aboral pole of the embryo becomes shifted toward the anterior end of the body. The brain then arises in that region. If the displacement were not to take place, then the brain would arise at the aboral pole, and would consequently have the same position as the apical plate of the Ctenophora. Even the otocysts of the Turbellaria, which in certain forms (Monotidæ, Otomesostoma, according to v. GRAFF) lie close to the brain, are perhaps to be looked upon as the remains of the otocysts of the Ctenophora.

Nevertheless it is to be emphasized that the Turbellaria and Ctenophora, even if they proceeded from a common root, have become so much altered that the comparison can be of only a general nature. We have already mentioned (p. 157) that we do not ascribe to the intermediate forms Cœloplana and Ctenoplana (Nos. 10 and 11), proclaimed as uniting links between the Ctenophora and Turbellaria, any such meaning. Nevertheless such forms are, in our opinion, valuable in showing how the transition from free-swimming, radial animals into creeping, bilateral forms could have been accomplished.

II. TREMATODA.

The egg of Trematodes is a product of the ovarium and the vitellaria. The latter supply to each egg a number of cells, which surround the egg-cell, and in the course of development are consumed by the embryo. [The conditions are, therefore, much the same as in the Turbellaria, and what we call the egg in the Trematodes is a composite structure similar to the cocoon of the Triclads and Rhabdocœles, save that there is only a single egg-cell and that the number of yolk-cells is much smaller.—K.] The embryo leaves the egg usually at a stage of development which is still far removed from the organization of the parent. Before it reaches this it still has to undergo a complicated process of development.

I. DISTOMIDÆ.

The **embryonic development** has been the most elaborately treated in the investigations of SCHAUINSLAND (No. 8). In *Distomum tereticolle* the egg-cell lies at that pole of the egg which is marked by the operculum of the egg-shell (Fig. 87 *A*). The remaining part of the egg is formed by the yolk-cells, which still show their cellular structure, but gradually undergo degeneration. The egg-cell divides into two cells, four cells, etc., until the germ extends over a large part of the entire egg (Fig. 87 *B* and *C*). At the apex of the embryonic mass a cell is soon distinguished from the rest by its losing its spherical shape and covering the uppermost cells like a kind of cap (Fig. 87 *C, Kz*). It soon divides into two cells, which grow downward, becoming in this way attenuated into a thin membrane. Still other cells take part in the formation of this delicate enveloping membrane as soon as the nutritive yolk is entirely displaced by the cleavage cells (Fig. 87 *D* and *E*). At this stage the germ is a solid mass of cells surrounded by the enveloping membrane, which is separated by a narrow space from the cell-mass (Fig. 87 *E*). Under the enveloping membrane is developed around the entire circumference of the embryo a layer of flat cells, which SCHAUINSLAND looks upon as

ectoderm, and which he believes has arisen, like the enveloping membrane, as the result of an overgrowth coming from one side and surrounding the cell-mass. This, then, would be an epibolic gastrula (Fig. 87 *E* and *F*).

The further changes of the embryo consist, in the first place, in the gradual disappearance of the nuclei of the ectoderm cells and transformation of the entire ectoderm into
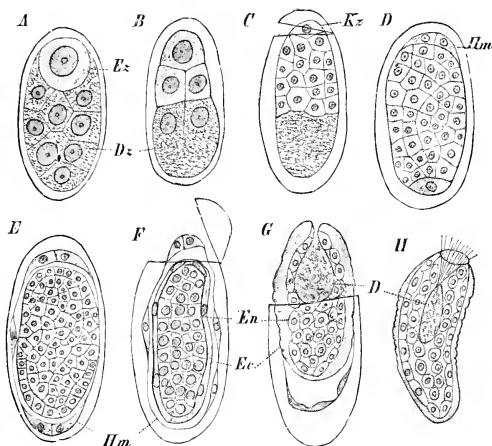
Fɪɢ. 87.—*A* to *H*, embryonic development of *Distomum tereticolle* (after Sᴄʜᴀᴜɪɴs-ʟᴀɴᴅ). *D*, intestine; *Dz*, yolk-cells; *Ez*, egg-cell; *Ec*, ectoderm; *En*, entoderm; *Hm*, enveloping membrane; *Kz*, cap-cell.

a thin cuticula-like layer, on the surface of which bristle-like structures make their appearance (Fig. 87 *H*). A number of the cells of the entoderm have united for the formation of the intestine, which fills about one half of the body (Fig. 87 *G*). Other entoderm cells are applied to the ectodermal membrane, whereas the remaining cells, lying between these and the intestine, retain the character of embryonic cells. They are germ cells, from which the new generation subsequently arises. Since in the present stage the cells of the ectoderm, as well as those which form the

intestine, have separated from those lying between them, the latter can be considered as belonging to a third germ-layer, the mesoderm.

When the embryo has reached the stage described, it breaks through the enveloping membrane, which has become a delicate transparent pellicle, the operculum of the egg-shell opens, and the embryo reaches the outside world (Fig. 87 F and G). Here it creeps about actively, and for this purpose it makes especial use of the proboscis. The anterior part of the intestine has become metamorphosed into an organ of this kind, for it can be everted and retracted. In the embryo represented in Fig. 87 H, the proboscis, together with the anterior end of the body, is retracted. A kind of funnel arises in this way which is surrounded by the chitinous bristles.

The embryos of other *Distomidæ* develop on the cells of the ectoderm cilia, by means of which they swim in the water (Figs. 88 and 89 A). The development of an enveloping membrane was observed by SCHAUINSLAND in various genera of *Distomidæ*. Two *Distomidæ* (*D. cylindraceum* and *D. mentulatum*) on leaving the egg-shell appear to cast off the ciliated ectodermal layer in addition to the enveloping membrane.

We shall meet with similar processes in considering the development of tapeworms. The significance of this will be considered there more at length.

FIG. 88.—Embryo of *Distomum globiporum*, pressed out of the egg (after SCHAUINSLAND). The ectodermal cells (*Ec*) are partly detached ; *Hm*, enveloping membrane.

The Further Course of Development.—The distomid larva, in order to develop further, must seek another host. The processes which are enacted during its growth we describe first for *Distomum hepaticum*, whose course of development has been made known chiefly through the prolonged investigations of LEUCKART, as well as those of THOMAS.

The eggs of *Distomum hepaticum* are found in great numbers in the gall-bladder of the host inhabited by the worm. From here they pass into the intestinal canal, to be voided together with the fæces. Their development begins only after they are outside the host. If by chance the egg reaches the water, then the favourable conditions for development are present. In from three to six weeks afterwards the embryo abandons the egg-shell (variations in the time of development are caused by higher or lower temperatures). By means of the cilia which thickly cover it, the embryo, or better the larva, easily moves about in the water. It possesses an x-shaped eye-spot (Fig. 89 *A*). Under this lies a ganglion. The intestine is only slightly developed. Two ciliated funnels already represent the beginning of the excretory system. The remaining part of the body is filled with the germ cells, the origin of which has already been considered in treating of the embryonic development, and the significance of which consists in the production of the subsequent developmental stages of the *Distomum.*

In this condition the larva may swim about for as many as eight hours; then it perishes, unless it meets with a snail, into whose respiratory cavity it bores. In this process its cephalic protuberance (also interpreted as tactile organ) is said by THOMAS to render good service. *Limnæus minutus* (*S. truncatulus*) is now to be regarded with certainty as the intermediate host of *Distomum hepaticum*, as the investigations of LEUCKART, confirmed by THOMAS, have shown. Having arrived in the respiratory cavity or other organ of the snail, the larva casts off its coat of cilia and secretes about itself a cuticula-like envelope. It now grows and becomes a sac-like body, which is called a *sporocyst* (Fig. 89 *B*). In it the germ cells become enlarged, and by repeatedly dividing produce the cell-masses which give rise to a new generation. The sporocyst besides has the power of reproducing itself by transverse division. To this end it constricts itself in the middle of the body, and produces two new sporocysts.

The generation produced in the sporocyst consists in turn of creatures which are sac-like, but which are more highly
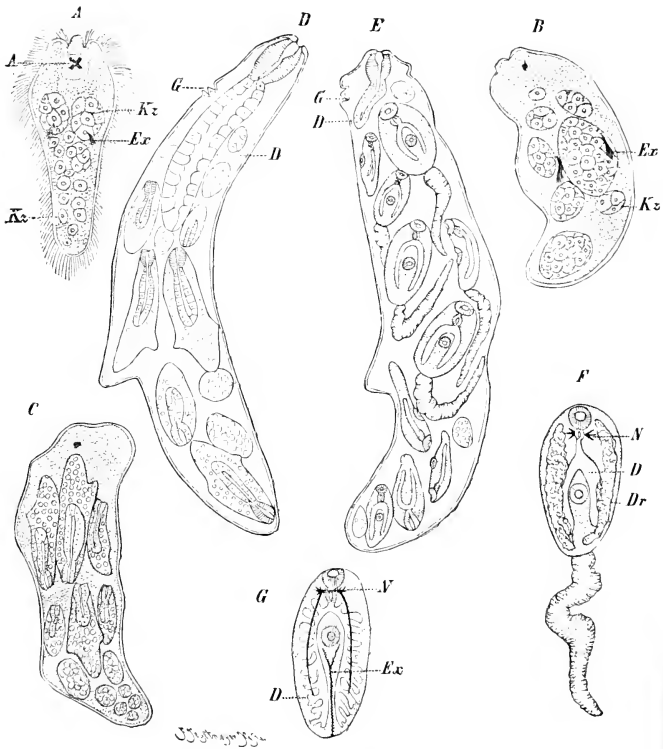
FIG. 89.—*A* to *G*, course of development of *Distomum hepaticum* (after LEUCKART):
A, larva with eye-spot (*A*), with ganglion lying under it and germ cells (*Kz*); *B*,
young sporocyst, with masses of germ cells inside of it, from the respiratory cavity
of the snail; *C*, older sporocyst, with young Rediæ; *D*, Redia, with Rediæ and
germ balls inside of it, from the liver of the snail; *E*, Redia, with Cercariæ
and germ balls, from the liver of the snail; *F*, free-swimming Cercaria; *G*,
young liver-fluke from the bile-duct of the sheep, with branching of the in-
testine already begun. *A*, eye-spot; *D*, intestine; *Dr*, glandular mass on either
side of the body of the Cercaria; *Ex*, excretory system; *G*, birth aperture of
the Redia; *Kz*, germ cells; *N*, nervous system.

organized than the sporocyst, since they are provided with
a mouth and an intestinal canal, and since the different
portions of the body, as well as its organs, appear to be
better differentiated (Fig. 89 C). The mouth is, in fact,
surrounded by a kind of sucker, which enables the animal to
attach itself to the organs of the host. Moreover, the
pharynx executes swallowing movements, and the intestine
appears at some times more, at other times less, filled;
hence it is functional. This new generation has been called
by the name of *Rediæ* (Fig. 89 D and E).

As regards the origin of the Rediæ, there are two opposing views; some
observers (LEUCKART, SCHWARZ) trace them directly to the germ cells,
while others (WAGENER, BIEHRINGER) maintain their origin from cells of
the body-wall. Although SCHWARZ argues strongly for the one and
BIEHRINGER for the other mode of origin, yet this difference does not
seem to us to be important, for we have already seen that the parietal
cells and the germ cells are embryologically of the same origin. In a
portion of the cells of the body-wall even, a differentiation into separate
histological elements appears not to have taken place, and for this
reason they may continue to develop in the same way as the real germ
cells. In harmony with this view is the statement of THOMAS, who de-
rives the Rediæ from both the germ cells and the cells of the body-wall;
if the supply of the former were exhausted, then the latter might take
their place.

In regard to the way in which the *Rediæ* (and later the *Cercariæ*)
arise, SCHWARZ explains this process as corresponding to the cleavage of
the egg. The single germ cell divides and produces a *morula*-like heap
of cells, from which the Redia (or the Cercaria) arises. The germ cell
therefore corresponds to the egg, and this would thus be a case of par-
thenogenetic development (LEUCKART). The entire process of development
is therefore to be considered, not as an alternation of generations *s. str.*
(*metagenesis*), but as *heterogony*, as already suggested by GROBBEN
(*Literature* on Cestoda, No. 4).

When the Rediæ have attained the proper stage of
development, they abandon the sporocyst by rupturing its
walls. They migrate from the respiratory cavity into the
other organs of the snail, especially the liver. Here they
increase in size, and there can soon be recognized in them
in turn spherical masses of germ cells, from which arise
again, if the season be cold,—that is to say, in winter—*Rediæ*
of nearly the same form as before (Fig. 89 E). If, on the

contrary, this stage of development happens in the warm
season, then creatures of another shape are developed from
the germ cells: the tailed *Cercariæ* (Fig. 89 *E* [contained
individuals] and *F*). In other cases the Cercariæ arise only
in the Rediæ of the second generation.

The mode of origin of the *Cercariæ* has been thoroughly studied by
Schwarz (No. 9). As has already been mentioned, this investigator finds in
their origin a great resemblance to the development of the embryo. The
morula-like heap of cells which arose from the germ cell is further
developed in such a manner that there are differentiated a peripheral
cell-layer, a central compact mass of cells, and a layer between the two.
The first supplies the dermal layer, which is to be considered as a meta-
morphosed epithelium; from the central mass arise the genital organs,
whereas the intermediate parts of the embryonal tissue (the " meristem "
of Schwarz) give rise to the other organs. Anterior to the central cell-
mass a number of cells are arranged in a regular manner. This is the
fundament of the intestine, which later becomes hollowed out and con-
tinuous with the two branches of the intestine, which have arisen in the
same way. The central part of the excretory apparatus is also formed
by means of such a regular arrangement of cells in the posterior part of
the body. The dermo-muscular layer and the fundament of the nervous
system arise nearer the periphery. The remaining part of the " meri-
stem " becomes the parenchymatous tissue of the body.

The *Cercaria* already exhibits to a certain extent the
organization of the adult *Distomum*, e.g., in the presence of
an anterior sucker and one situated on the ventral side
(Fig. 89 *F*). In the centre of the former lies the mouth,
which leads into the muscular pharynx, and thence into the
forked intestine. The œsophageal ganglion, with the two
lateral stems, and also the bipartite excretory system are
present. But a long muscular tail is attached to the
posterior portion of the body. In this condition the Cercaria
leaves the Redia through the birth aperture, which lies at
the anterior end (Fig. 89 *E, G*), and seeks an escape by work-
ing its way through the tissues of the host by means of its
suckers and tail. Its free life in the water lasts for only a
short time. It soon attaches itself to plants which are
found at the water's edge. It casts off the tail, and secretes
about itself a cyst. A large number of glands which lie on
either side in the body of the Cercaria, and which give a

characteristic appearance to the animal, serve for this purpose (Fig. 89 *F*). These glands appear on the free Cercaria as white opaque masses; but when their contents have passed out during the encystment, the body of the young worm becomes entirely transparent (Fig. 89 *G*). If the cyst, together with the plant to which it is attached, is swallowed by a sheep, the envelope is dissolved in its stomach; the young worm becomes free, and finally reaches the liver, where, in the course of about six weeks, it develops into the sexually mature *Distomum hepaticum.*

The different Distomidæ present great differences as to the course of their developmental processes. The eggs from which embryos are to emerge do not always become free, but may be taken up directly by the intermediate host, and hatched out only when they have reached its intestine (*Distomum ovocaudatum*, according to LEUCKART). It is not necessary that a sporocyst should be first developed out of the embryo, and a Redia out of it, as in *Distomum hepaticum*, but the sporocyst may become metamorphosed directly into a Redia. Sporocyst and Redia in most cases beget directly Cercariæ. The sporocyst in *Distomum macrostomum* and *Gasterostomum fimbriatum* is very aberrant in shape. In this species it develops tubular processes, which serve for the reception of the Cercariæ. The sporocyst of *Distomum macrostomum*, known as *Leucochloridium*, which inhabits the liver and other organs of *Succinea amphibia*, attains an extraordinarily large size, for it sends out processes into the antennæ of the snail, where, on account of their external resemblance to insect larvæ, they are seen and eaten by birds (ZELLER, HECKERT).
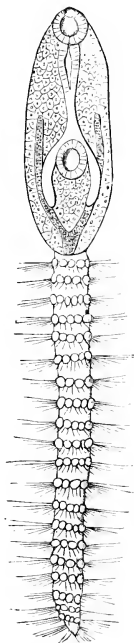
FIG. 90.—*Cercaria Villoti, Monticelli* (after VILLOT).

The Cercariæ produced in germ tubes present a variety
of forms. This applies chiefly to the caudal appendage,
as can be recognized in the peculiarly formed Cercaria
represented in Figs. 90 and 91. One of these, *Cercaria
setifera Villot*,[1] a marine form, which arises from a sporocyst
inhabiting *Scrobicularia tennis*, possesses an extraordinarily
large tail, beset with bristles. The other (Fig. 91) has
two tails, which are directed forwards, however, in swim-
ming. This is the Cercaria of *Gasterostomum fimbriatum*,
and is known under the name of *Bucephalus polymorphus*.
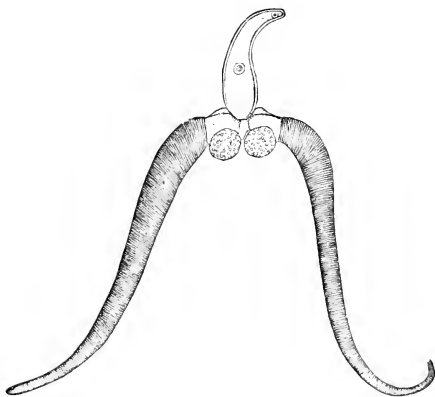
FIG. 91.—Cercaria of *Gasterostomum fimbriatum* (after ZIEGLER).

Under certain conditions the tail is entirely wanting in
the Cercaria stage. This is the case when the Cercariæ
are not compelled to undertake a migration, but remain in
their host until, along with it, they are consumed by another
animal, the final host. Since they do not pass through a
free stage, they do not require any special organs of loco-

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[1] The *Cercaria setifera* of VILLOT is called *Cercaria Villoti* by MONTI-
CELLI, for the term *setifera* occurs in another species (MONTICELLI,
" Sulla *Cercaria setifera* Müller," *Bolletino di Naturalisti in Napoli*,
vol. ii., 1888).

motion. The tailless Cercariæ of *Distomum macrostomum*
(produced in *Leucochloridium paradoxum*), together with
parts of the germ tubes, arrive in the intestine of the final
host [birds], in the cloaca of which they become sexually
mature (ZELLER). As a rule the Cercaria passes, by an
active migration, from its first intermediate host into a
second, which naturally is also an aquatic animal, either
another snail or a worm, crustacean, insect, mollusc, fish, or
amphibian. In this second intermediate host it casts off the
tail and becomes encysted. The young worm awakens to
new life only after its host has been taken as food and
digested by some other, usually higher, animal. In this
way the cyst is dissolved, and the young
Distomum now reaches the stage of the
sexually mature animal. But we have
seen that in *Distomum hepaticum* the
second intermediate host may be omitted,
and that the Cercaria, after becoming
encysted in the free condition, passes
directly into the final host. The state-
ment, often made, that tailed Cercariæ
could migrate directly into the final host
(for example, the *Cercaria macrocerca* of
Distomum cygnoides into the urinary
bladder of the frog), has not been sub-
stantiated. On the contrary, these Cer-
cariæ appear to be obliged to pass
through the encysted stage.
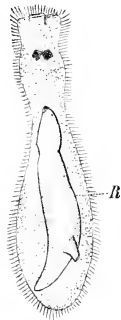
FIG. 92.—Embryo of
Monostomum mutabile,
shortly after hatching
(after v. SIEBOLD). *R*,
Redia.

A most remarkable condition is presented by
the embryos of *Monostomum mutabile* and *M.
flavum*, two *Distomidæ*, which are found in the
thoracic and orbital cavities of various aquatic birds. The embryos
abandon the egg-membrane when still in the uterus of the parent. These
Distomids are therefore viviparous. In each embryo a Redia-like
creature is already present (Fig. 92). In this case, therefore, the
embryo produces the new generation even before it has time to find an
intermediate host, within which to develop into a sporocyst. There is
scarcely a doubt but that the bud is formed from the germ cells of the
embryo.

II. POLYSTOMIDÆ.

The eggs in the Polystomidæ also are composed of the
egg-cell proper and yolk-cells (Fig. 93). Their egg-mem-
brane is provided with an operculum, and occasionally with
a long filiform, and twisted process, which serves for the
attachment of the eggs (*Diplozoön*). The course of develop-
ment is simpler than in the Distomidæ, for the embryo
while still in the egg-membrane attains nearly the form of

FIG. 93.—Egg of *Microcotyle Mormyri*.
Within its operculated shell lies an egg-
cell surrounded with yolk-cells (after
LORENZ, from HATSCHEK's *Lehrbuch*).

FIG. 94.—Embryo of *Polystomum
integerrimum*, shortly after hatch-
ing (after ZELLER).

the parent (*Gyrodactylus*), or at least passes through only a
single metamorphosis, not an alternation of generations
(heterogony).

The early development has been but little studied. We
are best acquainted with it (ZELLER, Nos. 16 and 17) in the
case of *Polystomum integerrimum*, which inhabits the urinary
bladder of the frog. The eggs of this species are voided into
the water, where cleavage soon begins. The result of this

is a spherical mass of cells, which subsequently becomes elongated, and thereby exhibits, even at this stage, the form of the embryo. The fundaments of the eyes, the sixteen hooks of the clasping disc [retinaculum], the cavity of the intestine, and the pharynx soon make their appearance (Fig. 94). The newly hatched embryo possesses in addition five rows of cilia, of which the three anterior belong to the ventral surface, the two posterior to the dorsal surface. Furthermore there is a fringe of cilia in front on the head (Fig. 94). The embryo, leaving the egg at this stage, now seeks the tadpole of the frog, to the gills of which it attaches itself by means of the hooks and suckers. Here the ciliated cells, which are no longer of any use to the animal, degenerate, and the Polystomum larva approaches more and more the form of the parent. In extraordinary cases it can attain this condition even in the branchial cavity, but as a rule this is not the case; on the contrary, the young *Polystomum*, upon the degeneration of the gills of the tadpole, penetrates into its mouth-cavity, migrates through the entire length of its intestine, and finally passes from the cloaca into the urinary bladder, where it attains sexual maturity.

Diplozoön paradoxum, which is remarkable on account of its subsequent habits, also leaves the egg as a ciliated larva (ZELLER, No. 18). The larva, known under the name of *Diporpa*, bears suckers and hooks, by the aid of which it attaches itself to the gills of fresh-water fishes (*Phoxinus levis*, for example). It can remain here for weeks and months, gradually approaching the organization of the adult. But before it arrives at this condition it is necessary for one individual to unite with a second, and, in fact, for the rest of their existence. This takes place by the larva seizing with its ventral sucker a knob-like outgrowth situated on the back of the other animal. Then the second individual turns and twists its body, so that it too may grasp the dorsal prominence of its mate with its ventral sucker. In this position the two animals grow together firmly, and in this condition reach sexual maturity.

The course of development in *Gyrodactylus elegans*, one of

the *Polystomidæ*, also living on the gills of fishes, is very remarkable. Its reproduction approaches that of *Monostomum*, already described, for in this species also the embryo while still in the body of the parent contains another embryo; indeed, the latter already exhibits within itself traces of a new individual, so that four generations are included one within the other (WAGENER, METSCHNIKOFF). Accordingly here, as in *Monostomum*, the germ cells produce the new generation very early; but otherwise this developmental process is not very different from that of the other Trematoda. In order to understand the cause of this accelerated production, one would have to know more accurately the processes themselves, as well as the habits of the animal.

III. CESTODA.

The eggs of the Cestodes exhibit a close resemblance to those of the Trematodes. Like these, they are composed of the egg-cell proper and a number of yolk-cells; where the latter are wanting, an accessory yolk-mass corresponding to them appears to be present. The eggs are surrounded by a thin egg-membrane, which occasionally possesses a movable lid. The development of the eggs takes place for the most part in the uterus of the parent, but in many forms it occurs only after the eggs are laid. In the latter case the membrane is thicker.

The investigations of E. VAN BENEDEN and VILLOT on the *Tæniadæ*, and especially those of SCHAUINSLAND on the *Bothriocephalidæ*, have shown that the embryonic development of the Cestoda takes place in a manner quite similar to that of the Trematoda.

According to SCHAUINSLAND, the development of the *Bothriocephalidæ* is accomplished in two different ways, depending upon whether the embryos are developed *before* or *after* oviposition. The undeveloped eggs which are deposited in the water are thick-shelled, operculated, and provided with a large number of yolk-cells. From them emerge larvæ which bear a thick coat of cilia. The eggs of the second kind are thin-shelled, without an operculum, and provided with only

a relatively small amount of yolk material. The embryos contained in them are naked.

The embryonic development of the Bothriocephalidæ approaches closely that of the Distomidæ. Cleavage takes place in much the same way as there. At an early period two cells are differentiated at the two poles of the elongated germ, upon which they rest like a cap. They then grow around it, and constitute the enveloping membrane (*Hüll-membran*). Afterwards another cell is separated off from the spherical cell-mass surrounded by the enveloping membrane, and this at first also covers the germ like a cap, and then grows around it. Later this external layer consists of several cells. It is in this way that the ectoderm is formed. The embryo now consists of a single layer of ectoderm and a solid entodermal mass (Fig. 95). Six chitinous hooks make their appearance in the latter. With this the formation of the embryo is completed. It is said to be composed of the inner (entodermal) mass only. The ectoderm separates from it, so that a space arises between the two. The embryo is now surrounded by two envelopes in addition to the egg-membrane, the ectodermal mantle, and the enveloping membrane. In this

Fig. 95.—Embryo of *Bothriocephalus latus* pressed out of the egg. *Ec*, ectoderm; *Hm*, enveloping membrane (after Schauinsland).

respect, too, the conditions described for the Distomidæ are repeated, and a comparison of Fig. 95 with Fig. 88 (on p. 180) shows without further comment the close agreement of the two groups at this stage of development.

Whereas the embryo quitting the egg leaves the enveloping membrane behind in the egg-shell, it takes the ectodermal mantle with it (Fig. 95). The latter either serves actively in locomotion when it possesses cilia, or it swells up so much in the water that it serves the larva both as a protective

envelope and as a means of making it of nearly the same weight as water, thereby enabling it to float. Where cilia are present, they are at first short, and only gradually increase in length. In *Bothriocephalus latus* the exceedingly delicate cilia attain a very great length. After the larva has floated about in the water for a time, under certain conditions for several days, it divests itself of the mantle, whether ciliated or not. In many cases (as sometimes even in *Bothriocephalus latus*) it may at the very beginning strip off the mantle with the enveloping membrane. Even in this naked condition the larva may live free for a time, but finally perishes, if it finds no suitable host.

SCHAUINSLAND explains the circumcrescence of the germ by the cap-shaped cells, which occurs twice in nearly the same way, as an epiboly. Accordingly he is compelled to assume a complete loss of the ectoderm in the casting off of the superficial layer. The embryo is developed out of the entoderm alone. He finds a support to this view in the fact that up to the present time no actual body epithelium has been found either in the Cestoda or in the Trematoda. This fact is in his opinion an argument that ectodermal structures are not present in these cases, a view that LEUCKART (No. 8) also maintains. In any event the origin of the cuticula-like dermal layer merits a thorough investigation. If, as is to be conjectured, it arises by the metamorphosis of a superficial cell-layer (E. ZIEGLER, SCHWARZE, *et alii*), then it would correspond to the body epithelium. The question whether in the casting off of the outer layer the entire ectoderm is removed, or whether certain of its cells still remain behind, must be difficult to determine on account of the small size of the egg.[1]

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[1] [As is well known, a distinct epithelium could not be found on the external surface in Cestodes and Trematodes. It was natural to connect this fact, the absence of the body epithelium, with the casting off of the external cell-layers in the embryo, and thus to assume that the entire ectoderm was lost. A body epithelium, therefore, could not be present. This question has often been considered, and even recently has been resumed. While some investigators assume that the cuticula which covers the body is secreted by the subcuticular layer, and that the latter is a part of the body parenchyma (BRANDES, LOOS), others maintain that it is a metamorphosed epithelium, and believe they see, more or less distinctly, cell nuclei retained in it (BRAUN, MONTICELLI). The most of these observations refer to the Trematodes, although investigations in this direction have also been made on Cestodes (ZOGRAFF, GRASSI; see Appendix to *Literature* on Cestoda). ZOGRAFF in particular finds that in various Ces-

The formation of the larval membranes in the Trematodes and Cestodes recalls in a striking manner the *Amnion* and *Pilidium* in the *Nemerteans*. Since, however, similar processes do not occur in the *Turbellaria*, —to which relationships are shown by the Trematodes and Cestodes on one side, and by the *Nemerteans* on the other,—and since the Turbellaria are to be considered as the more primitive forms, we have here to do with only analogous phenomena.

The embryonic development of the Tæniadæ differs to some extent from that of the *Bothriocephalidæ*, but leads finally to a similar result (LEUCKART, No. 8; MONIEZ, No. 9; E. VAN BENEDEN, No. 2). A difference is caused from the very beginning by the yolk-material bestowed upon the egg being less abundant, or not in the form of distinct cells. In *Tænia serrata* the egg-cell lies embedded in this yolk-material. In other cases the yolk appears to enter into still more intimate relations with the egg-cell; however, it appears from the somewhat various statements of the authors concerning the different forms that even in these cases the nutritive material becomes separated as early as the first divisions of the egg. There are one or several rather voluminous, generally granular cells, which are thus at first constricted off and then consumed, while the other cellular matter multiplies further. In *Tænia cucumerina*, it is true, the entire egg is said to be transformed directly by means of a rather regular cleavage into the embryonic cell-mass (MONIEZ). In the further development of the Tæniadæ we can find again the characters which we observed in the Bothriocephalidæ, although the details of the process are somewhat different. In the Tæniadæ also certain cells detach themselves at an early period, and grow around the germ as its enveloping membrane. In the Tæniadæ known as the Bladder-tapeworms, the second membrane may present an appearance somewhat different from that with which we have thus far acquainted ourselves. It becomes cuticularized, assumes a radially striated appearance, and thus finally forms a firm membrane about the embryo, which even in this stage is

todes the subcuticular matrix is independent of the connective-tissue body parenchyma, and explains how in the embryo an ectodermal cell-layer still remains behind after the casting off of the ciliated mantle.—K.]

equipped with three pairs of hooks. Furthermore, according to van Beneden, a cortical layer can early be distinguished from the differently constituted internal cell-mass; and Schauinsland also speaks of smaller peripheral cells and larger central ones. It is natural to regard this as a differentiation into the two germ-layers, though Schauinsland believes that such is not the case. According to him, the entire ectoderm, with the two membranes, is excluded from further participation in the formation of the embryo, which consists exclusively of a homogeneous cell-mass: the entoderm. This point, and especially the origin of the layers of the embryo, appears to us in urgent need of renewed investigation.

With Schauinsland, we regard the homology of the embryonal membranes of the *Bothriocephalidæ*, *Tæniadæ*, and *Distomidæ* as unquestionable. The different development of the second membrane—in the one case into a ciliated layer, in the other into a chitinous layer—is determined by the mode of life of the particular worms. Some of them inhabit animals which continually come in contact with water. In these the deposited eggs develop very quickly and require no special protection. The others inhabit land animals. Their eggs reach the outside world while still within the *proglottis*, and the more the already developed embryos are protected against desiccation, the better their prospects for existence. Hence the development of the chitinous membrane. In such *Tæniadæ*, on the contrary, as inhabit aquatic animals, the chitinized embryonal membrane may be absent, and in place of it there may appear a thin membrane, similar to the non-ciliated ectodermal mantle of many *Bothriocephalidæ* (Schauinsland, No. 12).

The further development of the six-hook *embryo* (Fig. 96 *A*) takes place only after it has migrated into an intermediate host. Either this may take place directly,—when the embryo, as in the *Bothriocephalidæ*, is a free-swimming larva, and so at once migrates into an aquatic animal,—or the embryos, still enclosed in the egg-membrane, may enter by passive means into the intermediate host. Generally this happens by the segment of the tapeworm, which crawls about on plants, being swallowed with the food. The proglottis is digested in the stomach, the eggs thereby become free, their membrane ruptures, and the embryos now find themselves within the intestinal canal. They do not remain there long, but penetrate into the in-

testinal wall by means of the boring movements of their hooklets. In this way apparently they arrive in the blood-vessels, and are probably carried along by the blood current, finally to take up their permanent abode in various organs, very frequently in the liver, sometimes in the brain, in the musculature, etc. There a vigorous growth soon begins; this is connected with a simultaneous activity of the sur-rounding tissues, which form a membrane about the intruded foreign body. The latter now casts off its hooks, and on its surface there appears a rather thick cuticula, under-neath which circular and longitudinal muscle fibres are differentiated. Beneath these there follows a cortical layer resembling connective tissue, which differs from the central parenchymatous tissue (Fig. 96 *B*). The latter soon exhibits spaces, in which an aqueous fluid makes its appear-ance. By the coalescing of these spaces with one another, a large cavity filled with fluid finally arises within the body. Herewith the development of the tapeworm has reached the stage which is known as the *Cysticercus, bladder-worm,* or *hydatid.* It has been compared to the sporocyst of the Trematoda, although it presents no particular resemblance to it either in structure or in regard to its further develop-ment.[1]

The excretory system has the same organization in the bladder-worm as in the tapeworm. It is composed of capil-laries which arise in ciliated funnels in the tissues, and discharge into larger stems. The latter unite into the chief trunks, which may fuse to form a short sac at the posterior end and there open to the exterior (G. WAGENER, LEUCKART).[2]

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[1] [In many cases the formation of a cavity in the Cysticercus is greatly reduced or becomes entirely suppressed. There are found in the lungs of crows and in the body-cavity of Lacerta vivipara, for example, Cysticerci of this kind (*Pietocystis variabilis* and *P. dythiridium Diesing*), the body of which is filled with a continuous connective tissue (LEUCKART). Such Cysticercus stages of Cestodes have been designated by the name *Plerocerci* and *Plerocercoids* (M. BRAUN),—by the latter when the scolex is only marked off from the bladder. Such, to a certain extent aberrant, bladder-worms are found in the Tæniadæ, as well as in the Bothriocephalidæ and other Cestodes.—K.]

[2] [The Cysticerci with long caudal appendages, which occur in in-

The Cysticercus may remain for a longer or a shorter time in the condition described, but may increase meantime in
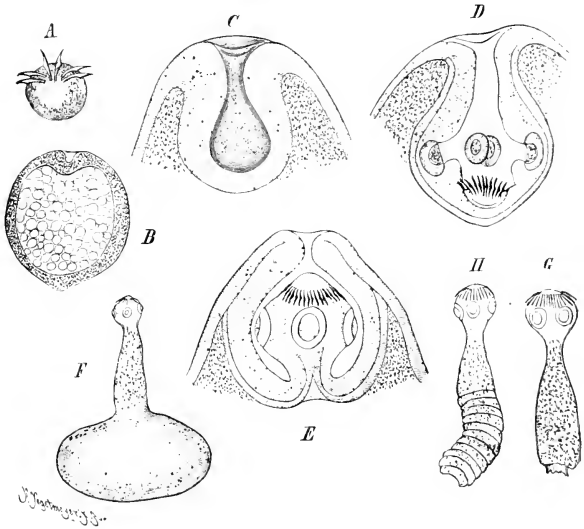
FIG. 96.—*A* to *H*, development of the tapeworm from embryo to scolex (after LEUCKART). *A*, six-hook embryo ; *B*, Cysticercus of *Tænia saginata* ; *C* to *E*, cephalic process of the hydatid (*Cysticercus pisiformis*) of *T. saginata* : *C*, before the fundaments of the suckers and hooks have made their appearance, *D*, with fundaments of the hooks and suckers, *E*, in the partially evaginated condition ; *F*, fully evaginated cephalic process with attached vesicle of *T. solium* ; *G*, scolex of *T. serrata* with the remains of the vesicle, which has fallen away ; *H*, young tapeworm (*T. serrata*), which has only just left the scolex stage, and in which there are therefore only a few segments.]

vertebrated animals, especially in Crustacea (*e.g.* Gammarus and Cyclops), are very noteworthy ; their relationships, however, are not yet sufficiently understood. The caudal appendage, which sometimes attains a very considerable length, carries about with it the remains of the embryonal envelopes. This stage in the development of the Cestodes thereby acquires to a certain extent the appearance of a Cercaria. Such tail-bearing Cysticerci, which belong especially to the genus Tænia, have been repeatedly discovered in recent years, and carefully studied by HAMANN, MRAZEK, and GRASSI E ROVELLI (see Appendix to *Literature* on Cestoda).—K.]

volume. The Cysticercus of *Echinococcus*, which remains for several months in this stage, attains during this period about the size of a walnut, but, as is well known, it may become much larger; that of *Tænia cœnurus* grows in five weeks to the size of a pea. Most of the Cysticerci reach in the course of three weeks or so the diameter of about 1 mm. Then a rapid cell-growth is noticeable at the anterior pole. This grows inward in the form of a knob (Fig. 96 *B* and *C*). Corresponding to the cell-proliferation, there is a pit-like depression on the surface of the vesicle, which increases in depth with the growth of the knob. The entire growth represents the fundament of the head of the tapeworm (*scolex*), which therefore arises as an invagination of the wall of the vesicle (Fig. 96 *B* to *F*). It appears that the want of space, to which the tapeworm is subjected as the result of its mode of life, has the effect of preventing the scolex from arising as an [external] appendage of the body, as would seem most natural, and causes it to be formed as an invagination of the vesicle, which is only subsequently evaginated.

The suckers arise as pit-like depressions of the lateral walls of the cavity of the cephalic knob, and the hooks of the head of the tapeworm are developed at the bottom of this cavity (Fig. 96 *D*). The head is now completely formed in negative. Beginning with the deepest part, the future rostellum (Fig. 96 *E*), the head is completely reversed by evagination (Fig. 96 *F*), and thus attains its permanent form. It then appears as an evagination of the vesicle, which is attached to its posterior end (Fig. 96 *F*).

Before the later developmental processes and the metamorphosis into the tapeworm can be completed, it is necessary for the Cysticercus to enter into another animal. This takes place by its host being eaten in part or in whole by the final host of the tapeworm. In the stomach of the final host the scolex loses the caudal vesicle by its being digested. In Fig. 96 *G* a small remnant of the bladder is still seen attached to the scolex, which has just become free. The scolex usually passes farther back in the intestine, sinks its hooks and suckers into the mucous membrane, and upon the appearance of segmentation becomes an adult tapeworm

(Fig. 96 H). Ordinarily only the neck portion of the
scolex, which is immediately attached to the head, is said
to be included in the adult worm, whereas all the rest dis-
integrates. LEUCKART observed such young stages of *Tænia
solium*, which moved about freely in the intestine of their
host by extending their suckers like arms and again retract-
ing them. They were no longer so much elongated as is
the case after their evagination from the Cysticercus (com-
pare Fig. 96 F), but had only a short stump-like appendage.
The formation of the segments takes place in such a way
that the terminal segment is the oldest, and the youngest
ones are always interpolated in the vicinity of the head.
Growth and formation of segments take place so rapidly
that the tapeworm soon attains a great length, and the
posterior segments become detached from the others. With
the fæces of the host they reach the outside world, where
they are encountered creeping about slowly.

In the younger proglottides nothing can as yet be recognized of the
genital apparatus. This arises out of the parenchymatous tissue in the
central part of the proglottis, which to a certain extent still remains in
an embryonic condition, as the result of a more compact massing of the
cells. This cell-mass, which is at first spherical, later elongates and is
differentiated in such a manner that three cords of cells occupying the
longitudinal axis of the worm can be distinguished. F. SCHMIDT, who
studied these conditions in *Bothriocephalus latus*, found that these three
cell-cords produced the sexual ducts, which, therefore, begin to develop
earlier than the germ glands. In consequence of a luxuriant cell-proli-
feration, these cords increase in length, the ventral one, which is earliest
differentiated, becoming the vagina, the dorsal becoming the vas deferens,
and the extensive cell-mass lying between them becoming the uterus.
In proglottides of *Bothriocephalus* which lie about 50 cm. behind the
head, the sexual ducts have become connected with the surface of the
body, and the sexual openings can be recognized. About 10 cm. behind
the head the genital fundaments appear simply as a dark longitudinal
streak in the middle line of the segments. The germ glands and vitel-
laria likewise arise from the parenchymatous tissue, but independently
of the ducts, with which they become connected by means of cords of
parenchymatous cells, which afterwards become hollow.

General Considerations.—The course of development in the
Cestodes has met with various interpretations. The older conception,
established by STEENSTRUP, looks upon it as a true alternation of
generations. According to this theory, inasmuch as the scolex buds

out from the Cysticercus by non-sexual methods, and then itself sepa-
rates by division into proglottides, each sexual generation, the product
of which is the embryo (Cysticercus), is followed by two non-sexual
generations. On the other hand, in view of the circumstance that in
all probability the continuity of the individual persists, the course of
development in the tapeworm has more recently been explained as a
metamorphosis (Grobben, No. 4; Claus, No. 3). Certain very simply
organized tapeworms, such as *Archigetes*, and a tapeworm living in the
body-cavity of *Cyclops* (Leuckart, No. 7 ; A. Gruber, No. 5), are evidence
in favour of this view. These Cestodes appear to reach the permanent
condition without first passing through the typical Cysticercus stage.
The one last mentioned is converted directly into the sexually mature
animal ; the other is metamorphosed into the sexual animal, simply by
its body becoming separated into an anterior and posterior portion,
whereby the worm acquires a *Cercaria*-like appearance (Leuckart, No.
7). If one considers the posterior portion of the body as equivalent to
the bladder of the Cysticercus, this tapeworm arrives at sexual maturity
even in the Cysticercus stage.

Like *Archigetes*, the unsegmented *Caryophyllæus*, which is provided
with a single set of sexual apparatus, represents throughout life a stage
which is equivalent to the *scolex* of other tapeworms, together with a
single accompanying segment. Therefore the development of the
embryo into the scolex would correspond to a metamorphosis, in which,
however, it is to be noted that with the bladder are cast off parts of the
body which originally represented the body of the entire individual. But
a similar state of affairs exists in the origin of the Nemertean from the
Pilidium, and the starfish from the *Bipinnaria*, without our calling these
processes alternation of generations.

As regards the second process of non-sexual reproduction—namely, the
division into proglottides—those cases are particularly noteworthy in
which, as in some *Acanthobothridæ* and *Echeneïbothridæ*, the proglottides
after detachment are able to live for a long time, and increase to
several times their former volume. They give the impression that one
has to do with independently living individuals resembling somewhat
Distomum. However, one must consider even here the earliest origin
of the Cestodes, and go back to forms which, like *Caryophyllæus* and
Amphiptyches, exhibit only one set of genital apparatus. They might be
traced back through transitional forms like *Amphilina* (comp. *infra*,
p. 201) to forms resembling *Trematodes*. In the beginning only one set
of sexual apparatus was present, later numerous sets made their appear-
ance, and this condition led, by reason of its advantage, to the detach-
ment of individual segments of the body. The *Ligulidæ* may perhaps
give us some foothold in this connection. Even if the conditions which
we find in them are to be considered as regressive, they may, neverthe-
less, be looked upon as reversions to an earlier condition. In the
Ligulidæ the genital organs are repeated without the appearance of an

outward segmentation of the body. The entire animal, therefore, corresponds to an individual with a segmented arrangement of the organs, and not to an animal stock. The genital organs themselves agree with those of the externally segmented Cestodes, and it appears, therefore, as if we had before us in this case a condition which corresponds to a more primitive stage of the Cestodes.

Although, from what has just been said, the course of development of tapeworms would have to be considered as a metamorphosis, it is nevertheless certain that in some forms it represents a real alternation of generations. This is true of those forms in which more than one scolex arises in the Cysticercus. The Cysticercus of *Tænia cœnurus* produces within itself a large number of tapeworm heads (about 500), and in the bladder-worm of *Tænia echinococcus* even daughter-vesicles are formed, which in turn give rise to tapeworm heads. Here, where the embryo produces many individuals, each one of which acquires the organization of the tapeworm, there is unquestionably an alternation of generations. The heads arise by means of budding in the Cysticercus; they grow up into segmented worms, and produce the sexual elements. In this case, therefore, a sexual generation alternates with a non-sexual. The conditions are still more complicated when there is interpolated a generation of daughter-vesicles, which bud from the parent vesicle and in turn alone give rise to the heads.

In conclusion we refer once more to the relation between Cestodes and Trematodes. In addition to other anatomical characters, it is especially the structure of the genital apparatus which brings the two groups very close to each other. In both, the yolk glands, in addition to the germ glands, contribute to the production of the eggs, which are therefore composed of two kinds of cells. The development, too, proceeds in a homologous manner, and shows, above all, a great similarity in the formation of the embryonal membranes. In considering the further stages of the developmental cycle, we are led by such forms as *Archigetes* (see *supra*, p. 199), which must be considered as a sexually mature cysticercoid larva, to the comparison of the Cysticercus stage of the Cestodes with the Cercaria of the Trematodes, in which the caudal appendage of the Cercaria is to be considered as the equivalent of the vesicular posterior end of the Cysticercus (CLAUS). In such an interpretation we must consider the sporocysts and Rediæ as secondarily interpolated links of the developmental cycle. They are essentially larval organisms, reproducing parthenogenetically, in which the organization and the form of the Cercaria have secondarily undergone an alteration and partial degeneration. In most of the Cestodes therefore the development from the egg to the complete tapeworm must be considered as a simple metamorphosis; an alternation of generations being recognizable only in the Echinococcus bladders, where the young forms (Cysticercus stage) possess the power of reproduction by means of budding. The development of the Trematodes, on the contrary, appears under the form of heterogeny, in which

several parthenogenetically reproducing generations of larval forms have been interpolated into the life-cycle. The close relationship of the Trematodes and Cestodes is supported not only by their anatomical and embryological agreement, but also by the existence of a form—*Amphilina foliacea*—which in its external shape more nearly resembles the Trematodes and was formerly reckoned among them (under the name of *Monostomum foliaceum Rud.*), but which, owing to the absence of an intestinal canal and on account of the structure of the genital organs, must be placed among the Cestodes (G. WAGENER, No. 15). Its body is of a leaf-like form, and there is only a single sexual apparatus present. The embryonic development takes place as in the Trematodes and Cestodes (SALENSKY, No. 11). The egg is composed of an egg-cell and yolk-cells. An embryonal membrane is formed, which the embryo breaks through. This is armed with ten hooks, similar to those of the tapeworm embryos.

As regards the derivation of the Trematodes, they are to be referred to free-living, Turbellarian-like Plathelminthes, which adapted themselves to a parasitic life.

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CHAPTER V.

ORTHONECTIDÆ AND DICYEMIDÆ.

THE Dicyemidæ were discovered as early as 1839 by KROHN, the Orthonectidæ in the sixties by KEFERSTEIN and MᶜINTOSH. They were more than once after that the object of investigation (v. KÖLLIKER, G. WAGENER), but a more thorough knowledge of their structure and development was not acquired until recent times. Our knowledge of the latter division of these most simply constructed, parasitic creatures is due principally to the exertions of A. GIARD, METSCHNIKOFF, and JULIN, whereas the Dicyemidæ have been thoroughly studied by E. VAN BENEDEN and WHITMAN.

I. ORTHONECTIDÆ.

SYSTEMATIC : There are only two species known :—

(1) *Rhopalura Giardii Metschn.* (*Rh. ophiocomæ Giard.*, *Intoshia gigas Giard.*), from *Amphiura squamata* ;

(2) *Rhopalura Intoshii Metschn.* (probably synonymous with *Intoshia Linei* and *Leptoplanæ Giard.*), from *Nemertes lacteus.*

The Orthonectidæ, which live parasitically in *Turbellarians*, *Nemerteans*, and *Ophiurans*, exhibit a striking sexual dimorphism. Male and female differ both in form and size (Fig. 97 *A* and *B*). The organization is very simple. The females are composed of only a peripheral cell-layer and a central cell-mass (Fig. 97 *A*). They are spindle-shaped and covered on the surface with vibratile cilia. However, two forms are distinguishable : those with a cylindrical body (*formes cylindriques* of JULIN) and those with a flattened body (*formes aplaties*). Both forms exhibit a kind of external segmentation. They probably migrate out of the body of the Ophiuran (*Amphiura squamata*) which they inhabit, in

order to seek a new host. In the body cavity of the latter, again an Amphiura, their life-history is continued, but in a different manner in the two forms. The *flattened* females are said by JULIN to break up into a number of fragments, each one of which is composed of several central and peripheral cells. These ciliated offspring develop into the "plasmodial sacs" of METSCHNIKOFF (No. 6). These are sac-like structures, which consist of a granulated mass, and exist in large numbers within the body cavity of *Amphiura* and *Nemertes*. The central cells contained in them are to be considered as eggs, and (in consequence of a kind of parthenogenetic reproduction) supply both forms of females. The *cylindrical* females while still in their new host expel their central cells—*i.e.*, the eggs—and these develop into individuals which differ considerably in shape from the females already described. They are the males of *Rhopalura Giardii*, which, according to JULIN, are brought forth by the cylindrical females only. Whereas the body of the female is segmented externally into nine rings, there are

FIG. 97.—*A*, cylindrical female; *B*, male of *Rhopalura Giardii* (after JULIN); *H*, testis; *M*, muscle fibres.

only six rings in the male (Fig. 97 *B*). The second ring, as in the females, is without cilia. The five rows of cells which constitute it contain peculiar highly refractive bodies. Within the animal there is differentiated an oval, sac-like organ of a granular appearance. From it fine cords, which are interpreted as muscle fibres, extend in the body forward and backward. The organ itself corresponds to the testis;

it is found to be full of spermatozoa. The latter present the typical appearance of flagellate seminal filaments (METSCHNIKOFF).

It has not yet been observed in what manner fertilization takes place. JULIN saw that the superficial cells of the male detached themselves, and that in this way the spermatozoa became free. Since males and females swim about free in the water, it is possible that the seminal filaments penetrate into the female, and that consequently fertilization is internal. The eggs destined to produce females develop inside the "plasmodial sacs," those producing males, free in the body cavity of the *Amphiura*. The statements of authors differ greatly regarding the embryonic development.

Development of the Male.—According to JULIN, there arises as the result of the unequal cleavage an epibolic gastrula (comp. Fig. 98 *A* and *B*), the inner layer of which is at first represented by only one large cell. Later, cells are separated from this above and below (Fig. 98 *C*). While the large central cell, by subsequently dividing many times, becomes the fundament of the testis, the muscle fibres arise from the cells that were previously separated off from it, and which at first rest upon it in the form of a cap (Fig. 98 *D* and *E*). The larva assumes the type of the adult animal as the result of the appearance of the characteristic division of the surface of the body into rings, the loss of cilia on the second ring, and the formation in it of the highly refractive bodies.

FIG. 98.—*A* to *E*, stages in the development of the male of *Rhopalura Giardii* (after JULIN); *H*, testis.

According to METSCHNIKOFF, an epiboly does not take place, but there arises a solid heap of cells of rather uniform size, from which the outer layer and the genital fundament are subsequently differentiated. On the

other hand, GIARD in his first communication described the formation of an epibolic gastrula.

Development of the Female.—The first stages of cleavage are not known. According to JULIN, there is produced here also an epibolic gastrula, the entoderm of which consists even at an early stage of a large number of cells. A peripheral layer is said to be differentiated from it into a layer of cylindrical cells, which, situated under the ectoderm, surrounds the central mass of polyhedral cells. When the embryo has elongated and acquired its coat of cilia, it presents a great resemblance to the embryos of the *Distomidæ* and *Bothriocephalidæ*. The outermost of its three cell-layers would then correspond to the enveloping membrane (*Hüll-membran*). Out of the second cell-layer, which later becomes flattened, there is said by JULIN to arise a system of extremely delicate muscle fibres, which are found under the ectoderm in the adult female.

According to GIARD and METSCHNIKOFF, during the development of the female a regular blastula makes its appearance, out of which the two germ-layers are formed possibly as the result of delamination.

The above presentation of the life-history and development of the Orthonectidæ does not rest wholly upon reliable observations, but many gaps in it have been filled by the speculations of the authors. We have adhered chiefly to the account of JULIN, for his work is the most complete and is an advance upon that of GIARD and METSCHNIKOFF.

II. DICYEMIDÆ.

SYSTEMATIC : VAN BENEDEN distinguishes four genera : *Dicyema, Dicyemella, Dicyemina,* and *Dicyemopsis,* which are distributed among four genera of Cephalopods : *Octopus, Eledone, Sepia,* and *Sepiola.* They are found in the appendages of the branchial veins. WHITMAN admits only two genera : *Dicyema* (with eight cells in the head region) and *Dicyemennea* (with nine cells in the head region).

The body of the *Dicyemidæ* is elongated. It consists of an outer layer of ciliated cells and a single large axial cell, the latter surrounded by the former (Fig. 99 *D*). At the anterior end the outer cell-layer is differentiated into a kind of cap [polar calotte]. Elsewhere the outer cells are nearly alike.

A certain difference in individuals is manifested in the manner of their reproduction. The latter consists in the production of embryos in the axial cell. But these are of different shapes; vermiform and infusoriform (rhomboid) embryos can be distinguished (Figs. 99 and 100). They arise in different individuals, which, according to VAN BENE-DEN, are recognizable even by their outward form. The *nematogenous* individuals are longer and more slender, the *rhombogenous* shorter and more compressed.

According to WHITMAN, in addition to the forms that bring forth only vermiform embryos, and which he designates as *primary Nematogens*, there also occur forms in which at first infusoriform and later vermiform embryos are produced (*secondary Nematogens*).

Development of the Vermiform Embryos.—There

can hardly be any doubt that the cells which constitute the earliest fundament of the reproductive elements, and which correspond to the genital cells of the other Metazoa, take their origin by the division of the axial cell of the parent. The products of this process of division are, however, not equivalent; moreover, the newly formed cells remain in the axial cell (Fig. 99), whereby the appearance of an endogenous cell-proliferation is produced. The production of the germ cells begins very early, for even in embryos there is to be seen inside the axial cell and behind its nucleus a new cell undergoing differentiation, the first germ cell (Fig. 99 *A*), and a second one soon arises in its anterior part (Fig. 99 *B* and *C*). Their nuclei have very probably arisen by division from the nucleus of the axial cell. Subsequently the latter takes absolutely no part in the formation of new nuclei. It appears to preside over the other cell functions only. The two germ cells, on the contrary, begin to increase by division, and soon furnish a large number of genital cells, from which the embryos subsequently arise.

The development of the germ cells, which are eventually present in large numbers within the axial cell of the parent, takes place *in situ* after the manner of cleavage. An epibolic gastrula is formed here, as in the *Orthonectidæ*, except that its inner large cell remains undivided. It becomes the axial cell.

By increasing in length the embryo becomes vermiform, whence its name (Fig. 99 *B* and *C*). These embryos are not essentially different from the adult animal, whose shape is soon fully assumed by the accomplishment of the slight differentiations in the outer layer of the body and in the head region, and by the elongation becoming more pronounced (Fig. 99 *C* and *D*). Then the formation of new germs in the axial cell begins very early, in fact while the embryo still remains within the parent. The processes described apply therefore to embryos which are still found within the parent (Fig. 99 *A* to *D*). When they have arrived at maturity, they break through the outer layer of the parent, but remain in the venous appendages of the Cephalopods, where they still grow considerably and produce other embryos.

FIG. 99.—*A* to *D*, stages in the development of the vermiform embryos of *Dicyema*; *A*, of *Dicyemennea eledones* (after WHITMAN); *B* to *D*, of *Dicyema typus* (after E. VAN BENEDEN). *Ax*, axial cell; *K*, nucleus of the axial cell; *Kz*, germ cells.

Structure and Development of the Infusoriform Embryos. — The infusoriform embryos differ widely from the vermiform in shape. Of a shorter, more compressed form, they also present numerous internal differentiations (Fig. 100 *D* to *F*). In swimming, the broader end of the embryo is directed forwards. Whereas the anterior end is naked, the rest of the body is ciliated (Fig. 100 *C* and *D*). The entire embryo is constructed on the bilateral plan, for two lateral parts as well as a dorsal and ventral side can be distinguished. Anteriorly and more dorsally lie two highly refractive bodies (Fig. 100 *D*, *r*), somewhat behind them, and lying more ventrally, the organ called by VAN BENEDEN the "urn." This peculiar organ, the function of

which is not clear, is composed of a shell-like envelope, a
granulated body contained in it, and a lid. The shell lies
with its cavity toward the ventral side (Fig. 100 F). It
consists of two parts and, owing to small comma-shaped
bodies embedded in its free edge, acquires a striated appear-
ance (Fig. 100 D, E). Its contents consist of four large
cells of nearly equal size, which lie close together, and are
granular. Finally, the lid, which corresponds to the ventral
part of the urn, consists in turn of four cells, which unite, at
the point where they all abut on one another, to form the
knob of the lid (Fig. 100 D to G, l). Within the urn VAN
BENEDEN sometimes observed a ciliation, which he ascribed
to the granulated cells.
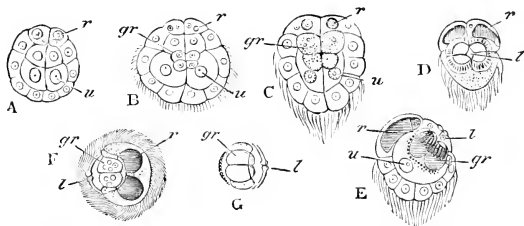
FIG. 100.—A to G, infusoriform embryos and their development—A to D, of *Dicyema
typus*; E to G, of *Dicyemella Wagnerii* (after VAN BENEDEN, from BALFOUR's *Compara-
tive Embryology*). A to C, stages of development; D, embryo seen from the ventral
side; E, from the right side; F, from the front; G, the "urn" isolated; gr, granu-
lated cells contained in the urn; l, its lid; u, the shell, which forms the floor of
the urn; r, highly refractive bodies at the anterior end of the embryo.

The origin of the infusoriform embryo, although at first
sight quite different from that of the vermiform embryo,
can perhaps be referred to this. It takes place in the axial
cell of the rhombogenous individuals, though not directly,
being introduced by a preparatory process (WHITMAN).

Near the nucleus of the axial cell there arise two new
cells, the nuclei of which in all probability originate from the
nucleus of the axial cell. These two cells soon multiply, but
not so rapidly as in the formation of the vermiform embryos.
They never exceed eight in number, and often only a few
are present. Before these cells develop further they undergo

a process which WHITMAN compares to the formation of the polar globules in the eggs of the Metazoa. As the result of a process of division a considerable portion of the nucleus is said to be cast out of them, which, as the "paranucleus," can be recognized for a long time in the axial cell (Fig. 101 *B*). Then ensue a cleavage of the cells and, as its result, the formation of cell-masses which have quite the appearance of an epibolic gastrula with a central cell. Such stages had already been observed by van BENEDEN (Fig. 101 *A*). They are entirely like those which occur in the development of the vermiform embryos. WHITMAN compares them directly to these, and looks upon them as special individuals, which appear early in the course of reproduction. For in their central cells there are soon formed new cells (Fig. 101 *A* and *B*), which subsequently give rise to the infusoriform embryos. On this account WHITMAN calls this gastrula stage an *Infusorigen*. Compared to the nematogenic developmental series, the gastrula stages would correspond to the vermiform embryos, which, as we saw, also produce embryos at a very early period.

From the central cell (*cellule ger-migène* of van BENEDEN) of the gastrula stage, which increases in size, arise several generations of germ cells, which surround it in the form of a rosette.[1] The larger of these cells become infusoriform embryos; the smaller ones are said subsequently to divide repeatedly, and vermiform embryos are said to arise from them when, after the formation of the in-
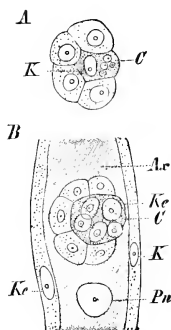
FIG. 101. — *A*, "Infusorigen embryo" (after van BENEDEN); *B*, the same lying in the axial cell (*Ax*) of the rhombogen individual (after WHITMAN). *A*, of *Dicyema typus*; *B*, of *Dicyemennea eledones*. *C*, the central cell of the "Infusorigen embryo," which has already produced new germ cells; *K*, nucleus of the central cell; *Ke*, nuclei of the outer layer of the rhombogen individual; *Pn*, paranucleus. On the right side of Fig. 101 *B* the references *K* and *Ke* are transposed.

[1] The central cell itself is to be looked upon as the homologue of the axial cell of the vermiform embryos.

fusoriform embryos, the rhombogen individuals have entered upon the second phase of their development (*secondary Nematogens* according to WHITMAN).

The formation of the infusoriform embryos from the germ cell also begins with a process of cleavage, the result of which is an epibolic gastrula (E. VAN BENEDEN). However, in this case several cells make their appearance in the centre, at first four large ones (Fig. 100 *A, u*). Two of these become the shell and two the lid of the urn ; whereas four smaller cells, which arise later, supply the four granular cells contained in the urn (Fig. 100 *B* and *C, gr*). In the meantime the two highly refractive bodies have made their appearance in the outer layer of the embryo (Fig. 100 *A, D, r*), and its posterior portion has become covered with cilia. Whereas at first the embryonal cells which become the urn lie side by side, they subsequently alter their position so that the granular cells become enclosed above and below by the lid and shell of the urn.

Nothing definite is yet known about the significance of the infusoriform embryos. From the fact that they can be kept alive in sea-water for days (E. VAN BENEDEN), it was thought that these forms were probably for the purpose of transferring the species from one cephalopod individual to another, where they would develop into a form which, like the vermiform embryos, produces new germs. Besides this view, there is a second one, which compares the infusoriform embryos to the male of the Orthonectidæ. VAN BENEDEN is inclined to see in the granular and vibratory contents of the urn the homologue of the testis of the Orthonectidæ. WHITMAN several times observed the penetration of infusoriform embryos into nematogen individuals, which is perhaps to be compared to a process of fertilization.

Related to the Dieyemidæ are the *Heterocyemidæ* (*Conocyema* and *Microcyema*), observed by VAN BENEDEN (No. 2), which also inhabit the appendages of the veins of *Octopus* and *Sepia*. Their shape differs from that of the Dicyemidæ inasmuch as they do not nearly attain the length that these do, and wart-like structures are present at the anterior end, which can be extended and withdrawn. Nematogen and rhombogen individuals are also distinguished here. Although the vermiform embryos

differ somewhat from those of the Dicyemidæ, yet on the whole they develop like them. The infusoriform embryos of *Conocyema* resemble those of the Dicyemidæ.

General Considerations.

There are so many common features in the structure and development of the Orthonectidæ and Dicyemidæ that we cannot doubt the relationship of the two groups. Their relations to the other divisions of the animal kingdom, on the contrary, are more difficult to understand. In view of the fact that they are said to be composed of only two germ-layers, an attempt was made to create out of them a new division of the animal kingdom, that of the *Mesozoa*, which would be interpolated between the *Protozoa* and the *Metazoa* (E. VAN BENEDEN, JULIN). Since it is only parasitic forms with which we have to do, such an explanation seems to us venturesome at least, and we consider it more probable that these simply constructed animals are Platyhelminthes which have become degenerated through parasitism (LEUCKART, METSCHNIKOFF, WHITMAN).

The resemblance of the female of the Orthonectidæ to the embryos of the *Distomidæ* has already been pointed out. The theory that such embryos have reached sexual maturity has nothing improbable about it, for such cases are also known elsewhere in the animal kingdom. Thus *Dinophilus* is evidently to be regarded as an annelid larva which has become sexually mature, and it is appropriate for comparison here, inasmuch as its males have degenerated to nearly the condition of the Orthonectidæ and Dicyemidæ (comp. *infra*, p. 313). The intestine and other features of a higher organization having been lost, they present within the body only a large testicular sac, similar to the males of the Orthonectidæ, which, to be sure, remain at a somewhat lower stage.

If we regard the Orthonectidæ and Dicyemidæ as degenerated forms, then the Orthonectidæ, with their central cell-mass, would represent the higher grade, whereas the Dicyemidæ, in which only *one* central cell is present, are more degenerate. However, in these also the inner portion becomes multicellular as soon as the formation of the germ cells by the division of the axial cell begins.

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CHAPTER VI.

NEMERTINI.

The Nemerteans lay their eggs enclosed in gelatinous enve-
lopes, either singly or balled into large masses of spawn. It
appears that fertilization may take place either outside or
inside the body of the female. In the latter case the sperma-
tozoa penetrate into the female genital organs (egg sacs)
through their efferent ducts. In many forms (*Monopora
vivipara*) the eggs are there developed up to the maturity of
the embryo. The development takes place either directly or
by means of a metamorphosis. The latter is of various kinds,
according as a free-swimming larva differing very much from
the ultimate shape of the animal is produced, or merely a
larval form which does not differ essentially from the young
animal, but which nevertheless produces the latter within
it. In the first case, in view of the shape of the larva, one
speaks of a *Pilidium larva*, in the latter case, of development
after the *type of Desor*, thus named from its discoverer.

I.—Development through the Pilidium Larva.

As the result of the equal cleavage a regular *blastula* arises
from the egg of *Lineus lacteus*. It loses its regular shape,
owing to a considerable increase in the size of the cells of
the lower half and to the occurrence at the same time of a
flattening on the under-side of the blastula (Fig. 102 *A*).
The outer and inner germ-layers can be distinguished on the
blastula as early as this, for the cells of the ectoderm are
smaller than those of the entoderm. The first trace of the
middle germ-layer is likewise already present. In the cleav-
age cavity and in contact with the entoderm are found a
number of cells (Fig. 102 *A*) which to all appearances take
their origin from the entoderm (Metschnikoff, No. 20), and

subsequently prove to be mesenchymatous migratory cells
(Fig. 102 *B* and *C*), like those which arise in the develop-
ment of the *type of Desor*.

After the blastula becomes covered with cilia, has assumed
its characteristic shape, and has acquired a large flagellum
at its apex (Fig. 102), it may break through the egg-mem-
brane to swarm about at large. More often, however, the
larva reaches the outside world only after invagination has
taken place, *i.e.* as a gastrula. This is accomplished by the
symmetrical invagination of the already-formed entoderm
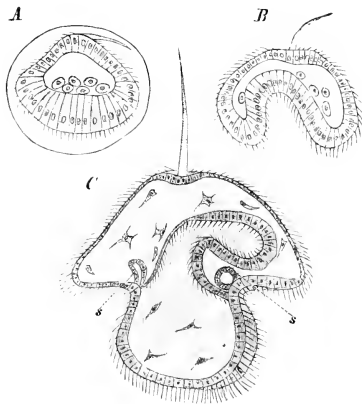
FIG. 102.—*A* to *C*, blastula, gastrula, and pilidium of *Lineus lacteus* (after METSCH-
NIKOFF); *C*, combination of two of METSCHNIKOFF's figures; *s*, ectodermal in-
vaginations, which subsequently grow around the intestine as the prostomial and
metastomial discs.

(Fig. 102 *B*). The *blastopore* is circular, and the entire larva
presents a radial form. This is soon changed, however, for
the blastopore elongates somewhat and becomes oval, while
the archenteron bends to one side, and its blind end grows
more and more toward one wall (Fig. 102 *B*). In this way
the form of the larva becomes bilaterally symmetrical. The
larva assumes its permanent shape—*i.e.*, the one which its
discoverer, JOH. MÜLLER, designated as *pilidium*—by the

downgrowth of a lobe on either side of the blastopore (Figs.
102 *C* and 103). It now consists therefore of an upper bell-
shaped part, which we call the umbrella, and the two pen-
dent lateral lobes. Between the two latter, on the under-
side of the umbrella, lies the wide mouth-opening (Figs. 102 *C*
and 103). It leads into the œsophagus, which corresponds
to an ectodermal invagination, whereas the real entoderm is
represented by the intestinal sac back of it (Fig. 102 *C*).
The intestine of the larva, the cells of which are provided
with cilia, remains closed.

Like Turbellarian larvæ, the pilidium is encircled by a
continuous band of cilia, which fringes the periphery of the
umbrella and the margins of the lateral lobes. The ciliation
of the band is distinguished from that of the rest of the
body by its longer cilia (Figs. 102 *C* and 103). The par-
ticularly stout flagellum already mentioned takes its origin
in a depression at the apex, corresponding to which there is
a thickening of the ectoderm. The latter has been compared
to the apical plate of the *Trochophore* larvæ of the Annelida
(comp. *infra*, p. 266).

As in the annelid *Trochophore*, two muscle strands, which also seem to
contain nerve fibres, issue from the apical plate (SALENSKY, No. 25). The
presence of these cords would not constitute, however, the only resem-
blance to the annelid larva, but, according to SALENSKY, the ciliated band
is also accompanied by a nerve cord, which would correspond to the
ring-nerve in the ciliated zone of the Trochophore. This nerve cord, which
is composed of nerve fibres and ganglionic cells, is said indeed to present
a more varied histological differentiation than the ring-nerve of the an-
nelid larva. At the point where the nerve cord passes from the lateral
lobes to the umbrella, it forms ganglionic swellings, which SALENSKY
interprets as the central organ of the nervous system.

The inside of the larva, between ectoderm and entoderm,
is filled with a gelatinous mass, in which the variously
shaped mesenchymatous cells are found embedded (Fig. 102).
These become at first the muscle-bands which traverse the
larva at regular intervals; subsequently they become in part
the mesodermal elements (connective tissue, musculature,
etc.) of the adult animal (BÜTSCHLI, No. 2).

The pilidia of different Nemerteans differ from one another in shape as the typical form described above *is more or less distinctly developed.* In place of the flagellum, *Pilidium gyrans* bears a tuft of cilia at the apex (Fig. 103). In *Pilidium auriculatum* (LEUCKART UND PAGENSTECHER) the two lateral lobes are only very slightly developed, and the *Pilidium brachiatum* described by E. B. WILSON, which resembles *P. auriculatum*, possesses, in addition to the two slightly developed lateral lobes, three
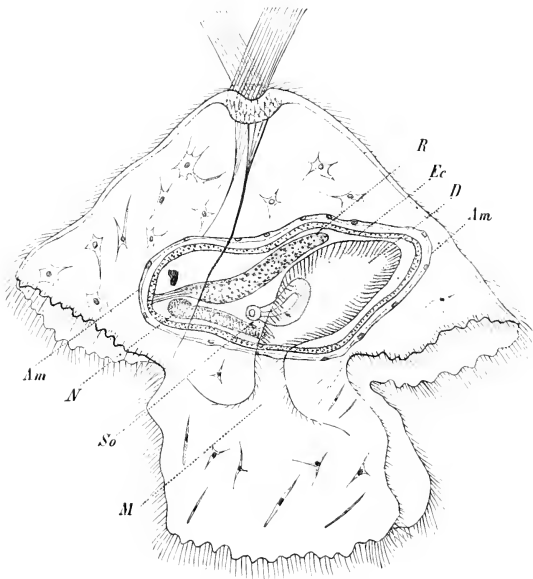
FIG. 103.—*Pilidium gyrans*, with completely formed worm inside (combined from two of BÜTSCHLI's figures). *Am*, amnion; *D*, intestine of the pilidium already surrounded by the worm; *Ec*, ectoderm of the worm; *M*, mouth of the pilidium; *N*, fundament of the nervous system; *R*, proboscis; *So*, lateral organs.

additional ones, which have arisen by indentations of the edge of the umbrella.

The *Pilidium recurvatum* found by FEWKES (No. 5) at Newport exhibits a very aberrant form, which, by the absence of the lateral lobes, by the lateral curvature of the upper part, and by the presence of a row of cilia at the posterior end, acquires a striking resemblance to the *Tornaria* larva

of *Balanoglossus*. Moreover, the metamorphosis of this larva is said by Fewkes to be accomplished in a manner different from that of other Pilidia. Whereas usually the larva remains intact even after the maturity of th worm, and in this condition is abandoned by it, in the present case the collapsed Pilidium, after the withdrawal of the *Nemertean*, is said to hang to its posterior end, where it is gradually resorbed, in the same way as the *Pluteus larva* is drawn into the body of the young sea-urchin.

After Gegenbaur had expressed the view that possibly a new animal was developed within the *Pilidium*, this idea was more precisely defined by Krohn, who maintained that regularly a young Nemertean arises from the pilidium. Leuckart und Pagenstecher were able to raise this view to a certainty, for they (No. 17) followed the development of the Nemertean inside the pilidium. The accompanying processes were then fully elucidated by Metschnikoff (No. 19) and Bütschli (No. 2).

The formation of the Nemertean in the pilidium is initiated by the appearance of four pit-like depressions of the ectoderm in the region of the mouth. Externally these present the appearance of round suckers, for which at one time they were mistaken by Joh. Müller. As the depressions become deeper they become sac-like in shape (Fig. 102 *C*), and the wall directed toward the intestine of the larva is much thicker than the outer one. The further changes of the invaginations consist in their being constricted off from the ectoderm, becoming considerably expanded and growing around the intestine of the larva (Fig. 104 *A* and *B*). They have now assumed more of a discoid shape. At the points where they come together the discs fuse, and their thicker wall, the one directed inwards, constitutes the superficial layer of the body of the Nemertean, whereas their thin outer layer forms around the body an envelope, which is known as the *amnion* (Fig. 103 *Am*). This separates from its connection with the body of the worm, which it surrounds as a delicate membrane. The anterior pair of discs becomes the head of the Nemertean (as far back as the lateral grooves), whereas the posterior pair gives rise to the ectoderm of the rest of the body (Fig. 104 *A* and *B*). Consequently the anterior discs, which, moreover, are the first to fuse, are known as the *head-* [*prostomial*] *discs*, the posterior as the *trunk-* [*metastomial*] *discs*. The union of the anterior with the

posterior pair does not take place until the components of
each pair have completely united with each other. At the
point where the two prostomial discs first come together an
invagination is formed, the fundament of the proboscis,
which soon grows backward a long distance (Fig. 104 *A* and
B, R).
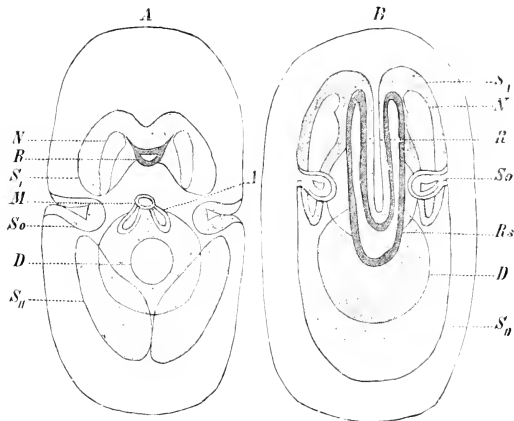
FIG. 104.—Diagrams to show the formation of the Nemertean (after SALENSKY).
A, evaginations of the œsophagus (considered by HUBRECHT to be the fundaments
of the nephridia); *D*, intestine ; *M*, mouth ; *N*, fundament of the nervous system ;
R, proboscis; *Rs*, sheath of the proboscis; *S*, prostomial [head-] discs ; *S_{II}*, meta-
stomial [trunk-] discs ; *So*, lateral organs.

The position of the young worm in the *pilidium* is illus-
trated by Fig. 103. The larval intestine is entirely included
within the worm. Meanwhile the œsophagus continues to
pass through the body-wall of the worm, still terminating in
a wide opening, until at a later stage it fuses with the ecto-
derm of the worm and is displaced to a position relatively
further forward.

The lateral organs are said by SALENSKY and HUBRECHT to arise in the
same way as the somatic discs. They originate as two invaginations of
the wall of the pilidium, one on either side of the œsophagus (Fig. 104
A, So), then grow out toward the somatic discs, and finally separate from

their connection with the primary ectoderm of the *pilidium*, in order to fuse with that of the somatic discs (Fig. 104 *B*). Thus they are said to be formed directly as parts of the pilidium.

The nervous system of the young worm makes its appearance in the form of two ectodermal thickenings (Fig. 104 *N*), which arise in the region of the anterior pair of discs on either side of the invagination of the proboscis. At this place the ectoderm cells are differentiated into several layers, of which the more superficial are said to become the body epithelium and the ganglionic cells, the deeper, the *Punktsubstanz*. The anterior thickened parts of the fundaments correspond to the brain, and their backward prolongations to the lateral nerve-trunks (Fig. 104 *A* and *B*). According to this, the fundament of the central nervous system would have nothing to do with the apical plate of the larva.

Even before the discs had separated from the ectoderm, mesenchyma cells were applied to their inner (deeper) layer; and since such cells were also found in the region of the larval intestine, a considerable number of them came to be enclosed within the worm (BÜTSCHLI, SALENSKY). Like the separate fundaments of the cephalic and somatic parts, the fundament of the mesoderm is double. In the first place, a mass of mesenchyma cells is formed on each of the two prostomial discs, and a similar one at the apex of the invagination of the proboscis. It could not be determined whether the latter originated from the former. Then each disc has its own mesenchyma layer, which likewise has arisen by an accumulation of mesenchyma cells. The anterior and posterior parts of the body are established, therefore, quite independently. The mesenchyma of the trunk is said by SALENSKY to split into two layers, one of which is applied to the intestine as the splanchnic layer, the other to the body-wall as the somatic layer. A kind of cœlom thus arises, which, to be sure, subsequently becomes reduced and breaks up into small cavities, owing to the cells of both layers sending out processes which unite with one another. In the head that part of the mesoderm which is applied to the prostomial discs becomes the musculature, whereas the layer in contact with the proboscis splits into two cell-layers, one of which is applied to the proboscis, while the other forms the sheath of the proboscis. Accordingly the cavity of the proboscis-sheath would be a portion of the cœlom (SALENSKY). The proboscis and its sheath attain their subsequent great length by growing backwards (Fig. 104 *B*).

[The results of a recent investigation by BÜRGER (Appendix to *Literature* on Nemertini) differ in several particulars from the account given above. The formation, and especially the differentiation, of the head- and trunk-discs, the formation of the head itself, and the development of the nervous system are there described quite differently. The musculature of the dermo-muscular sac appears to be of double origin, inasmuch as the outer layer of it arises from the ectoderm, but the remaining portion from the mesoderm.

Similar statements are also made regarding the Annelids.—K.]

When the development of the worm has progressed as
far as this, it breaks through the *amnion* and *pilidium* and
swims about free in the water by means of its covering of
cilia. At this stage it lacks the anus, which arises only
later. In some cases eye-spots are present; in others they
are absent.

II.—Development after the Type of Desor.

For the more intimate knowledge of the mode of develop-
ment in the type known as that of DESOR, we are chiefly
indebted to J. BARROIS (No. 1). Recently HUBRECHT (Nos. 9
to 11) has reinvestigated the subject.

Here also, as in the development of the pilidium, an
invagination gastrula arises, which at first is radial, subse-
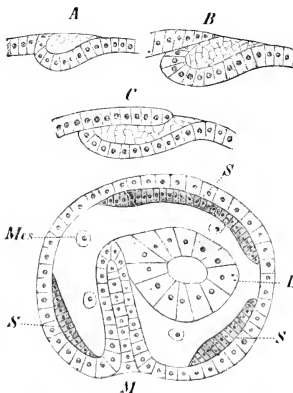
FIG. 105.—*A* to *C*, formation
of the somatic plates by in-
vagination in *Lineus obscurus*
(after J. BARROIS).

FIG. 106.—Section of an em-
bryo of *Lineus obscurus* (after
HUBRECHT). *D*, intestine; *M*,
mouth, which, however, like
the œsophagus, is closed by
cells; *Mes*, mesenchyma cells;
S, discs which subsequently
form the ectoderm of the worm.

quently bilaterally symmetrical. According to HUBRECHT,
cells (the mesenchyma cells) are said to migrate into the
blastocœle from both ectoderm and entoderm (Fig. 106).
On the ventral surface of the ectoderm BARROIS found a pair
of invaginations in front of the mouth and another behind
it. He saw that these invaginations were closed by the
growth of the ectoderm over them, and that finally their
floor became separated from the rest of the ectoderm (Fig.

105 *A* to *C*).   In this way there arose under the ectoderm four
cell-plates, corresponding to the prostomial and metastomial
discs of the pilidium, but distinguished from them by the
fact that they are not composed of two layers, but of only
one cell-layer (Fig. 106).   When subsequently they grow
around the embryonic intestine, there is thus formed only
one cell-layer, the body-wall.   The amnion is wanting (Fig.
107 *B*).   The body, of course, is still surrounded by the
larval skin, the original ectoderm.   At the place where the
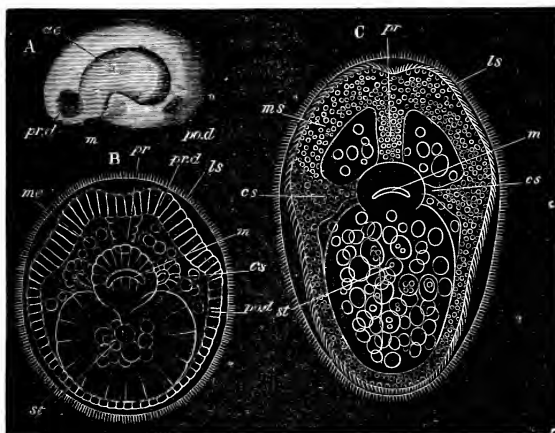
Fig. 107.—*A*, gastrula stage of *Lineus obscurus*, seen from the side; *B* and *C*,
older embryos of *Lineus* seen from the ventral surface (after Barrois, from Bal-
four's *Comparative Embryology*); *ae*, archenteron; *cs*, lateral organs; *ls*, larval
skin; *m*, mouth; *me* and *ms*, mesenchyma; *pr.d*, prostomial disc; *po.d*, meta-
stomial disc; *pr*. proboscis; *st*, stomach.

prostomial discs come together, the proboscis arises as a
solid ingrowth of the ectoderm, which subsequently becomes
hollow (Fig. 107 *C*).

HUBRECHT describes a fifth plate, derived from secondary ectoderm, in
addition to the four plates found by BARROIS (Fig. 106 *S*).   It is said to
be formed on the dorsal side of the embryo, but in a different manner

from the four ventral plates, namely by delamination. HUBRECHT derives the epithelium of the young Nemertean from the fusion of these five plates.

HUBRECHT likewise differs from BARROIS and SALENSKY in his description of the mode of origin of the proboscis. The latter authors derive it from the secondary ectoderm, but according to HUBRECHT it arises from the primary ectoderm and subsequently separates from this and fuses with the secondary ectoderm. When one considers that the lateral organs, according to the concordant statements of HUBRECHT and SALENSKY, take their origin from the primary ectoderm, then such a mode of origin of the proboscis might perhaps be intelligible. Small argument, it is true, is to be got from the fact that in the *pilidium* the proboscis arises from the secondary ectoderm. *Pilidium* evidently represents the more primitive state, and on this account one must also expect in it the more primitive condition as regards the mode in which the organs originate. As to the lateral plates, which are to be considered as sensory organs, it is easier to suppose that they were already present in the larva, whereas this is scarcely probable for the proboscis.

The statement of BARROIS that the mesenchyma cells are detached from the somatic discs seems to need revision. We have already become acquainted with the origin of these cells in the pilidium. In the cephalic part of the embryo they are applied in part to the proboscis (as its musculature), and in part they are arranged in the vicinity of it to form the proboscissheath. In this particular also HUBRECHT differs from SALENSKY, for he considers the pocket of the proboscis to be the remains of the *blastocœle*, whereas SALENSKY maintains that it arises (as a kind of cœlom) by means of a splitting of a mesenchyma-layer. HUBRECHT also looks upon the blood lacunæ and the cavities of the vessels, the walls of which as well as the body musculature are of a mesenchymatous nature, as remnants of the blastocœle. He likewise derives the fundament of the nervous system from the mesenchyma, a conclusion which is wholly discredited by SALENSKY, since in the development of *Pilidium* this observer recognized the nervous system to be ectodermal in nature; this, moreover, agrees with the ordinary mode of origin of this system of organs. On the other hand, HUBRECHT is inclined to derive the genital organs, which make their appearance at an early period, from the ectoderm.

While the proboscis and its sheath have grown considerably farther backwards, striking changes have taken place in the intestine. It consists, as in the *pilidium*, of a posterior wider part and an anterior narrower portion, although in this type even the latter is said to be of entodermal nature. The anterior part becomes solid as the result of cell-growth (Fig. 106), but subsequently is hollowed again, and its lumen

then communicates both with the lumen of the intestine and with the outer world. Therefore the permanent mouth still lies at the place of the *blastopore*. At about the time of the closure of the blastopore the ciliated embryo breaks through both the embryonal envelope, which is likewise ciliated, and the egg-membrane, to continue its development in the free condition.

According to HUBRECHT, the paired fundaments of two nephridia (?), which only later would come into connection with the outer world, arise as vesicular structures from the œsophagus, and consequently from the entoderm (for the œsophagus is said to be of entodermal nature). In the development from the *pilidium* these structures are found on the anterior intestine (Fig. 104 *A*), which here is of ectodermal nature.[1]

III.—Direct Development.

A transition from the indirect to the direct development is afforded by the Nemertean studied by DIECK: *Cephalothrix galatheæ*. Here a ciliated *blastula* arises as the result of the tolerably regular cleavage. DIECK is inclined to look upon a wide cup-shaped depression, which makes its appearance on the blastula, as evidence of relationship with the *pilidium form*, for an extension of the edges of the depression would result in the lateral lobes of the *pilidium*. But a process which is accomplished later recalls far more the indirect mode of development of other Nemerteans than this outward shape of the embryo does. *After the embryo has elongated and has assumed a rather worm-like shape, the layer of ciliated cells covering it begins to be cast off, and under it a new coat of cilia is immediately developed.* Apparently here also, as in the type of DESOR and in the *pilidium*, the new covering of the worm is formed under the larval skin; a great simplification in the mode of development has, however, taken place. Special plates, which enlarge and unite to form the new body-covering, are no longer formed as the result of invaginations of the larval skin, but the body-covering is

[1] [These organs have also been recently recognized by BÜRGER (Appendix to *Literature* on Nemertini) to be nephridia, and their origin is likewise referred by this author to the ectodermal anterior intestine.—K.]

split off directly from the larval skin. This process takes
place on the free-swimming larva, for long before this the
embryo had broken through the egg-
membrane. Even at the time of its be-
coming free, it exhibits at its anterior
and posterior ends stout cilia (Fig. 108),
which are likewise a reminiscence of the
pilidium stage.

Stout cilia, or tufts of cilia, arise at
the ends of the body of the embryo even
in those forms in which the development
has become quite direct (*Amphiporus,
Tetrastemma, Malacobdella*), and in which
no other points in harmony with indirect
development are still found,—apparently
an indication that development by
means of a ciliated free-swimming larva
is the more primitive mode, direct de-
velopment, on the contrary, the derived
method.

FIG. 108.—Embryo of
Cephalothrix galatheæ
just hatched (after
DIECK).

Cleavage and the production of the germ-layers in the forms developing
directly do not appear always to take place in the manner which we have
hitherto considered. In *Monopora vivipara*, it is true, after an irregular
cleavage there arises from the *blastula* an *invagination gastrula* (SALEN-
SKY); other forms, on the contrary (*Amphiporus lactifloreus, Polia car-
cinophila, Tetrastemma varicolor*), are said to possess a *delamination
gastrula* (BARROIS, HOFFMANN). The sheet of long prismatic cells which
forms the blastula splits into an outer and an inner layer. The former
corresponds to the ectoderm, whereas the latter again separates into a
double layer, the outer the mesoderm, the inner one the entoderm.
In *Tetrastemma* the differentiation of these cell-layers takes place in a
solid mass of cells, a part of which remains at the centre and is employed
only as food material. In *Malacobdella* also the germ is said to consist
of a solid cell-mass, from which the ectoderm becomes detached. Indi-
vidual cells migrate from the inner cell-mass into the cavity thus pro-
duced, and constitute the middle germ-layer. The remaining cells
correspond to the entoderm, and finally arrange themselves into an
intestinal epithelium, which fuses with the ectoderm to form the mouth
and anus. The embryonic development is now completed. The ciliated
embryo reaches the outside world to develop directly into the Nemertean
(HOFFMANN).

The origin of the different organs in the Nemerteans with direct development has recently been studied by SALENSKY (No. 24) on *Monopora*. It corresponds essentially with what we have learned as occurring in the indirect process of development. At the anterior end the central nervous system arises in the form of two ectodermal thickenings, which soon become detached from their connection with the ectoderm. The fundaments of the two brain ganglia grow backwards as the two lateral nerves.

The proboscis and the œsophagus arise in the vicinity of the ganglionic fundaments, both of them as bud-like thickenings of the ectoderm and both of very similar appearance. The proboscis in this form lies, even in the adult animal, very close to the œsophagus, whereby the relation of the fundaments of the two organs is explained. The proboscis, which lies above the œsophagus, opens with it into a common atrium. In spite of this, however, relations [genetic] between œsophagus and proboscis should hardly be sought for here, as HOFFMANN and BALFOUR supposed; but the condition in *Monopora* is much more likely of a secondary nature. The proboscis, at first located at the anterior end of the body, was only subsequently [phylogenetically] united with the œsophagus by moving backwards. Moreover, the union is a very loose one, for the proboscis and œsophagus do not actually unite, but rather open independently of each other into the common atrium.

In the further course of development the fundament of the œsophagus becomes hollow and unites with the intestine. The latter, after the closure of the blastopore, consists of a closed sac. Entodermal cells migrate into its lumen, thereby entirely filling it. Later they become arranged into an epithelium, and then the œsophagus also unites with the wall of the intestine. Afterwards the anus is formed.

The proboscis in this case also is composed of ectoderm and mesoderm, the latter giving rise to the envelope of the ectodermal invagination and to the proboscis-sheath. SALENSKY argues for a formation of the body-cavity by means of a splitting of the middle germ-layer in *Monopora* also. Even before the appearance of the body-cavity, two lateral bloodvessels and one dorsal are said to be formed, corresponding to the conditions of the adult animal. To all appearances they owe their origin to the inner part of the mesoderm, for they are located in the vicinity of the intestine.

We find no statements in SALENSKY regarding the formation of the genital system.

GENERAL CONSIDERATIONS.

In conclusion, we must once more point out how closely the different modes of development of the Nemerteans approach one another. In the *pilidium* the worm arises by the formation of four vesicular ectodermal invaginations, which assume a discoid shape, and, growing around the

larva, unite to form the epidermis of the worm. Since
the discs, owing to their mode of origin, are bilaminar, the
body-covering of the worm, formed by the inner layer, is
enclosed by an envelope (amnion), the outer layer of the
discs. The larva itself goes to pieces. In the *type of Desor*,
the discs, which likewise arise from the ectoderm, are from
the beginning unilaminar only; the amnion, therefore, is
absent, whereas in other respects the developmental pro-
cesses are quite similar. Finally, the discs are no longer
formed at all. However, as a suggestion of the former
mode of development, the outer ectodermal layer separates
from the embryo and is cast off (Cephalothrix). Moreover,
the embryo bears rigid cilia, as in Pilidium. This is also
the case in those embryos which are metamorphosed directly
into the worm without having their ectodermal covering
undergo any important changes.

Accordingly the *pilidium* appears as the older type of
development, from which the others are derived by becom-
ing at the same time simplified. But even the development
of the pilidium cannot be the original form. The origin of
the worm within the larva is a secondary process, which has
probably arisen through adaptation to the conditions of life.
Originally the larva was certainly metamorphosed directly
into the worm, as is still the case in the *Turbellaria* and
Annelida, for example. If the statements of FEWKES (No. 5)
should be verified, those forms in which the *pilidium* is said
to be resorbed by the body of the worm could best explain
the original mode of development (comp. p. 220).

The shape of the Nemertean larva, irrespective of the *Tornaria*-like
form (FEWKES), points to relationships of two kinds. One of these con-
cerns the *Turbellaria*. The resemblance is clear without further
comment, if one considers the Stylochus-larva of GOETTE (Fig. 80, p.
168). This larva exhibits the two typical lateral lobes of the *pilidium*.
We have shown in treating of the *Turbellaria* how it can be referred to
MÜLLER's larva. In the comparison of larval forms caution is of
course necessary, and especially in the case under consideration, where
the first stages of development in the two groups differ very much from
each other. Thus one might be inclined to maintain the similarity in
the outward shape to be accidental, if the adult animals did not also
possess many similar characters in their organization.

The pilidium resembles the *Trochophore* of the *Annelida* (comp. p. 266), as well as the Turbellarian larvæ. In common with this, it possesses the apical plate, the cords radiating from it, and the ring-nerve which extends under the ciliary apparatus. The apical plate, to be sure, does not give rise here, as in the *Annelida*, to the œsophageal ganglion, for it is lost with the *pilidium*. For this reason, it does not seem allowable to homologize the brain of the *Nemerteans* directly with that of the *Annelida*. Apart from this, the lateral nerves of the *Nemerteans* arise by the growing out of the cerebral ganglion, which is already separated from its connection with the ectoderm, whereas the ventral ganglionic chain of the Annelida appears to take its origin by means of progressive differentiation of the ectoderm.

The nervous system of the Nemerteans is most closely allied to that of the Platyhelminthes, and particularly to that of the Turbellaria, with which the Nemerteans also present other common features, such as the uniform ciliation of the entire surface of the body, the body parenchyma, and the lateral organs. But the shape of the proboscis appears to us to be of particular value for the comparison of the two groups. The proboscis, situated at the anterior end of the body, apparently having arisen by the metamorphosis of the latter into a tactile organ and being withdrawn into the inside of the body, presents in the two groups a position and structure too much alike not to challenge comparison.

Other conditions separate the Nemerteans from the Turbellaria. The intestine possesses an anal opening, which is wanting in all Platyhelminthes. The presence of a differentiated blood-vascular system indicates a higher organization of the Nemerteans. The genital organs are constructed quite differently from those of the Platyhelminthes, whereas those of the Turbellaria, Trematoda, and Cestoda show great agreement in structure. In the position of the sexual organs a segmental arrangement can be recognized. Whether the indications of segmentation furnished by the presence of the septa which constrict the intestine and the numerous openings of the water system have any higher meaning cannot be said in the present state of our knowledge. What we have hitherto learned in regard to the excretory system (v. KENNEL and OUDEMANS) entitles us neither to recognize therein a higher degree of organization nor to place the Nemerteans nearer to the Platyhelminthes, though the presence of two longitudinal vessels might point to the latter. On account of their numerous relations to the Turbellaria (although their organization is much higher than that of the latter), it does not seem justifiable to separate the Nemerteans from the Platyhelminthes altogether and to place them, as has already been done, nearer the segmented worms. The Nemerteans would have to be separated much more sharply from the Turbellaria, if the statements regarding the segmentation of the body and the occurrence of a true body cavity were verified.

Finally, we cannot leave unmentioned in this place a theory which places the Nemerteans in relation with the *Vertebrata*. HUBRECHT, the

expounder of this view, compares to the central nervous system of the
Vertebrata the dorsal nerve cord found by him. The cerebral ganglia of
the Nemerteans are held to correspond to the series of ganglia of the
cranial nerves of the Vertebrata, and the lateral nerves to the nervi
laterales which occur so constantly in the latter group. In the chorda
HUBRECHT sees the metamorphosed sheath of the proboscis, while the
remnant of the proboscis itself would be recognized in the hypophysis.
For this view HUBRECHT finds support in the fact that in certain Nemer-
teans the proboscis opens out in the vicinity of the œsophagus, and that
in Tetrastemma it is said even to arise from the wall of the œsophagus
(HOFFMANN, No. 7). For the present these explanations have only the
value of a mere hypothesis.

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CHAPTER VII.

NEMATHELMINTHES.

SYSTEMATIC : I.   NEMATODA S. STR.
            II.   GORDIIDÆ.

I. NEMATODA S. STR.

Embryonic Development.

THE eggs of the Nematoda, which are usually oval, but occasionally spherical, are laid at very different times. Sometimes they are deposited very early, even before cleavage begins, and then are surrounded by a thick shell (*Ascaris lumbricoides*, *Trichocephalus dispar*), whereas thin-shelled eggs begin their development when still in the parent, and may even continue to develop here to a quite advanced stage. Still other Nematodes, as, for example, *Trichina spiralis* and some species of *Ascaris*, are viviparous. The embryonic development of a number of forms is known, though, it is to be regretted, not perfectly. As far as ascertained, the cleavage appears in general to be fairly alike in all cases. It is total and approximately equal, and leads to the formation of a *blastula*, which, to be sure, may be somewhat variously shaped. It may have the form of a mere cluster of cells, designated by GOETTE as a sterroblastula (*Rhabditis nigrovenosa*), or it may be a true vesicle, with, however, only a very small cavity (*Ascaris megalocephala*), or, finally, it may appear in the form of a bilaminar plate of cells (*Cucullanus elegans*).

At a very early period the fundaments of the germ-layers and the differentiation of the various regions of the body can be recognized on the segmenting egg (GOETTE, HALLEZ). As early as the first cleavage the

egg is divided into an ectodermal and an ento-mesodermal half. In *Rhabditis nigrovenosa*, according to GOETTE, the ventral and dorsal sides and the anterior and posterior ends of the embryo can be recognized even at this time. The ento-mesoderm divides first into two blastomeres. The ectodermal blastomere sends out a process dorsally over both of these (Fig. 109 *A*), and a newly formed ectodermal sphere is then situated at this point. In the further division of the ectoderm and ento-mesoderm the elements of the former push themselves more and more over those of the latter, and thus as a whole come to lie more dorsally (Fig. 109 *B*). In subsequent stages two cells lying close together at the former ectodermal pole of the egg indicate the tail-end of the embryo (Fig. 110 *A*, *B*), while the head-end lies opposite.

Whereas GOETTE makes the separation of the mesoderm from the entoderm take place later, it occurs, according to HALLEZ (in *Ascaris* and *Rhabditis aceti*), even in the eight-cell stage, in which two mesoderm cells are constricted off from two entoderm cells. In the twenty-four-cell stage, the *blastula*, with a small cleavage cavity, is formed, the dorsal part of which is composed of the ectodermal cells, the ventral of the entodermal and mesodermal cells.

FIG. 109.—*A* to *D*, cleavage stages and formation of the germ-layers in *Rhabditis nigrovenosa* (after GOETTE). *ect*, ectoderm; *ent*, entoderm; *mes*, mesoderm.

Gastrulation takes place in various ways, according to the form of the *blastula*. In *Ascaris megalocephala* an *invagination gastrula* is formed, the archenteron of which is very shallow, owing to the shape of the thick-walled blastula (HALLEZ). The process of gastrulation in *Cucullanus elegans* takes place in a peculiar manner, as was demonstrated by BÜTSCHLI. In this form the *blastula stage* consists, as has been mentioned, of a bilaminar cell-plate. This shape is soon lost, however, for the cells of one layer multiply more rapidly than those of the other, and therefore a bending toward the latter ensues. Finally a kind of tube is formed,

which presents an elongated fissure on one side. This con-
stitutes the *blastopore* of this peculiar *gastrula*. Also in the
forms observed by HALLEZ and in *Rhabditis nigrovenosa* the
blastopore exists in the form of a long slit (Fig. 110 *B*, *bl*).
In the last-mentioned Nematode the gastrula arises by
the more active proliferation of the ectoderm cells, which
produce an epibolic overgrowth, embracing the ento-meso-
derm (Fig. 109 *B*, *D*), whereby a long slit, the blastopore,
persists on the ventral side (Fig. 110 *B*). Subsequently this
closes gradually from behind forwards. A transition between
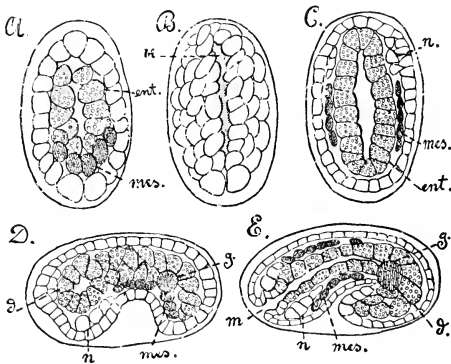
FIG. 110.—*A* to *E*, different stages of development of *Rhabditis nigrovenosa* (after
GOETTE). *bl*, blastopore ; *d*, intestinal canal ; *ent*, entoderm ; *g*, fundament of the
genitalia ; *m*, mouth ; *mes*, mesoderm ; *n*, fundament of the nervous system.

gastrulation by *invagination* and by *epiboly* exists, according
to HALLEZ, in *Oxysoma*.

As regards certain facts of the subsequent embryonic
development which are not yet wholly clear, we have to
abide chiefly by the statements of GOETTE for *Rhabditis
nigrovenosa*. According to him, when the circumcrescence is
already far advanced, the formation of the mesoderm takes
place by the squeezing out of two cells from their connection
with the ento-mesoderm at the posterior end of the embryo
(Fig. 109 *D*). A comparison of these two cells with the

primitive mesoderm cells [teloblasts] of the Annelida is suggested, especially since in multiplying they extend toward the anterior end, and then constitute two rows of cells lying by the side of the entoderm, resembling the mesodermal bands of the Annelida (Fig. 110 *A* and *C*). Their subsequent development, however, is not the same as in that group, for single cells afterwards separate from them and take up various positions between the intestine and the body-wall, without giving rise to a cœlom homologous to that of the Annelida (comp. p. 268).

The embryo, which up to this time has possessed an oval form, changes in shape, for it becomes curved toward the ventral side (Fig. 110 *D*) and more elongated. The shape of the entoderm should be considered in connection with this. At first it forms two layers of cells, between which only a narrow lumen exists (Fig. 110 *A* and *C*). The latter soon disappears in the posterior part of the embryo, and the cells now arrange themselves one after the other in a row (Fig. 110 *D*). The lumen is retained only in the anterior portion; there is formed here a depression of the ectoderm, the fundament of the fore-gut, which unites with the entoderm (Fig. 110 *D* and *E*). The mouth lies in the same place where the last trace of the slit-like blastopore, which closed from behind forwards, was visible. Later a lumen is again formed in the remaining part of the intestine by the splitting of the entoderm (Fig. 110 *E*). The entoderm cells at the posterior end, according to the statements of GOETTE and HALLEZ, fuse with the ectoderm to form the anus, without any depression of the ectoderm being noticeable, whereas STRUBELL (No. 10) maintains the existence of such a depression. The central nervous system arises by a thickening of the ectoderm in the region of the mouth (Fig. 110 *C* and *D*, *n*); the dorsal and ventral parts of the œsophageal ring are said to sever their connection with the ectoderm earlier than do its lateral parts (GANIN). The ventral longitudinal nerve appears to arise from a paired fundament, a condition which has led to a comparison with the ventral longitudinal nerve cords of the Platyhelminthes. In pursuing this idea, there has also been an inclination to refer the dorsal longitudinal

cord to the dorsal nerves of the Platyhelminthes, and to
compare the lateral nerves of the latter to the two nerves of
the lateral lines in Nematoda. It must be noted, however,
that the facts actually established offer no certainty that
this comparison is justified. More uncertain still are the
observations on the further changes of the mesoderm. The
mesoderm cells multiply greatly, separate from the two cell-
rows, and migrate in various directions. They also penetrate
between the fundaments of the nervous system and the skin,
separating these from each other (Fig. 110 E, mes). Finally,
the mesoderm forms a rather even layer between the in-
testine and the epidermis, so that the originally bilateral
arrangement thus disappears. It would be important to
know more accurately about the formation of the body cavity
in the Nematoda.

The origin of the sexual organs, which in the early stages
is the same for both sexes, is better known. In each of the
mesodermal bands, which at first consists of only a few cells,
one of these cells is distinguished by its remarkable size
(Fig. 110 D and E, g). It constitutes the fundament of the
genital organs. In *Rhabditis* a cord of cells is developed
from it by division, the individual elements of which divide
further, and finally become the sexual products (GOETTE).
In other Nematoda the original cell multiplies, it is true, but
the protoplasmic bodies of the newly formed cells do not
separate from one another; on the contrary, a *syncytium* with
many nuclei is formed. The sexual fundament, which is at
first saccular, grows and differentiates into germ glands and
ducts. While in the former the protoplasmic mass with the
nuclei persists as the germarium, in the latter a peripheral
epithelium is formed (ANT. SCHNEIDER).

The shape of the ripe embryo resembles on the whole that
of the Nematode, although it still has to undergo, especially
in the parasitic worms, many changes before it attains the
adult form. Several moultings are often necessary for this.
In some cases the embryo possesses provisional organs, which
appear to be adaptations to its mode of development. Thus
in *Spiroptera obtusa* and *Cucullanus elegans* a boring-tooth is
found at the edge of the mouth, and the posterior end of

the larva of the last-named worm is prolonged into the form of an awl, whereas the adult worm possesses a conspicuously blunt posterior portion.

Post-embryonic Development.

The post-embryonic development in the parasitic Nematoda is very diverse. It appears to be simplest in those cases where the eggs of the Nematode reach the outside world from the place where the parasite lives—for example, from the intestine of the host with its fæces—and then are taken up by another animal of the same species along with its food. The eggs may be more or less developed at the different stages of this migration, but in any event their envelopes are first destroyed in the intestinal canal of the new host, and the embryo here finds at once the conditions of life suitable to it. LEUCKART has observed such a direct conveyance of the eggs into the intestine of the host in *Trichocephalus affinis* and *Heterakis vesicularis*.

The conditions are somewhat less simple when the eggs are enveloped by only a thin shell, from which the embryos hatch as larvæ. These then live and take food in damp earth or water, like those Nematodes which always lead a free existence. In general they resemble the members of the genus *Rhabditis* so closely that they are not distinguishable from them (LEUCKART). During its free existence the worm attains a certain size and development. Only when it arrives in its host do the organs needed for a free existence degenerate; it now adapts itself to the parasitic mode of life. Such is the case, for example, in *Dochmius trigonocephalus* and *D. duodenalis*. The *Rhabditis*-like larvæ of these worms undergo several moultings during their free existence, are then swallowed by the dog along with its drinking-water or by man, and, as the result of a gradual metamorphosis, acquire the sharp mouth armature which is peculiar to them in the adult condition. The process of development is somewhat different in the *Mermithidæ*, which are found as sexually immature forms in the larvæ of insects. After prolonged periods of residence, they abandon this place of habitation by breaking through the body-wall,

and then remain in the damp earth.   Here they moult and
metamorphose into the sexually mature animals.   These
copulate, deposit their eggs in the earth, and the young
worms developing from them then migrate into insect larvæ
again, that of *Mermis albicans*, for example, into young
caterpillars.

The mode of development just described for many
Nematodes, in which the worms pass through a *Rhabditis*
stage, may well be regarded as most nearly resembling that
form in which parasitism in the Nematoda originated; that
is to say, a more or less fully developed worm resorted to the
body of another animal, or at first only became attached
to it in order to gain nourishment from its juices.   The
parasitism only gradually became permanent; it is precisely
the Nematodes that offer all transitions from a partial to a
complete parasitic life, which eventually leads to a total
transformation of the form of the body.   Such a metamor-
phosis of the most extreme kind is realized in *Sphærularia
bombi*, which was first investigated by ANT. SCHNEIDER and
more recently in detail by LEUCKART (No. 7).   This worm in
the adult condition consists of a thick warty sac, which
lies in the body cavity of female humble-bees.   To it is
attached a diminutive worm, which can be recognized as a
Nematode only upon careful examination.   The entire sac
owes its origin to the fact that the vagina of the worm
became everted, and, growing to an enormous size, included
the other sexual organs in it.   The entire animal now con-
sists, with the exception of the small attached worm, simply
of a sac filled with sexual products.   In it the eggs develop.
The young worms reach the body cavity of the humble-bee,
and from there the outside world, where they attain to
sexual maturity.   They copulate in the free condition, and
probably the fertilized females migrate into the humble-bees
when these seek their winter quarters in the ground.   Then
the remarkable transformation of the female begins.

A transition to *Sphærularia* is represented by *Atractonema
gibbosum*, discovered by LEUCKART, in which an eversion of
the vagina likewise takes place, although it attains no
greater size than about that of the worm itself.   It is

appended to the worm as a hernia-like body. The intestine of the latter degenerates, so that here also nutrition must take place by endosmosis. The course of development of *Atractonema* resembles that of *Sphærularia*. The eggs arrive in the body cavity of the host, and the young worms from here repair to the outside world, where they develop into sexually mature animals and copulate. The fertilized females penetrate into the larvæ of a gall-fly, *Cecidomya pini*, where they undergo their further development.

To the developmental processes of the forms last considered can be added that of the Beet Nematode, *Heterodera Schachtii*. Swellings containing a spherical worm filled with eggs, which can be recognized as a Nematode by its development, are often found on the lateral roots of the sugar-beet. The eggs of the worm develop within it, and pass into a slimy brood-sac, secreted by its genital ducts and attached to its posterior end. From here the larva passes to the outside world, and undergoes a development which differs somewhat according as a male or a female arises from it. The female, which is provided with a stiletto-like structure on the pharynx, bores into a beet-root, moults here, and sucks up such a large amount of nourishment that it becomes swollen into a plump body, and thereby causes the epidermis of the root to burst. In this way the hind end of the female is exposed, and it is probable that copulation does not take place until this time (STRUBELL).

Probably the most profound metamorphosis undergone by any Nematode is exhibited by *Allantonema mirabile*, likewise discovered by LEUCKART (No. 7), a worm of a sausage-like, stubby shape, which lives in the body cavity of one of the Curculionidæ (*Hylobius pini*). Except for the form of the sexual apparatus and its products, resemblance to a Nematode could be recognized neither from the external nor internal conditions of this intestineless structure. This worm is said to be hermaphroditic, and it is maintained that self-fertilization takes place. The eggs are developed in the uterus into young Nematodes, which are set free in the body cavity, and subsequently reach the outside world through the intestine. For a considerable time the larvæ lead a free life, for

which their organization fits them. They develop into males
and females, which copulate and lay fertilized eggs. These
develop in the free condition, and a generation of *Rhabditis*-
like Nematodes arises from them. The latter most likely
migrate into the larvæ of the weevil, and here change into
the *Allantonema* form described above. Here therefore the
process of development is further complicated by embracing
two differently formed generations, of which one is free
throughout life; the other, however, leads in part a parasitic
life. This condition, long known as heterogeny, corresponds
to the mode of development of *Rhabditis nigrovenosa*, only
that in the latter case no such fundamental metamorphosis
of the parasitic generation takes place. The hermaphroditic
form, ordinarily known as *Ascaris nigrovenosa*, inhabits the
lung of the frog. It produces eggs, the development of
which we have described above. The eggs are developed in
the parent, from which the embryos emerge in the lung of
the frog. From there the embryos pass into the intestine
and then out with the fæces, and then develop into males
and females, the true *Rhabditis* form. After copulation,
there are developed within the female a small number
of young, which abandon its body after they have been
nourished by its contents. These young worms likewise
exhibit the *Rhabditis* form, and do not lose it until they
have migrated into the lung of the frog, where they are
metamorphosed into the hermaphroditic form. The course
of development in *Rhabdonema strongyloides* is, according to
the discovery of LEUCKART, also similar; the hermaphroditic
form, hitherto known as *Anguillula intestinalis*, inhabits the
intestine of man, whereas the diœcious *Rhabditis* form (*Rhab-
ditis stercoralis*) is found in a free condition.

Those forms also which, in order to reach their complete
development, must live parasitically in two different hosts,
show a very high degree of adaptation to a parasitic mode of
life. This applies, for example, to *Cucullanus elegans*, which
is found in the intestine of the perch. The young of this
viviparous Nematode pass from the intestine of the host into
the water, where they may live free for several weeks, until
they meet with some suitable host. This is not the perch,

as one might imagine; but the worms migrate into a *Cyclops* by first penetrating into the intestine through the mouth and then into the body cavity of the Crustacean. Here they undergo several changes in form, but attain their permanent shape only after the Cyclops which harbors them is swallowed by a perch, and they are set free in its intestine, where they soon become sexually mature, and in turn bring forth young, which undergo the same course of development. *Dracunculus medinensis*, a Nematode parasitic in the human body, appears to have a quite similar mode of development. *Dracunculus* inhabits the subdermal connective tissue, and by its pressure against the skin causes a tumor and finally an abscess, through which it is able to pass out. In this way also the embryos, which are present in the worm in countless numbers, may reach the outside world. During the bathing of persons afflicted with the disease they get into the water, and, like the larvæ of *Cucullanus*, migrate into Cyclopidæ; however, they penetrate directly through the body-covering to the interior of the host. These infected Cyclopidæ are probably swallowed along with the drinking-water by the inhabitants of those regions where the parasite abounds.

Spiroptera obtusa has a development very similar to that of the two forms last considered, only it is still more adapted to parasitic life, for the eggs of this worm do not develop into a free organism, but are directly received by an intermediate host. *Spiroptera obtusa* inhabits the intestine of the mouse. The eggs, in which the embryos are already developed, reach the outside world with the fæces. They are swallowed by the larvæ of the mealworm, *Tenebrio*, which feed on the dung balls. The embryos hatch out in their stomach, break through the wall of the intestine, and become encysted in the fat-bodies of the mealworm. When a mouse devours a mealworm, it becomes infected with the *Spiroptera*, which wakes up to a new life in the intestine of its host, becomes sexually mature and reproductive.

The course of development in *Trichina spiralis* is one of those which are most completely adapted to parasitic life, for this Nematode accomplishes its entire life-history within the

bodies of two hosts. Its development differs from that of
other Nematodes in that the young born of the sexually
mature females in the intestine of the host do not reach the
outside world, but break through the walls of the intestine
and migrate into the muscles of various parts of the body of
the host, to become, after sufficient growth, encysted. In
order to wake the muscle Trichina into new life and bring
about its sexual maturity, it is necessary that the infected
muscle be consumed by some other animal, in whose intes-
tine the Trichinæ then attain their complete development
and power of reproduction (LEUCKART).

II. GORDIIDÆ.

The accounts of the development of the Gordiidæ are still
superficial. The eggs are not deposited singly, but are united
into large balls or strings; for during oviposition a tenacious
mass is poured over the eggs, which are already surrounded
by a shell. The mass hardens in the water. Since the egg-
strings are heavier than water, they sink to the bottom and
remain there until their embryonic development is completed.
This does not begin until after the laying of the eggs, and
requires quite a long time, according to MEISSNER about a
month or more. As regards the first stages of development,
the statements of the authors (VILLOT, No. 16, and CAMERANO,
No. 11) do not agree. According to CAMERANO, the cleavage
is unequal, and leads to the formation of a bilaminar cell-
plate, which, by the bending in of the edges, is metamor-
phosed into a gastrula with a long slit-like blastopore, in a
manner similar to that described above (p. 235) for Cucul-
lanus. The gastrula closes, exactly as in Cucullanus, from
behind forwards. The observations of CAMERANO on *Gordius
Villoti* extend up to this stage, and it appears as if the
figures given by VILLOT for *Gordius aquaticus* could be ap-
plied to CAMERANO's observations. VILLOT describes the
cleavage as regular. A solid heap of cells arises which,
after further multiplication of the cells, splits into a central
cell-mass and a peripheral layer (VILLOT). The hitherto
spherical embryo elongates somewhat, and a deep depression

now arises at one end. In this the head of the embryo is formed in such a way that it can subsequently be everted. The head is composed of a thicker basal portion and a slender proboscis. The former bears three circles of six hooks each, the latter three long stylets, so that the embryo appears well armed. 'At the time of hatching, the head, with its armature, is everted (Fig. 111 B), but can at any time be retracted as before (Fig. 111 A). In the mean-time the intestine is formed, and leads from the mouth, at the tip of the proboscis, to the anus, situated somewhat in front of the posterior end. The efferent duct of a remark-ably extensive gland opens into the œsophagus, at the base of the pro-boscis. Externally the embryo pre-sents an annulated appearance (Fig. 111). The embryo after hatching lives as a larva for a long time free
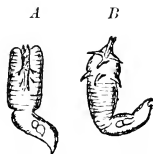
FIG. 111.—A and B, two larvæ of *Gordius subbifurcus*, with retracted and with everted proboscis (after MEISSNER).

in the water, and then, with the aid of its sharp armature, penetrates through the skin into the interior of *Chironomus* larvæ, as was observed by VILLOT. This observer regards as simply an exceptional case MEISSNER'S statement (No. 13) that the larvæ of *Ephemeridæ* are also infected with *Gordius* larvæ. The parasite becomes surrounded by an envelope formed from the tissue of the Chironomus larva, and re-mains there until the larva happens to be swallowed by a fish (VILLOT, No. 16). Becoming free in its intestine, the Gordius larva perforates the intestinal wall and again be-comes encysted. It remains here for a long time without undergoing essential change. Finally (at the beginning of spring) it returns to the intestine, which it leaves with the fæces, and then gradually assumes the form of the adult worm, during which the cephalic armature is lost, the an-nulation of the surface of the body is smoothed out, and the sexual organs are developed. At the same time its intestine suffers a partial degeneration, and the mouth becomes closed. However, it appears to be by no means certain whether the mode of development described is the one realized, or

whether the life even in a single host may not prepare the *Gordius* for further development (VILLOT, No. 17).

In addition to fishes, the Gordius larvæ may also get into frogs, insects, spiders, and Crustacea, although, according to VILLOT, fishes are their most common hosts. As is well known, the Gordiidæ are often found also in terrestrial insects, for example beetles and grasshoppers; but nothing is accurately known concerning the conditions of infection in these animals. In insects of prey it can be explained as the result of swallowing infected insect larvæ. The extraordinary size and development of the Gordiidæ in such terrestrial animals is explicable by the fact that they so long lacked the opportunity of reaching the water, the place of their final development.

General Considerations.

The systematic position of *Gordius* must be briefly considered here. VEJDOVSKY has recently reverted to the idea, prevalent in former times, that the Gordiidæ present much closer relationships to the Annelida than to the Nematoda, and perhaps are even to be looked upon as degenerate Annelids (Nos. 14 and 15). The segment-like arrangement of the ovaries, and more especially the structural conditions of the body cavity, give rise to this conception. The latter is said, according to VEJDOVSKY, to be bounded, on its somatic wall at least, by a well-marked epithelium, and the intestine, as well as the genital organs, is said to be united to the body-wall by means of mesenteries. VILLOT denies the existence of the mesenteries, and refers the epithelium seen by VEJDOVSKY to a kind of mesenchymatous tissue, which in young stages of development fills up a large part of the space between the intestine and the body-wall. Therefore the *body cavity* of the Gordiidæ, like that of the Nematoda, is bounded on one side by the musculature of the body-wall, which arises from that [mesenchymatic] tissue, and on the other by the entodermal wall of the intestine itself. On the latter VEJDOVSKY even could recognize no lining epithelium, a condition which he explained, however, by the great reduction of the intestine. However, v. LINSTOW has also denied recently the presence of an epithelium lining the body-wall (No. 12), and CAMERANO, in consequence of the early stages of development of the *Gordiidæ* observed by him, argues for their relationships to the *Nemathelminthes* (No. 11). Nevertheless the Gordiidæ are distinguished from the Nematoda by the peculiar condition of their genital organs and their deviations from them in other systems of organs, especially the nerve-ring, which is prolonged into the ventral cord, and they can be co-ordinated with them as a separate division. What was said in considering the Nematoda must

be repeated here, namely, that for the determination of the position of this division a better knowledge of the mode of origin and metamorphosis of their middle germ-layer is most desirable.

Embryology gives no satisfactory basis for the determination of the position of the Nemathelminthes in the system, and it is hardly possible, in the present state of our knowledge, to decide this. It cannot be determined whether on the one side they have relationships to the Platyhelminthes or to the Nemertini, and whether on the other to the Annelida. It appears to follow from the structure of the adult animal that there exist resemblances to the organization of the Echinoderes and Gastrotricha. But the latter are unquestionably related to the Rotatoria, so that in this way relations of the Nemathelminthes to the *Trochophore* would be brought about (comp. p. 259).

More obscure still than the position of the *Nemathelminthes* is that of the *Acanthocephali*. We have not, as is customary, considered these along with the *Nemathelminthes*; it is for the reason that their association with this group rests upon grounds of purely external nature, and is required neither by their organization nor by the manner of their development. Even the musculature, which has ordinarily been made use of for the comparison of these two groups, does not appear to be the same in the Nemathelminthes and Acanthocephali either in its arrangement or structure (Säfftigen, Koehler [*Literature* on Acanthocephali, Nos. 6 and 3]).

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CHAPTER VIII.

ACANTHOCEPHALI.

THE eggs of the Acanthocephali are detached from the ovarium as membraneless, usually spindle-shaped cells, and then come to lie in the interior of the body of the female. Here they are fertilized, after which each egg is surrounded by a delicate transparent membrane, and then begins to cleave. When this (in *Echinorhynchus gigas*) has advanced as far as the formation of twelve blastomeres, a second membrane is formed under the first, which has separated some distance from the egg, and to which are added in the course of the development two more protective envelopes, so that finally four of them are present. This applies to *Echinorhynchus gigas* (Fig. 113 *A*). Ordi-
narily three such embryonal mem-
branes are formed, the middle one of
which acquires a considerable thick-
ness and firmness by the deposition
of concretions of a brownish colour.
These structures are particularly
noteworthy, for the reason that they
first make their appearance during
cleavage, and therefore are not to be
looked upon as egg-membranes, but
as a kind of embryonal membrane ;

FIG. 112.—*A* to *D*, four
cleavage stages of *Echinor-
hynchus proteus* (after LEUC-
KART); *eh*, first embryonal
membrane.

still they do not appear to have any cellular structure.
They recall the embryonal membranes occurring in the
Tæniadæ, which may also acquire a considerable firmness.

During the formation of the embryonal membranes the
cleavage has continued.[1] It is unequal, and, according to

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[1] In this connection we follow, in addition to the older observations of
GREEFF and especially LEUCKART, the newer investigations of KAISER on

LEUCKART, takes place in *Echinorhynchus proteus* and *angustatus* in such a manner that the spindle-shaped egg is divided at right angles to its long axis into a number of cells which are not quite equal in size (Fig. 112 *A*, *B*). After five blastomeres have been formed in this way, they are divided in the direction of the long axis, and a rather irregular arrangement of the cleavage spheres ensues (Fig. 112 *C*, *D*). As the result of cleavage an epibolic gastrula is produced (KAISER), the outer layer of which is formed of a large number of polyhedral cells, whereas the inner layer consists of much larger cells and encloses a remnant of yolk in the centre. Even at this stage the embryo acquires its armature. In the middle of every group of four contiguous ectoderm cells is formed, as the product of their secretion, a recurved hooklet which protrudes into the space bounded by the embryo and the innermost protective envelope. The entire surface of an embryo of *Echinorhynchus gigas* is beset with small spines, and in addition five larger hooks are found at the anterior end (Fig. 113 *A*). The anterior end of the body, on which they are located, can be retracted, forming a funnel-shaped depression. In *Echinorhynchus angustatus* it is truncated, and five to six hooks are always found on the disc thus formed (Fig. 113 *B*). As in *Echinorhynchus gigas*, it also can be drawn in.

FIG. 113.—*A*, embryo of *Echinorhynchus gigas* in the embryonal membranes (*eh*); *B*, larva of *Echinorhynchus angustatus* with the disc (*s*) at the anterior end bearing the armature (after LEUCKART); *ek*, "embryonic nucleus."

After the central yolk is entirely consumed, there begins a process called by KAISER histolysis. This consists in the following changes: the boundaries between the cells disappear, the bodies of the cells flow together, and the cell nuclei move to the middle of the embryonic body, where

Echinorhynchus gigas, which, however, have as yet been published only in a preliminary way and without illustrations, but which nevertheless afford an insight into the development of these forms.

they accumulate to form the structure called by Leuckart the embryonic nucleus or core. Moreover, layers of two kinds can still be distinguished in the syncytium : an outer tough one and a less firm inner one, which encloses the embryonic nucleus. Leuckart had already shown that later the greater part of the worm arises from this central portion of the embryo. Furthermore, he compared it to a rudimentary intestine, and showed how the solid body which he found lying between the cephalic disc and the embryonic nucleus (Fig. 113 *B*) could be interpreted as a rudimentary pharynx. This conception seemed satisfactory in view of the relationship of the intestineless Acanthocephali to other worms (Nematoda).

In the condition above described the embryos, enclosed in their firm envelopes, pass out by means of the complicated mechanism of the sexual conductive apparatus. They now find themselves in the intestinal canal of the host—a fish in the case of *Echinorhynchus angustatus* and *protens*, the hog in the case of *Echinorhynchus gigas*—and then reach the outside world with the faeces of the animal. The embryos of the latter species are swallowed by the larvæ of *Cetonia aurata* along with their food, whereas those of the two worms first mentioned are swallowed in the same way by *Asellus aquaticus* and *Gammarus pulex*. The embryonic envelopes soften in the stomach of the new host, and the embryo becomes free ; it immediately penetrates into the intestinal wall, and comes to rest either here (*Echinorhynchus gigas* and *angustatus*), or in the body cavity of the host. The larva of *Echinorhynchus angustatus* also reaches the body cavity later, but in a more passive manner as the result of its active growth and the rupturing of the intestinal musculature. Here (in *Gammarus pulex*) are also found the young stages of *Echinorhynchus polymorphus*, which as an adult worm inhabits the intestine of ducks and other aquatic birds (Greeff).

The further development of the larva is connected with a metamorphosis of the external shape of the body, due to the formative processes which take place within. In *Echinorhynchus gigas* the middle part of the body swells greatly

as soon as the larva has located itself in the intestinal mus-
culature of the intermediate host. The developmental pro-
cesses proceed from the central part, the so-called embryonic
nucleus, for it is this which contains the formative material.
According to the observations of LEUCKART, it is differenti-
ated into four groups of cells lying one behind the other
(Fig. 114 *A*). The hindermost of these four groups soon
acquires a greater volume, sending out a peripheral layer,
which spreads out in front and on the sides, and encloses
the other groups, with the exception of the most anterior
one (Fig. 114 *A*). The Echinorhynchus is formed for the

most part out of these cell
groups. The most anterior is
said to become the proboscis,
the second the ganglion, the
third, which soon divides into
two, the sexual glands, and,
finally, the fourth the sexual
ducts. The cell-layer which
surrounds the groups subse-
quently splits into two layers,
which were treated by LEUC-
KART as answering to the soma-
tic and splanchnic layers of
the mesoderm. In the absence
of the intestine, the splanchnic
layer would be represented by
the so-called ligament and the
proboscis-sheath only, both of
which structures arise from it.
The somatic layer, after it has
separated farther from the
splanchnic, and has left the
body cavity between them,
would form the musculature

FIG. 114.—*A, B*, two larvæ of *Echi
norhynchus proteus*, in which the
"embryonic nucleus" is already un-
dergoing its metamorphosis (after
LEUCKART). *r*, proboscis; *rt*, pro-
boscis-sheath; *n*, ganglion; *g*, funda-
ment of the genital glands; *l*, ducts
of the genital system; *m*, the cell-
layers which are destined for the
formation of the musculature.

of the body, whereas the epidermis arises directly from the
larval skin. When the internal formative processes have pro-
gressed sufficiently to allow of it, the cuticula of the larva
is alone cast off. A new cuticula then arises. During these

processes the different parts of the " embryonic nucleus "
have also enlarged considerably, and thus have once more
approached somewhat nearer to the larva in size (Fig. 114
B). At the same time the differentiation and development
of the different organs begin.

From the preceding description, which contains the chief
features of LEUCKART'S discoveries, it is seen that the
largest part of the worm arises from that frequently men-
tioned central mass into which the nuclei are said to retreat
at the beginning of development. The more recent state-
ments of KAISER also agree in general with this conclusion.
Since it appears that, owing to improved methods, certain
processes have been more elaborately worked out by him,
and since these are of a most peculiar nature, his obser-
vations will be considered here more at length, although it
is difficult to obtain a clear idea of the complicated processes
from his brief communication, unaccompanied as it is by
illustrations.[1]

After the larva of *Echinorhynchus gigas* has attached itself to the
wall of the intestine, and the middle part of its body has become greatly
swollen, groups of cells are said to detach themselves one after the other,
to become surrounded with cytoplasm, and thus to form the cells which
produce the permanent hooks of the proboscis. The groups of cells
move forward and finally unite to form the proboscis, which at length
can be everted. At about the same time the permanent body-covering
of the worm is formed by the detachment of nuclei from the entire
periphery of the " embryonic nucleus " and their migration into the
outer layer of the body plasma (Fig. 114). Accompanying an active
division of the nuclei, there is soon formed a very regular body-epithe-
lium. Here also the cuticula of the larva appears to be cast off, just as
its provisional hooks are. The epithelium secretes a new cuticula, and
beneath it a colourless, tenacious product, the fibrous tissue of the so-
called subcuticula. The muscular elements which are found in the sub-
cuticula are said to be formed at the same time from the cells of the

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[1] [A paper by HAMANN (Appendix to *Literature* on Acanthocephali) and
especially a voluminous work by KAISER have furnished us with a new
exposition of the development of Echinorhynchus. These investigations
elucidate to a great extent the remarkable developmental processes, which
are here only briefly touched upon. We refer to these two works them-
selves, since it is not possible to give in this place the results of these
extensive studies.—K.]

body-epithelium. They arise as "primitive muscle-fibres" in the epithelial cells, and pass from these into the fibrous tissue of the subcuticula. When this process is completed, the body-epithelium degenerates completely and disappears. The formation of the lemnisci agrees with that of the skin. The nuclei, which have separated from the central mass and moved to the anterior end of the body, here form a circular swelling which at two diametrically opposite points is drawn out into slender processes, the fundaments of the lemnisci. In them the formation of the fibrous tissue takes place just as in the skin. Near the anterior end of the body, and immediately behind the rod-like proboscis, there also lies an extensive mass of nuclei, the fundament of the central nervous system, from which the peripheral nerves soon grow out to the different organs.

The organs the development of which has thus far been described are said to be of ectodermal origin ; this, indeed, is very probable, although sufficient grounds for this conclusion cannot as yet be recognized in Kaiser's description. The real body-musculature, the sexual glands, and the ducts of the genital apparatus arise, according to Kaiser, from the entoderm. Leuckart had spoken of a mesoderm, which splits into an outer and an inner layer, but as yet Kaiser has not given attention to this statement. Again, it is layers of nuclei which separate from the central mass to give rise to new structures. Three such layers of nuclei can be recognized, owing to their somewhat different shape. The two outer ones soon migrate to the body-wall, and here, after various metamorphoses, supply the circular musculature and the longitudinal musculature of the body.

Behind the proboscis, in the neighborhood of the ganglion, are found nuclei, arranged in definite order, concerning whose origin more accurate knowledge would be important, for out of them arise the proboscis-sheath and the retractors as well as other muscles of the proboscis, therefore structures which would be ascribed to the inner layer of the mesoderm did such exist.

The formation of the genital organs takes place in quite a peculiar manner. Behind the proboscis-sheath a prismatic protoplasmic mass makes its appearance, from the edges of which arise four thin plates, which divide the cavity of the body into four sectors. By this description one is involuntarily reminded of the mesenteries which unite the fundaments of the genitalia with the body-wall, and at the same time recalls the conditions which, according to Vejdovsky, exist in the Gordiidae. In the female the plates unite in the dorsal and ventral sectors to form the ligament ; in the male the plates of one sector degenerate. The germ glands themselves arise from the axial mass of plasma. The resemblance of the thin plates to mesenteries, referred to above, is increased, as far as can be judged from the brief statements of Kaiser, by the two lateral sectors being filled with a cellular mass ; subsequently, however, this degenerates and thus gives rise to the body

cavity. If then, provided we rightly understand KAISER's statements, a union of two plates were to take place dorsally and ventrally, the resemblance to mesenteries would indeed be strong. The plates could certainly arise only from the above-mentioned third or inner layer, which separated from the central mass at the time of the formation of the body-musculature. The two outer layers would then be applied to the body-wall, whereas the inner layer would perhaps assume the formation of the internal organs, the proboscis-sheath, and the ligament, in some such manner as was described by LEUCKART. This is the way at least in which we should interpret the statements of KAISER in the absence of his more detailed descriptions.

In regard to the origin of the genital organs, especially the extensive conducting apparatus, we refer to KAISER's communication, or, better still, to the awaited complete work, for it cannot be determined from the former what is the real origin of those elements which constitute the genital apparatus.

The *Echinorhynchus*, which even in the body of the intermediate host attains in general the form of the adult worm, becomes capable of reproduction only when the animal harboring it is consumed by another which is adapted to serving it as permanent host, thus, for example, the *Gammarus* by a fresh-water fish or a duck, if the species be *Echinorhynchus polymorphus*.

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CHAPTER IX.

ROTATORIA.

THE Rotatoria are peculiar in regard to their reproduction. Three different kinds of eggs occur among them : in the first place, thin-shelled summer eggs, which develop parthenogenetically into females ; then eggs similar to these, but of only half the size, from which arise the simply organized males ; and finally thick-shelled winter eggs or resting eggs, which, as it appears, require to be fertilized. The eggs are either deposited free in the water or cemented to the body of the female. The development of the thin-shelled eggs takes place in many forms even in the body of the mother ; that of the resting eggs occurs only a long time after laying.

The expulsion of the polar globules precedes cleavage. The parthenogenetically developing eggs, according to WEISMANN UND ISCHIKAWA, produce only one polar globule. Little is yet known concerning the development of the Rotatoria. The chief descriptions are from SALENSKY, JOLIET, and TESSIN ; they present, however, many gaps. In our presentation of the subject we follow principally TESSIN's work, which is occupied chiefly with the development of *Eosphora digitata*.

Cleavage is from the beginning unequal (TESSIN, JOLIET). In the stage of four blastomeres one large and three small cells can be distinguished (Fig. 115 *A*). At the time when the latter divide into six, the abstriction of a new portion from the large blastomere takes place, and when those cells which subsequently supply the mesoderm are differentiated from the cells at first produced, a division of the large blastomere is still in progress (Fig. 115 *B*). That part of it which is now left as a rather extensive remnant represents

the fundament of the entoderm, for it is subsequently over-grown by the other cells. The small blastomeres, which now divide repeatedly, are, however, to be considered as ectoderm and mesoderm.

Particularly striking is the statement that the mesoderm (in the form of three dark, granular cells) arises by division of the small blastomeres that were first to appear, and that it still remains united to the ectoderm, whereas even after its differentiation ectodermal elements continue to be separated off from the large blastomeres. According to O. ZACHARIAS, however, the mesoderm is supplied directly by the large blastomere, which on the whole corresponds more to the ordinary mode of formation of the mesoderm, but does not, it is true, appear to be well established in the case under consideration. The conditions of formation of the meso-derm hitherto known do not allow a comparison with the Annelida, as one would perhaps expect from the relationships of the *Rotatoria* to these forms.

The three meso-derm cells lie at the subsequently dorsal side of the embryo (Fig. 115 C). With the progressive division of the ectoderm cells and the commencing circumcrescence of the large blastomere by these, the mesoderm cells are pushed farther forward (Fig. 115 D). Meanwhile their number has doubled. Even before the formation of the epibolic gastrula is completed the enclosed entoderm cell has divided. As the result of
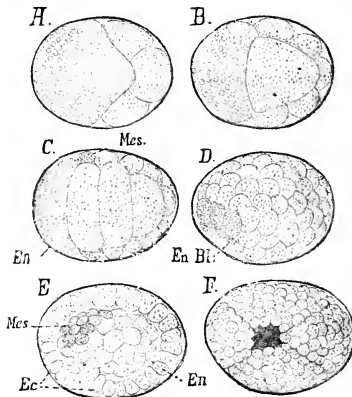
FIG. 115.—*A* to *F*, stages of development of *Eosphora digitata* (after TESSIN). *A* to *C*, cleavage stages; *D*, epibolic gastrula. The large blastomeres are already entirely overgrown; the mesoderm cells lie at the blastopore. *E*, the mesoderm cells have moved inward; an invagination of the ectoderm follows it; the entoderm cells have multiplied. *F*, embryo, on which the head-, tail-, and lateral lobes can be recognized. *Bl*, blastopore; *Ec*, ectoderm; *En*, ento-derm; *Mes*, mesoderm.

the forward growth of the ectoderm, the mesoderm cells
are now forced inward, and the invagination of ectoderm
cells, which succeeds it (Fig. 115 *D, E*), subsequently pro-
duces the trochal apparatus and the œsophagus.

The outer form of the embryo is now changed in such a
way that an anterior, posterior, and two lateral protuberances
can be distinguished (SALENSKY, TESSIN). On the surface
which bears the blastopore, these regions of the body are
seen to be separated from one another by shallow grooves
(Fig. 115 *F*). The posterior elevation bends forward, and
growing further in the same direction, forms the foot (or
caudal appendage) of the Rotifer.

TESSIN seeks to refer the anterior and lateral elevations (cephalic and
lateral lobes) to the lobular processes of the *Turbellaria*, especially to
those of the larva of *Stylochus*. Inasmuch as the Rotatoria do not pass
through any real larval stage, the lobular processes would have become
rudimentary. In the further course of development the cephalic and
lateral processes are again smoothed out, and can no longer be recog-
nized as special structures.

Concerning the origin of the inner organs even TESSIN can give little
definite information. We have already mentioned that he derives the
trochal organ and the most anterior part of the intestinal canal from an
ectodermal invagination. On the other hand, he combats the discoveries
of SALENSKY, for he derives the masticating stomach (pharynx), which
is provided with jaws, from the entoderm ; SALENSKY maintains that this
part is of ectodermal origin. According to TESSIN, by far the largest
part of the intestine (together with the appended glands) arises from the
entoderm, for the latter extends far backwards ; it is said even to send a
process into the caudal appendage. The hind-gut arises by means of an
invagination of the ectoderm (SALENSKY, JOLIET).

The further fate of the mesodermal fundament remained obscure to
TESSIN. The statements regarding the origin of the nervous system and
the genital organs are of too doubtful a nature for us to consider them.
Nothing is as yet known concerning the formation of the excretory
organs.

The development of the male of *Brachionus urceolaris*,
which, as is known, is very simply constructed, takes place,
according to SALENSKY, in the same way as that of the
female. The degenerative processes which characterize the

incomplete form of the male begin only after the trochal organ and the foot have been formed.[1]

General Considerations.

The development of the Rotatoria gives us as yet no information as to their doubtful position in the system. Such forms as that of *Trochosphæra æquatorialis* (Fig. 116), found by SEMPER in the Philippines, point with almost imperative force to relationships with the Tro-
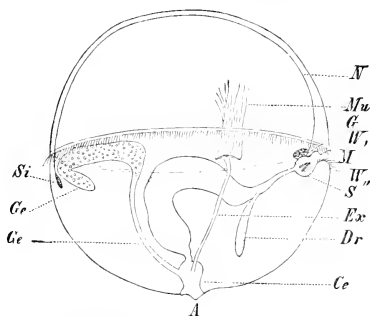
FIG. 116.—*Trochosphæra æquatorialis* (after SEMPER). *Ce*, cloaca; *Dr*, appendicular glands of the fore-gut; *Ex*, duct of the excretory organs; *G*, brain; *Ge*, female sexual organs with duct; *M*, mouth; *Mu*, musculature; *N*, nerve that emerges from the brain; *S*, œsophagus; *Si*, sense organ; W_A preoral, W_{AA} post-oral, ciliated band.

chophore larva of the Annelida (comp. p. 266). Like the latter, *Trochosphæra* possesses a complete preoral circle of cilia and an indication of a post-oral one. Both of these are also to be recognized in the trochal organ of other Rotatoria, the form of which is different from that of the Trochophore. The course of the intestine is similar to that of the annelid Trochophore. The structure of the excretory system also argues for a relationship with the *Trochophore*-like forms. The excretory canals of the *Rotatoria* begin with blind ciliated funnels in the body cavity, and the same

[1] [Our knowledge of the development of the Rotatoria has recently been much enlarged by the thorough investigation of ZELINKA, to which the reader is referred (see Appendix to *Literature* on Rotatoria).—K.]

is said to be the case in the *Trochophore*. In the Rotatoria
there are two trunks to the excretory system, which in the
Gastrotricha, which are related to the *Rotatoria*, open to the
exterior by means of two ventral openings (ZELINKA, No.
12), so that this organ thus acquires still greater resem-
blance to the so-called head kidney, the excretory system of
the *Trochophore*, for the two head kidneys also open directly
and separately from each other to the exterior (comp. p. 266)
The agreement of the *Rotatoria* with the *Trochophore* was
especially advocated by HATSCHEK (No. 1), with whom
recent investigators of the Rotatoria, such as PLATE and
ZELINKA, in the main agree (Nos. 3, 4, 11, 12).

TESSIN contends against the relationship of the Rotatoria to the An-
nelida or their ancestral form, which we have briefly indicated above,
because, owing to the origin of the trochal organ from the stomodeal
invagination and the position of the brain outside of the area included
within the trochal organ, a comparison of the trochal organ with the
ciliated rings of the Trochophore larva does not seem to him admissible.
TESSIN seeks rather relationships to the Turbellaria, being influenced by
the lobular structures of the embryo. His comparison of the caudal
appendage of the Rotatoria with the post-abdomen of the Crustacea,
which he supports with the fact that a process of the entoderm is said to
extend into the tail, seems weak. This perhaps indicates that the
Rotatoria have a tendency to increase in length. We would here recall
the growing out of the Trochophore into the worm. Relationships of
the Rotatoria to the Arthropoda have also been found in forms such as
Hexarthra polyptera, to which attention has recently been called by PLATE
(No. 4). This remarkable Rotifer, discovered by SCHMARDA, possesses on
the ventral side three pairs of movable setose appendages, which are like
extremities, and give to it almost the appearance of a *Nauplius*. In view
of the close relationships of the Rotatoria to the *Trochophore*, one will
certainly not think of a descent of the Rotatoria from the *Arthropoda*,
especially from the *Crustacea*; it is, however, interesting to see how
Trochophore-like beings can vary in the direction of the *Arthropod type*,
even if it be only in their outward shape.
    Still less justifiable than a comparison of the caudal appendage (foot)
of the Rotatoria with the abdomen of the Crustacea is such a comparison
with the foot of the Mollusca, which has been attempted by various
writers, who have based their conclusions principally upon the position
of both organs between the mouth and anus, which is particularly well
expressed in embryos and larvæ.

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Appendix to Literature on Rotatoria.

ZELINKA, C. Studien über Räderthiere III. Zur Entwicklungsgeschichte, der Räderthiere nebst Bemerkungen über ihre Anatomie u. Biologie. *Zeitschr. wiss. Zool.* Bd. liii. 1891.

CHAPTER X.

ANNELIDA.

I.—CHÆTOPODA AND ARCHIANNELIDA.

THE two chief divisions of the *Chætopoda* are unlike as regards development, this being in the *Polychæta* generally indirect, and involving a free-swimming larval stage, whereas in the *Oligochæta* it is considerably abbreviated, and free-swimming larvæ are absent. The *Archiannelida* are like the Polychæta.

1. Development through Free-swimming Larvæ

(*Polychæta* and *Archiannelida*).

In general the Polychæta develop from free-swimming larvæ which are provided with ciliated bands. Only a few forms bring forth living young. Such is the case in *Eunice sanguinea*, *Syllis vivipara*, and in a *Cirratulus* in which the eggs develop either in the body cavity or in the cavity of a segmental organ which has become a uterus. A kind of brooding also occurs in many forms, as, for example, in *Autolytus cornutus*, an extensive sac, in which the eggs are developed, being formed on the ventral surface by the distension of the skin of the body. In *Polynoë cirrata*, the eggs, which are stuck together in a single mass, are carried on the dorsal surface under the dorsal scales. Similar to this is *Grubea limbata*, in the females of which at the time of sexual maturity the entire back is thickly covered with eggs, while *Exogone gemmifera* and *Sphærosyllis pyrifera* carry their eggs on the ventral side, namely on the ventral cirri (VIGUIER, No. 46). In *Spirorbis Pagenstecheri* the tentacle which bears the operculum of the tube is enlarged, and thus serves as a brood-chamber; in *Spirorbis spirillum*, on the contrary, the

eggs are deposited inside the tube, and are found here between it and the body-wall. Similar to this is the brooding in the genus *Capitella*, in which one finds the eggs firmly attached like a mosaic, on the inner surface of the tube. Other tubiculous worms attach their eggs to their habitations on the outside; thus in *Sabella lucullaria* the eggs, which are enveloped in a slimy mass, form a thick ring around the tube of the parent. Many Polychæta deposit their spawn in the form of large gelatinous packets or clumps (*Aricia, Psygmobranchus*); others discharge the eggs into the sea-water without any other protection than the egg-membrane (*Eupomatus, Pomatoceros et al.*, likewise *Polygordius*). In such forms artificial fertilization can be employed with success.

Cleavage is unequal, but in some forms may approach very near to the equal type (*Pomatoceros* according to v. DRASCHE). In the latter case it produces a *cœloblastula*, the entodermic part of which can be distinguished by the greater thickness (*Sabellaria, Aricia*), or an epibolic *gastrula* is formed (*Nereis, Psygmobranchus*). The Polychæta, which have been studied with this object in view by HATSCHEK, GOETTE, v. DRASCHE, SALENSKY, and other investigators, offer all transitions between the different types of cleavage, and correspondingly the form of the gastrula also varies from a typical invagination to an epibolic *gastrula*. In *Terebella Meckelii*, for instance, we find a blastula with the wall thickened on one side, the cavity of which soon becomes filled by the intruding macromeres, so that we now have before us a so-called sterrogastrula (SALENSKY). [WILSON (Appendix to *Literature* on Annelida, No. XXVII.) has recently given a very detailed account of the early stages of development in *Nereis*, especially of the cleavage, in which the fate of the individual cells is established with great precision.—K.]

As an example of the embryonic development of a Polychæte, we select that of *Eupomatus* (according to HATSCHEK). The spherical egg is divided by means of the first two meridional planes and succeeding equatorial plane of division into eight blastomeres of almost equal size. Soon, however, the divisions at the animal pole take place more rapidly than

at the vegetative pole, and thus the blastomeres at the latter
remain more voluminous. In the resulting blastula, the cells
from which the three germ-layers arise are already differen-
tiated (Fig. 117 *A*). The upper hemisphere, composed of
smaller cells, gives rise to the ectoderm, and the greater
part of the lower to the entoderm; however, two cells here
are distinguished at an early period from the others by
assuming a more spherical shape: they produce the mesoderm,
and are called by HATSCHEK the primitive mesoderm cells
[mesodermal teloblasts (Fig. 117)]. The region where they
lie corresponds to the anal end of the larva. Even as early
as this stage a delicate equatorial circle of cilia makes its
appearance, the future preoral ciliated band of the larva.
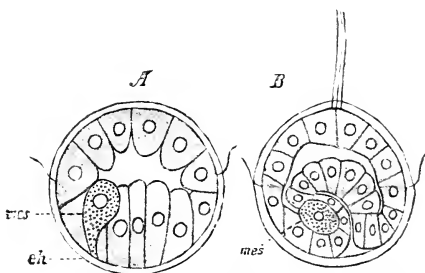
FIG. 117.—*A*, *B*, blastula and gastrula stages of *Eupomatus uncinatus* (after
HATSCHEK); *eh*, egg-membrane; *mes*, one of the two mesoderm cells.

Soon afterwards the tuft of cilia at the apex of the larva
makes its appearance (Fig. 117 *B*). The cilia perforate
the egg-membrane, which therefore most probably consists
of a soft mass.

The subsequent behaviour of the egg-membrane is of a peculiar nature,
for, according to the concurrent statements of various authors, it is pro-
visionally retained, increases in extent with the growth of the larva, and
is thus formed into a cuticula-like envelope (HATSCHEK, No. 20), which,
however, is replaced later by the permanent cuticula from the ectoderm.
Thus here the embryo is converted directly into the larva.

The entodermic part of the blastula now invaginates. At

the same time the two primitive mesoderm cells have moved
into the inside, having detached themselves from their con-
nection with the other cells. In the lateral aspects seen in
Fig. 117 *A* and *B*, only one of the two cells can be recognized.
It should be mentioned here that later they divide (Fig.
118). The two primitive cells still continue to be dis-
tinguished from the newly formed ones by their greater size.
HATSCHEK calls them the two *pole cells of the mesoderm*.
They lie at the ends of the two *mesodermal bands* formed
by cell-proliferation. In the further development of the
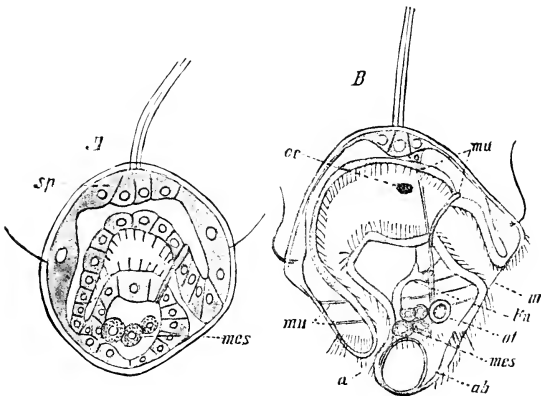
Fig. 118.—*A* and *B*, trochophores of *Eupomatus* in younger and older stages
of development (after HATSCHEK). *a*, anal opening; *ab*, anal vesicle; *kn*, head
kidney; *m*, mouth-opening; *mes*, mesodermal bands; *mu*, muscles; *oc*, eye-spot;
ot, auditory vesicle; *sp*, apical plate.

larva the intestine bends toward the anal side, in order
to fuse in later stages of development with the originally
slight depression of the ectoderm, which produces the hind-
gut and anus (Fig. 118). Some time before the completion
of this process, the blastopore had become considerably
narrowed. It assumed the form of a fissure which closed
(from behind forwards) and left only a small opening re-
maining in front. At the place of this last trace of the

blastopore, the ectoderm becomes invaginated, and forms the œsophagus. This is followed by an enlargement, the stomach of the larva, and this in turn by the small-gut and the hind-gut (Fig. 118 B).

The formation of the intestine takes place less simply in the cases where the gastrulation is epibolic and the entoderm at first consists of a compact mass of cells. The intestinal wall is only gradually formed, detaches itself from the central yolk-mass, and finally unites at the fore- and hind-guts with the ectoderm (comp. the figures 128 A and B, p. 280, of *Psygmobranchus*).

Trochophore.—Even during gastrulation the embryos rose, with the aid of their vibratile apparatus, from the bottom, and betook themselves to the surface of the water. Together with the internal changes described, alterations have also taken place on the outer body, the upper portion of which has become bell-shaped, while the under-portion tapers more conically (Figs. 118 B and 119). The band of cilia which lies in front of the mouth extends around the longest periphery. Thereby is reached the larval stage, designated by Ray Lankester as the *Trochosphere*, but now with Hatschek more generally known as the *Trochophore*. In addition to the organs already mentioned —ciliated band, intestinal tract, and mesodermal bands — still others can be seen in the *Tro-*
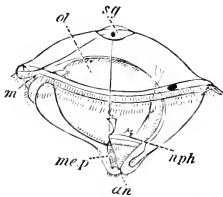
Fig. 119.—Larva of *Polygordius* (after Hatschek, from Balfour's *Comparative Embryology*). *an*, anal opening ; *m*, mouth-opening ; *me. p*, mesodermal band ; *nph*, head kidney ; *ol*, stomach ; *sg*, apical plate.

chophore. An ectodermal thickening at the upper pole, which bears the tuft of cilia, if such be present, is designated as the *apical plate* ; it represents the fundament of the super-œsophageal ganglion (Figs. 118 A and 119). The cells of the *preoral ciliated band* also form a similar thickening. These may consist of several successive circles of cells, and between or underneath them is placed a ring of fine nerve fibres, which is connected with ganglionic cells, and is considered by its discoverer, Kleinenberg, as the

central nervous system of the larva. At the base of the ciliated cells there also lies, according to KLEINENBERG, a ring of muscle cells, which, like the ciliated band itself, is made use of by the larva in locomotion. In addition, various other muscle strands traverse the inside of the body; thus some extend from the apical plate to the stomach, others are found in the lower part of the body, and one surrounds the intestine at the point where the stomach and œsophagus unite (Fig. 118 *B*). These muscle cells have become detached from the mesodermal bands (HATSCHEK). From the latter also arises the so-called *head kidney*, the paired excretory organ; it is formed from a few cells situated near the pole cells, which increase greatly in length and become hollow. The head kidney then extends from the pole cells, that is, from the vicinity of the anus, as far as the œsophagus (Fig. 118 *B*, *kn*). It consists of a ciliated canal, which may branch (as, *e.g.*, in *Polygordius*), and of one or more funnel-shaped terminations (Figs. 119 *nph* and 120 *B*, *kn*). These do not open freely into the blastocœle, but are said to end blindly (FRAIPONT), and in this regard therefore resemble more the excretory system of the *Platyhelminthes* and Rotatoria. The spot where each of the two head kidneys opens to the exterior can be seen from the figures 120 *A* and *B*.

Of the ectodermal structures of the larva there should still be mentioned as important, in the first place, the *eyespot*, consisting of an accumulation of pigment, which in the larva of *Eupomatus* is located in a cell of the apical region, but asymetrically on the right side (Fig. 118 *B*, *oc*). The two ectodermal vesicles which arise symmetrically on the posterior portion of the body, each from one ectoderm cell, also constitute sensory organs (HATSCHEK). They are provided with fine stiff hairs, which project into their lumina; highly refractive concrements are also found inside of them. Thus they are to be recognized as *otolith vesicles* (Fig. 118 *B*, *ot*). The large sac which in Fig. 118 *B* is seen lying at the posterior end of the larva arises by the enlargement of an ectodermal cell. This anal vesicle appears to have no important significance. In *Eupomatus* is developed another

(perianal) circle of cilia, which is situated on the posterior portion of the body (Fig. 118 *B*); this is lacking in many other Annelids. Furthermore there is added on the ventral side a ciliated area extending from the mouth backward, the adoral ciliated zone (Figs. 118 *B* and 128 *A*, p. 280).

The metamorphosis of the Trochophore larva into the adult worm will be followed in *Polygordius*, a form in which it takes place in a particularly clear manner. The Polygordius larva was first discovered by Lovén, and held to be that of a chœtiferous worm. Ant. Schneider showed that Lovén's larva belonged to *Polygordius*. It has the form of a typical Trochophore (Fig. 119). The ciliate apparatus, which encircles the larva at its greatest diameter, is composed of two rings, one in front and one behind the mouth. The preoral ring consists of a double, the post-oral of a single, row of cilia. A third ring, the perianal ciliated band, makes its appearance at the posterior end of the larva (Fig. 120 *B*), but it is not formed until the later stages of development. The development of the *Trochophore* into the perfect worm, which has been thoroughly studied by Hatschek, consists first of all in a growing out of the posterior section of its body and a gradual reduction of the anterior part.

At first a segmentation of the larva is noticeable (Fig. 120 *A*), which depends upon a marked change in the two mesodermal bands. These, which at first consisted of only a few cells, have become by active cell-proliferation much more voluminous. Each of them is separated into two cell-layers (Fig. 133 *A* to *C*, p. 290), and spreads out toward the ventral and dorsal lines. Then a segmentation makes its appearance in them, proceeding from in front backwards (Fig. 120 *A*), and at the same time the two layers of the bands separate from each other by the formation of a cavity in each segment. In this way the primitive segments arise, the outer and inner walls of which become in each segment of the worm the somatic and splanchnic layers of the mesoderm, and the walls, abutting on one another, form the segmental boundaries (dissepiments) of the body of the worm.[1] Since

[1] A more detailed description of these conditions will be found in the discussion of the formation of the body cavity (comp. p. 289).

to each segment of the body a pair of primitive segments belongs, these meet in the middle line of the ventral and dorsal surfaces, and form there a ventral and dorsal mesentery (Fig. 133 *C*, p. 290). In the figures 120 *A* and *B* (lateral views of the larva) the primitive segments can already be recognized in the form of an internal segmentation of the larva. The most anterior primitive segments are the oldest, the posterior ones younger. The body is seen to be already considerably grown out backwards, although the head portion has not yet diminished in circumference. Two ciliated tentacles, which are still very small, now make their appearance on the apical plate (Fig. 120 *B*). The originally sac-like mid-gut has grown in length with the body, and is now cylindrical in shape. Very near the posterior end of the body, a short distance in front of the anus, is the posterior ciliated band (Fig. 120 *B*).
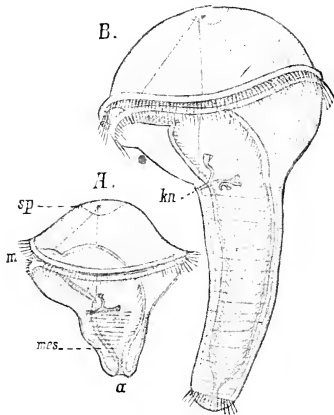
FIG. 120.—*A* and *B*, larvæ of *Polygordius* (after HATSCHEK). *a*, anus; *m*, mouth-opening; *kn*, head kidney; *mes*, mesodermal bands; *sp*, apical plate.

While the posterior part of the body of the larva is gradually passing from the earlier conical into the cylindrical form, the head portion attains its greatest volume, but thereafter soon diminishes. The metamorphosis of the voluminous cephalic vesicle into the slender cephalic process of the worm is effected by the thickening and conical outgrowth of the apical plate (Fig. 121 *A*), and by the contraction of the wall of the head generally. The previously flat cells become considerably thickened, whereby the circumference of the

entire head is diminished, until it is not much larger than the trunk. The apical plate has grown out forward in the form of a cone. The eyes are more conspicuous than in the larva. In the trunk the primitive segments have increased in number, and made the segmentation of the body still more distinct, since they have enlarged more and have applied themselves more closely to the intestinal and body-walls. At the posterior part of the trunk they are less clearly expressed. These changes are much more evident in the last stage of development (Fig. 121 B), which we introduce for comparison. There the segmental constrictions of the intestine cause the metamerism to be still more distinct. The cephalic vesicle and the vibratile apparatus have already entirely disappeared in this stage; and we have now before us in its chief features the adult worm, although it has not yet reached its complete development. The worm gives up the larval mode of life, that of floating upright in the water, and adapts itself to locomotion by creeping. The papillæ, which make their appearance in front of the posterior band of cilia, which has now disappeared (Fig. 121), serve the worm for the purpose of attachment.

Fig. 121.—A and B, larvæ of Polygordius (after HATSCHEK). a, anal opening; m, mouth-opening; kn, head kidney.

The Different Larval Forms.

—Polygordius was selected as an example because it shows in a particularly instructive manner the transition of the larva into the worm. It does not show, however, the ordinary condition

of the Trochophore larva, for the anterior bell-shaped part in the majority of cases is not retained unaltered for so long a time. Generally also it does not surpass the trunk so considerably in size, and it soon comes to be even smaller than the trunk. Since in many forms the typical shape of the Trochophore is not so strongly expressed, and, on the other hand, the segmentation of the body of the worm makes its appearance at an early stage, many deviations from the shape of the Trochophore are realized. The larvæ of Annelids are very variously shaped, for some of them, owing to the early appearance of the segmentation, are found in phylogenetically younger stages than the *Trochophore*, and others, although they stand at the same level with it, may be modified by the occurrence of various kinds of locomotor organs and by other external changes in form. The principal difference in the larvæ consists in the presence or absence of segmentation of the entire larva, not including that of the trunk part, which is acquired only during the metamorphosis. To be sure, this difference should not be overrated, for the segmented forms likewise must pass ontogenetically through an unsegmented stage. The Annelid larvæ have usually been distinguished according to the distribution of their cilia : as *Atrochæ* when a ciliated band is lacking ; *Monotrochæ* with a preoral band of cilia, to which, as in the Telotrochæ, there may be added a post-oral band lying directly behind the mouth ; *Telotrochæ* with an anterior and posterior (perianal) band of cilia ; *Mesotrochæ*, in which the ciliated band is situated in the middle of the body ; and, finally, *Polytrochæ*, which possess a greater or smaller number of ciliated bands, and as a result of this exhibit at an early stage a segmentation of the body. The ciliated bands of the *Polytrochæ* may form either closed rings, or only half-rings. In the latter case, according to their position on the dorsal or ventral surface, *Nototrochæ* and *Gastrotrochæ* are in turn distinguished. They are called *Amphitrochæ* when ventral and dorsal half-rings alternate with one another. This classification has been made use of by different investigators for distinguishing the larvæ. However, CLAPARÈDE and METSCHNIKOFF themselves, to whom we owe the most

thorough knowledge of the Annelid larvæ, point out that the characters cited have no great morphological value, for larvæ occur in the same family, and even in the same genus, which belong to more than one of these types. The differences in shape are probably due to differences in the mode of life. Variations in regard to the development of the locomotor apparatus—*i.e.*, in the distribution and stoutness of the ciliation—would easily follow, if the larvæ of closely related forms adopted different modes of life, as is actually the case. *Terebella* larvæ (*Terebella conchilega*) are known which must be placed among the *Nototrochæ*, while others belonging to this genus entirely lack the ciliated rings (*Terebella Meckelii*). The former are good swimmers, and lead a pelagic existence; the latter, on the contrary, never move far away from the masses of eggs from which they hatch, and may sometimes develop into young worms, even in the jelly surrounding the eggs.

The presence or absence of the preoral band of cilia may well be important in the interpretation of Annelid larvæ, for (according to KLEINENBERG) this alone possesses a ring-nerve, which is said to be lacking in all other bands of cilia that make their appearance, with the exception of the so-called post-oral band, which stands in close relation to the preoral. Even where posterior ciliated bands appear without the existence of an anterior one, as in the *Mesotrochæ*, the ring-nerve is said to be absent. But these conditions are as yet too little studied to allow one to base on them a distinction between the larvæ.

Out of the multitude of variously formed Annelid larvæ, only a few of the particularly characteristic forms can be chosen. We shall first consider the unsegmented larvæ.

The simplest larvæ of the Annelids are undoubtedly those whose body is covered with a
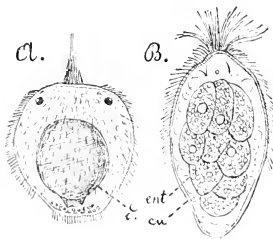
Fig. 122.—*A* and *B*, so-called atrochal Annelid larvæ — *A*, of *Lumbriconereis* (?) (after CLAPARÈDE UND METSCHNIKOFF); *B*, of *Sternaspis scutata* (after VEJDOVSKY). *cu*, cuticula ; *d*, intestine; *ent*, entoderm.

uniform coat of cilia, and which at the most possess at the anterior end of the body a tuft of cilia, which serves for steering (*Atrochæ*, Fig. 122 *A, B*).

CLAPARÈDE UND METSCHNIKOFF describe atrochal larvæ of *Lumbriconereis* (?), and VEJDOVSKY those of *Sternaspis*.[1] Both larvæ are at first spherical, but later become elongated (Fig. 122 *B*). The former possess eye-spots ; the latter do not. A differentiation in the ciliation appears even in these larvæ, for in *Lumbriconereis* narrow zones, one toward the anterior and one toward the posterior end, remain free from cilia, and in *Sternaspis* the entire posterior end is without cilia (Fig. 122 *A, B*). Inside one recognizes in the first form the sac-like fundament of the digestive tract, in the latter, on the contrary, only a compact mass formed of large entoderm cells.

The further development of Lumbriconereis is marked by the appearance of setæ in pairs at the posterior end of the body, thus giving expression to the segmentation. At the same time the degeneration of the cilia begins. In *Sternaspis* the entire ciliation of the body disappears, and the larva continues to live in this naked condition for some time, the segmentation of the body being as yet unrecognizable (VEJDOVSKY, RIETSCH). Its further development was not followed in detail.

It is difficult to say whether in the evenly ciliated larvæ we have to do with phylogenetically older stages than those represented by the *Trochophore*. The incomplete development of the intestinal canal, especially in the larva of *Sternaspis*, and also the subsequent development of this worm, make it appear as more probably a derived form. Although in *Lumbriconereis* the cilia in later stages are arranged into an anterior and posterior region, this distribution is altogether too indistinct to be referred to the anterior and posterior ciliated bands of the *Trochophore*.

Although we are not justified in looking upon these atrochal larvæ as primitive forms, still it appears to follow from the development of another Annelid that the larvæ which are provided with ciliated bands represent a stage succeeding the atrochal forms. In *Terebella Meckelii*, which was studied by MILNE-EDWARDS, CLAPARÈDE UND METSCHNIKOFF, and later by SALENSKY, there arises from a larva, which

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[1] *Sternaspis* has been classed with the Echiuridæ ; nevertheless in this form, which is provided with setæ, such a distinct segmentation is expressed, both externally on the body and internally, in the matter of the arrangement of the muscles and blood-vessels (RIETSCH), that this group of Annelids—very aberrant, it is true—must still be placed among the Chætopoda.

at first is rather evenly ciliated, one having a preoral and a perianal band of cilia, which is substantially in the *Trochophore* stage.

The young larvæ of *Terebella Meckelii* are at first spherical, then elongate a little, and become covered with an even coat of cilia, which leaves bare only the small part of the anterior end of the body lying in front of the eyes. Later they become pyriform, and the cilia now cover only the voluminous anterior part of the body, whereas the posterior region is destitute of them. It is only in a later stage of development that a perianal row of cilia makes its appearance. In this stage it resembles the previously described larva of *Lumbriconereis*. The ciliation is gradually confined to a preoral band, a perianal band, and a ventral ciliated groove (SALENSKY). To be sure, the outer form of the larva is in this case, on account of the small size of its bell, not that of a typical *Trochophore*; nevertheless nothing prevents us from comparing it to one that has already begun its metamorphosis into the worm. In front of the mouth lies the preoral band of cilia; the intestine has the usual shape; at the posterior end, in the vicinity of the anus, is found the perianal band of cilia. About midway between the anterior and posterior ciliated bands appear indications of the two first segments, behind which others soon follow. They become noticeable externally by the development of protuberances, which are studded with setæ. The worm grows in length; evaginations at its anterior end form the tentacles; it secretes the tube and attaches itself.

The larvæ of the *Chætopteridæ*, known as *Mesotrochæ*, also arise from uniformly ciliated embryos. In *Chætopterus*

pergamentaceus, which at first is evenly ciliated, there is formed a tuft of cilia at the anterior end of the larva, and gradually a ring also of cilia, encircling the body at about the middle (Fig. 123). The inside of the larva is pretty well filled by the large sac-like intestinal canal. The larva of *Telepsavus costarum* is similar, only that it lacks the anterior tuft of cilia. On the other hand, the larva of *Phyllochætopterus socialis* also exhibits stouter cilia at the anterior end; it possesses two ciliated bands which lie close to the posterior end. A preoral band of cilia is not present in these larvæ, and the middle one cannot be

directly compared to the perianal ciliated band of other An-
nelid larvæ, for it is not, like that, situated at the posterior
end, but a number of segments make their appearance be-
tween it and the hind end. The anus in these larvæ is
placed dorsally, for a pointed prolongation is formed pos-
teriorly on the ventral surface, a condition which also recurs
in polytrochal larvæ (comp. Fig. 127).

Noteworthy is the tuft of cilia at the anterior end which we met with
in the atrochal and mesotrochal larvæ, and which is also recalled by the
stout cilia found at the head end of many telotrochal and polytrochal
larvæ. Such a ciliation of the apical area occurs also in *Turbellarian*,
Nemertean, and *Molluscan larvæ*, and has perhaps a higher significance
than that of a merely secondary acquisition, connected with the larval
mode of life only.

Apparently aberrant larval forms, such as those of *Mitraria*
(Fig. 124 *A*, *B*), are referable to the *Trochophore*. *Mitraria*
would, therefore, have to be classed with the *Monotrochæ*, in
which a preoral, but not a perianal, band of cilia is de-
veloped (comp. the larva of *Psygmobranchus*, shown in Fig.
128, p. 280). *Monotrochæ* and *Telotrochæ* cannot be separated
from each other, inasmuch as in the beginning the larvæ
frequently possess only a preoral band of cilia, are therefore
monotrochal, whereas later a perianal ciliated band, which
gives them the character of *Telotrochæ*, is developed on them.

Mitraria, the Annelid larva discovered by JOH. MÜLLER, and subse-
quently more thoroughly studied by METSCHNIKOFF, can easily be recog-
nized in its young stages as a *Trochophore*, with a well-developed bell, but
much-reduced posterior portion (Fig. 124 *A*). As a result of this, the
anus and mouth are brought close together. The ciliated band lies in
front of the mouth. Later the posterior part of the body grows out
more, and the ciliated band, which acquires many outfoldings, there-
fore comes to lie more anteriorly (Fig. 124 *B*). In this figure the
beginning of the worm, which is gradually developed out of the
Mitraria, can be easily recognized. On the lower area, surrounded by
the ciliated band, two lateral protuberances, which bear long cilia, can
be recognized in the young larva. In the older larva they are seen
lying dorsally. The metamorphosis of the larva into the tubicolous
worm is due to the vigorous growth of the segmented posterior portion
and the degeneration of the chief part of the *Mitraria*, together with
its lobes and setiferous papillæ. Thereupon the larva sinks to the bottom,
secretes the tube, and becomes attached.

In *Mitraria* we recognized a larva which possesses provisional larval appendages in the form of long bristles,
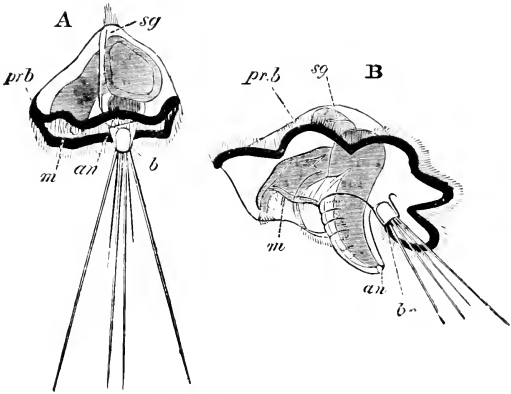
FIG. 124.—Lateral views of Mitraria larvæ (after METSCHNIKOFF, from BALFOUR'S *Comparative Embryology*). *an*, anus; *b* and *br*, the lateral elevations with the provisional setæ; *m*, mouth; *pr. b*, preoral ciliated band; *sg*, apical plate.

which also occur in other Annelid larvæ. *Trochophore* larvæ are known which exhibit a number of long denticulate bristles on both sides of the body, thus, *e.g.*, in the genera *Sabellaria, Spio*, etc. Figs. 125 and 126 show larvæ more advanced in development with richly developed, and in part extraordinarily long, provisional setæ. Setæ of this kind do not appear in adult recent Chætopoda, but, on the other hand, are found in fossil forms. It has been conjectured that they might have been inherited from unsegmented ancestors of the existing Chætopoda. This suggestion appeared to be supported by the fact that they are mostly found on the anterior unsegmented part of the larva (ALEX. AGASSIZ).

FIG. 125.—Larva of *Nerine* (after ALEX. AGASSIZ, from BALFOUR'S *Comparative Embryology*).

The larvæ of *Ophryotrocha puerilis* (Fig. 127) are *Polytro-
chæ*—segmented larvæ in the proper sense. They possess a
number of segments, each one of which
is provided with a ciliated band. In
addition, stouter tactile hairs are found
at the anterior and posterior ends of the
body. The first ciliated band belongs
to the head region of the larva. Next to
this is situated the mouth-opening, which
leads into a large pharynx provided with
a chewing apparatus. The intestine
extends straight backwards, and opens
to the exterior at the end of the last seg-
ment. The anus is situated dorsally, in-
asmuch as the last segment possesses a
pointed process on the ventral side (Fig.
127).

The next stages of development in *Ophryo-
trocha* remain much like the larva described,
since the new segments formed in front of the
anal segment are also provided with bands of
cilia. Knob-like parapodia then bud out on the
segments, and in them the setæ are developed.
The number of the segments is considerably in-
creased, yet this small Annelid, which never
becomes over 2·5 mm. long, remains, as it were,
in a larval condition, since the segments retain
their ciliation throughout life. Still another
ciliated band has been developed on the head,
and two small knob-like feelers have arisen there,
which bear long cilia, just as do the two cirri
which have made their appearance near the unpaired process on the
anal segment. The two most anterior segments remain without appen-
dages (CLAPARÈDE UND METSCHNIKOFF).

FIG. 126.—Annelid larva
with provisional setæ
(after ALEX. AGASSIZ,
from BALFOUR'S *Compara-
tive Embryology*).

In *Ophryotrocha* the ciliated rings surround the entire
segment. They appear to be arranged in the same way in
Arenicola marina; in other larvæ, on the contrary, they have
the form of half-rings only, and are confined to the dorsal
or ventral surfaces (*Nototrochæ* and *Gasterotrochæ*). *Noto-
trochal* larvæ are found, for example, in *Terebella conchilega*,

gasterotrochal in members of the genera *Magelona*, *Nerine*, and *Spio*. In the two last-named genera there are found *amphitrochal* larvæ—*i.e.*, such as possess dorsal as well as ventral half-rings—in addition to the *gasterotrochal*, just as *atrochal* and *polytrochal* larvæ appear in the genus *Terebella*.
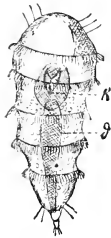
Fig. 127.—Polytrochal larva of *Ophryotrocha puerilis* (after CLAPARÈDE UND METSCHNIKOFF). *d*, intestine; *k*, jaws.

The polytrochal larvæ sometimes appear as a stage succeeding other larval types. Thus those of *Arenicola marina* arise from larvæ which at first were monotrochal, later became telotrochal, and finally, by the appearance of new ciliated rings between those already present, assumed the stage of polytrochal larvæ (MAX SCHULTZE). Also the true polytrochal larvæ—*i.e.*, those which possess only the ciliated bands, but do not yet, like many other polytrochal larvæ, exhibit the fundaments of the setæ and other parts of the body of the worm—appear as the stage succeeding the *Trochophore*. Thus we have just noted a stage entirely resembling a *Trochophore*, which preceded the polytrochal larva of an *Ophryotrocha*. This condition warrants the assumption that the segmented forms are to be looked upon as the younger, the unsegmented, on the other hand, as the phylogenetically older.

As may be inferred from the manifold shapes of the Annelid larvæ, their metamorphosis into the worm is also extremely varied.

This has already been briefly discussed in some forms while considering the larval stages. The segmentation may be expressed on the body of the larva in various ways. In some cases the body elongates and divides into segments, while the ciliated bands are still retained. In other forms the setæ alone first make their appearance in pairs, and indicate the segmentation of the body, or at the same time the parapodia are established in the form of protuberances. Thus larvæ are found which have still preserved the entire form of the *Trochophore*, and yet exhibit already the two lateral rows of setæ or parapodia. At first only a few

segments are present; new ones are, however, continually being interpolated behind. Since, moreover, the parapodia acquire more and more their permanent shape, and the larval organs, on the other hand, degenerate, the larva approaches the shape of the adult animal.

The segmental appendages do not arise in a uniform manner in the different divisions of the Polychæta. In the *Errantia* the dorsal and ventral parapodia arise from a common fundament, which afterwards separates into the dorsal and ventral parts. This has been observed, for example, in *Nereis*. Such a separation, however, does not take place in the *Sedentaria*, but their dorsal hook-bearing segmental appendages arise independently of the ventral parapodia (thus in *Terebella*). Accordingly it is maintained that only the dorsal appendages of the *Sedentaria* correspond to the common parapodal fundament in the *Errantia*, whereas the ventral appendages are to be considered as new formations of a secondary nature (SALENSKY).

The cirri and tentacles arise as elevations and evaginations of the ectoderm, into which continuations of the somatic mesoderm may also extend. Of these the unpaired median tentacle, as it occurs, for example, in *Terebella*, *Pileolaria*, and *Psygmobranchus*, usually extending forward beyond the head, is of an especially peculiar nature. It attains at first a large size, and is provided with a considerable cavity (*Terebella*), but may soon become reduced in size again (*Psygmobranchus*). When it is present, there are found near it, and on either side of the head, the lateral tentacles, the number and form of which are very variable in the different Annelida. The tentacles may attain a peculiar development by putting forth bud-like evaginations, which enlarge and become the gills. In *Psygmobranchus* the larva, by means of the trifid gills, acquires quite a peculiar shape (Fig. 128 *B*). [1] The median tentacle, which was present somewhat earlier and extended forward beyond the head, has already in this stage degenerated. As sometimes the tentacles, so also may the eyes, degenerate in the *Sedentaria*, since these sessile forms can scarcely have further need of them. In *Psygmobranchus* a peculiar organ is seen lying behind the gills (Fig. 128 *B*, *kr*), which is also developed in other Annelida (*Pileolaria*, *Spirorbis*). This is an annular fold of the

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[1] The larva which is here figured has developed from a so-called monotrochal larva (Fig. 128 *A*), which exhibits the form of the Trochophore, provided with a preoral and post-oral ciliated band, while the preanal band is wanting. The post-oral ciliated band is continued into the ventral (so-called adoral) ciliated groove. The Trochophore already possesses two eye-spots, but still lacks the intestinal canal, which is represented by only an entodermal mass of large cells. The mouth is already indicated.

skin, which grows out backwards, and surrounds like a mantle the part of the body lying behind the head.

The first two segments lying behind the head are conspicuous in many Polychæta (*Terebella, Oph-*

ryotrocha) by the fact that they are destitute of seg-mental appendages; this fact has caused them to be reckoned as belonging to the head, which is thus sup-posed to arise from several segments. However, the manner of formation of their internal organs (neural and mesodermal), which are begun like those of the body segments, is an argument against this (SALENSKY). Differences of opinion exist among the different investi-gators concerning the origin of the head itself, for some of these maintain that it is formed from the preoral por-tion of the Trochophore alone; while, according to others, post-oral parts of the larva also enter into its for-mation.

FIG. 128.—*A, B,* larval stages of *Psygmobran-chus protensus* (after SALENSKY). *A,* Trochophore with pre- and post-oral ciliated bands and adoral ciliated groove (seen from the ventral surface); *m,* region of the subsequently formed mouth-opening; *ent,* still undifferentiated entodermal mass within; *B,* later stage with gills (*k*); *b,* fundaments of the setæ; *kr,* collar; and *vd, md, ed,* fore-, mid-, and hind-gut.

In forms which, like *Exogone gemmifera* and *Grubea limbata,* brood their eggs, the stage of the free larva may be altogether omitted, the embryo breaking through the egg en-velope in the form of the young worm al-ready provided with a number of segments, parapodia, and cirri (VIGUIER). It is these conditions which recall those in the Oligochæta, more especially since one of

the forms mentioned (*Exogone*) is said to pass through a
stage of development which, according to the description of
VIGUIER, strongly resembles the "larvæ" of the Oligochæta.

2. Development without Free-swimming Larva

(*Oligochæta*).

The Oligochæta lay their previously fertilized eggs in firm
cocoons, consisting of a chitin-like substance. The cocoons
vary greatly in shape in the different genera, and, according
to the life-habit of the worm, are found either in the earth
or attached to aquatic plants. The slender, spindle-shaped
cocoons of *Criodrilus* attain a considerable length (as much
as 5 cm.). In the *Lumbricidæ* they are rounded or ovate,
and of different sizes in one and the same species, being
about as large as a pea or a bean. Correspondingly the
number of eggs which they contain is also variable. Some-
times only a very few eggs are found, while in other cases
the number may reach as many as twenty or thirty. Usually
not all of these eggs develop, but, as appears, some of them
develop at the cost of the others. Ordinarily the eggs float
in an albuminous mass. Their development is different
according as they contain a small amount of food-yolk
(*Lumbricus*, *Criodrilus*), or possess abundant yolk (*Rhyn-
chelmis*, *Tubifex*). Cleavage is always unequal, but in the
first case an invaginate gastrula is formed, while in the
second an epibolic gastrula occurs.

Cleavage and the formation of the germ-layers in the Oligochæta have
been thoroughly studied by various investigators (KOWALEVSKY, No. 27;
HATSCHEK, No. 18; KLEINENBERG, No. 24; VEJDOVSKY, No. 45). In
Lumbricus a blastula is formed which is thicker on one side, and which
may be flattened so that the cleavage cavity is small; and the gastrula,
which soon arises by invagination, is also at first rather flat (KOWALEVSKY,
Fig. 130 *A*). These characters are less marked in the case of *Lumbricus
trapezoides* (Fig. 129 *A*), in which occurs the peculiar phenomenon of the
division of the embryo in the gastrula stage, producing in this way two
embryos, which, separated from each other, develop further. Fig. 129
A represents such a stage of division of an embryo, and shows the two
embryos (which are in the same stage of development) only slightly
united.

In case the egg is very rich in yolk, as in *Rhynchelmis*, there arise, according to VEJDOVSKY, as the result of the first divisions, four blasto- meres, from which four much smaller blastomeres are constricted off, so that now four micromeres and four macromeres are present. While the micromeres increase rapidly by division, the hindmost and largest of the four large cleavage spheres buds off three cells of medium size : the mesomeres. Now the macromeres also divide further ; the micromeres, which, as well as the mesomeres, have meantime increased in number, grow over the latter, which thereby come to lie inside. Between micro- meres and macromeres a small cleavage cavity arises, which is soon obliterated, when the small cells grow over the large ones further, in this way forming an epibolic gastrula.

Ordinarily several, usually two, blastomeres are differen- tiated before the formation of the two primary germ-layers, but apparently exhibiting relations to both of them ; these withdraw from connection with the other cells and enter the cleavage cavity (Fig. 129 *A*). They constitute the fundament
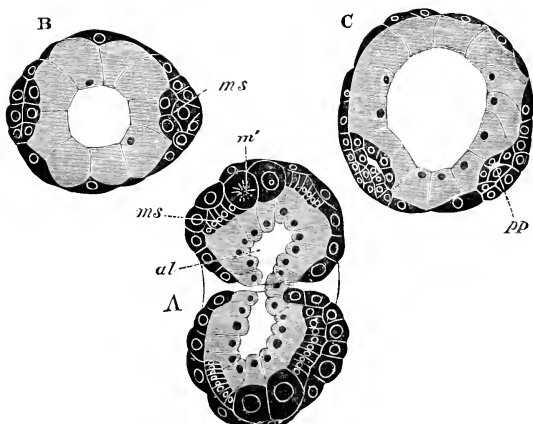
Fig. 129.—*A* to *C*, sections through embryos of *Lumbricus trapezoides* (after KLEINENBERG, from BALFOUR's *Comparative Embryology*). *A*, horizontal longi- tudinal section of an embryo in the gastrula stage, which is about to divide into two embryos ; between ectoderm and entoderm the two large pole cells of the mesoderm (*m'*) can be recognized, with the mesodermal bands (*ms*) arising from them on either side ; *al*, archenteron ; *B* and *C*, cross-sections of somewhat older embryos, which show how the mesodermal bands (*ms*) move toward the ventral side, and how the cavity (*pp*) makes its appearance in them.

of the mesodermal bands. These arise by the division of the
two cells, and by the smaller cells thus produced moving
away from them. This process can best be understood from
the figures of *Lumbricus* given by KOWALEVSKY and KLEI-
NENBERG (Figs. 129 and 130). The two large cells (pole cells)
from which the smaller cells of the mesodermal bands have
arisen by division are seen in the posterior part of the
embryo (comp. the interpretation given by KLEINENBERG, p.
286). The mesodermal bands extend on both sides of the
embryo towards the mouth ; whereas they at first diverge,
later they move from the lateral position toward the ventral
surface, and now lie on either side of the median line (Fig.
129 *B*, *C*).
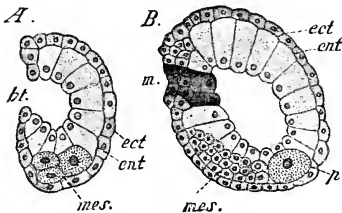
FIG. 130.—*A*, *B*, optical longitudinal sections of two embryos of *Lumbricus
rubeilus* (*Allolobophora fœtida* [?], Vejdovsky) of different ages (after KOWALEVSKY).
bt, blastopore ; *ect*, ectoderm ; *ent*, entoderm ; *m*, mouth-opening ; *mes*, mesodermal
bands ; *p*, pole cells of the mesoderm.

In the figures 130 *A* and *B*, the mesodermal bands are
seen in side view, and their first appearance (Fig. 130 *A*)
can be recognized. In this case they consist from the begin-
ning, not of one, but of several, cell-rows ; but even here the
pole cell of each band can be seen at the posterior end. The
bands extend further and further, and finally acquire the
considerable length which is represented in the figures 130
B and 131.

Together with the elongation of the mesodermal bands
already described, which are also, though inappropriately,
called germ bands, the formation of the embryo as a whole
has progressed further (Figs. 130 *B* and 131). It has en-
larged by the rapid multiplication of its cells, and now con-

sists substantially of a bilaminar cellular vesicle, between
the two layers of which are lodged on the ventral side the
mesodermal bands. The blastopore has become the per-
manent mouth, in the neighborhood of which a lip-like
thickening of the ectoderm makes its appearance. The
cells lying around the mouth appear to be of a contractile
nature, and accordingly execute swallowing movements, in
consequence of which the intestine becomes filled with the
albumen in which the embryo floats, and which serves it as
food. As a result of this nutrition the embryo becomes
more and more distended, and increases in volume. The
embryo in this condition may be compared with the free-
swimming *larvæ* of other Annelida, especially as it bursts
the vitelline membrane at about this stage, and now floats,
as has been mentioned, in the albumen of the cocoon. The
larva-like appearance of the embryo is increased by the fact
that in *Lumbricus trapezoïdes* (according to KLEINENBERG)
there is found a ring of delicate cilia, surrounding the
mouth and continuing into a ventral ciliated groove, which
extends in the middle line between the mesodermal bands.
HATSCHEK also found an adoral ciliated zone in the embryos
of *Criodrilus*. Furthermore VEJDOVSKY proved the existence
in *Rhynchelmis* of a paired head kidney, which BERGH also
found in *Criodrilus*. It consists of a long, semicircular tube,
the blind inner termination of which lies in the vicinity of the
mouth, whereas the external opening of the ciliated canal is
situated laterally at about the middle of the body. In view
of all this, the embryos of the Oligochæta appear to be
degenerate larval forms, which float free in the albumen of
the cocoon, and here feed independently. The absence of the
anus does not enter much into the question, for we see that
in many Trochophore larvæ also—for example, in *Psygmo-
branchus*—the anus, and even the mouth, may be wanting in
the early part of its free existence (comp. Fig. 128, p. 280).

The metamorphosis of the larva-like embryos into the
worm is accomplished principally as the result of the further
development of the mesodermal bands. These at first con-
tinue their growth forwards and surround the fore-gut,
which has been formed out of an invagination of the ecto-

derm (Figs. 130 *B* and 131). Also in the parts of the
embryo lying further backwards the mesodermal bands
advance from the ventral side, to which they were at first
confined, to the dorsal side, and thus separate the ectoderm
from the entoderm. The separation of the mesodermal
bands into primitive segments and the splitting of these into
somatic and splanchnic layers occurred even before this
(Figs. 129 *C* and 131). The posterior part of the embryo
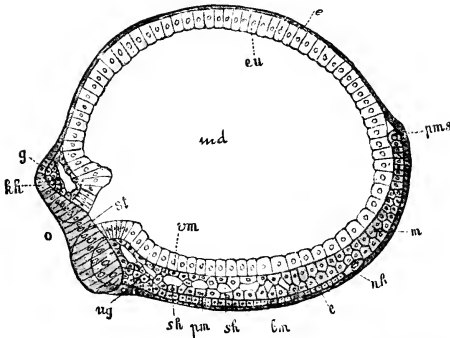
Fig. 131.—Optical longitudinal section of an embryo of *Lumbricus olidus* (after
WILSON, from LANG's *Lehrbuch*). *bm*, fundament of the ventral nerve cord; *e*,
ectoderm; *en*, entoderm; *g*, fundament of the supra-œsophageal ganglion; *kh*,
head cavity; *m*, mesodermal bands; *md*, cavity of the mid-gut; *nb*, neuroblast
cells; *o*, mouth; *pm*, parietal (somatic) layer of the primitive segments; *pms*, pole
cells of the mesoderm; *sh*, cavity of the primitive segments; *st*, stomodæum
(fundament of the fore-gut); *ug*, suboesophageal ganglion; *vm*, visceral (splanchnic)
layer of the primitive segments.

is greatly distended by the albumen taken into the intestine,
and bulges out like a yolk-sac on the embryo, which in the
meanwhile has grown longer (Fig. 132 *h*). Also in the
posterior distended part of the embryo the primitive seg-
ments are ultimately formed and grow around the ento-
dermal sac towards the dorsal side, so that finally it is
entirely surrounded by mesoderm; thus the most im-
portant parts in the development of the worm, as far as
regards its outer form, are completed. The anus is formed
later by an ectodermal depression at the posterior end of
the worm.

Both the origin and the further development of the mesoderm are disputed points in the development. In some cases, as, for example, in the *Lumbricus* studied by Kowalevsky (and in *Nereis*, according to Goette), it appears as if the first mesoderm cells had been derived from the entoderm cells, whereas in other cases they seem rather to have belonged to the ectoderm. Usually their origin cannot be referred to either one or the other of the two primary germ-layers, for they were established before the formation of these, or on the border-line of the two. Such is the case in various Oligochæta and also in Polychæta. In *Rhynchelmis* (comp. p. 282) the so-called mesomeres are separated off from the large blastomeres, which subsequently become the entoderm, and, together with the micromeres, overlie these; apparently therefore they belong to the ectoderm. It is only later that they are overgrown by the

ectoderm, and move to the inside here to develop into the mesodermal bands (Vejdovsky).

Just as the opinions of authors are divided in regard to the derivation of the mesoderm, so also are they in regard to the manner in which the mesodermal bands are formed. Whereas some authors derive them from proliferations of the primitive mesoderm cells (Kowalevsky, No. 27; Hatschek, No. 18; Goette, No. 15), others are of the opinion that the parts of the ectoderm which lie over the mesodermal bands also supply cells for the reinforcement of these bands, and that as a result ectoderm and mesoderm are in this region continuous (Fig. 129 *B*). Kleinenberg (No. 24) thus describes the conditions in *Lumbricus trapezoides*. Salensky (No. 37) agrees with him. Recently Kleinenberg (No. 26) has gone still further, for he considers that the entire mesoderm—the existence of which as a separate layer he, moreover, denies—has been gradually split off from the ectoderm. This point will be referred to again in considering the organogeny.
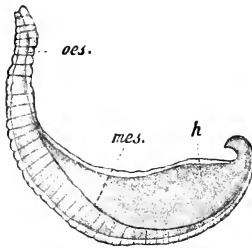
Fig. 132.—An embryo of *Lumbricus agricola*, already far advanced in development (after Kowalevsky). *h*, posterior part of the embryo, resembling a yolk-sac; its wall is formed of ectoderm and entoderm, and it gradually becomes overgrown by the mesodermal bands; *mes*, upper limit of the left mesodermal band; *œs*, œsophagus.

3. The Formation of the Organs.

So much of the formation of the individual organs as has not been considered in the two preceding sections upon the general form of the body will be added here. However, it

should be noted at the beginning that upon these matters
there prevails as yet among authors but little clearness, and
agreement to only a limited extent.

ECTODERMAL STRUCTURES.

The *epidermis* of the larva and of the adult worm arises
directly from the embryonal ectoderm, its cells multiplying
greatly, and becoming much flattened.

The *setigerous sacs* arise, according to the concurrent state-
ments of KOWALEVSKY, VEJDOVSKY, and BERGH, as club-shaped
ingrowths of the epidermis, inside of which the setæ are
secreted. According to other descriptions, the setigerous sacs
originate from the mesoderm.

Nervous System and Sensory Organs.—In considering the
origin of the nervous system it seems necessary to separate
the supra-œsophageal ganglion from the ventral cord. Both
arise as thickenings of the ectoderm (Fig. 133 C), the ven-
tral chain of ganglia either as a longitudinal, unpaired
or as a paired thickening, which detaches itself from the
ectoderm, and moves to the inside, where it may be sur-
rounded by mesoderm (KOWALEVSKY). The further develop-
ment proceeds from in front backwards. Opinions are very
far apart regarding the origin of the supra-œsophageal
ganglion, and especially its connection with the ventral
chain of ganglia.

In HATSCHEK's opinion, there first arises an ectodermal thickening at
the head end of the embryo: the apical plate. From this the ectodermal
thickening progresses backwards in the form of two cords, which extend
on either side of the mouth. From the œsophageal connectives thus
formed, the thickening process continues further and further. In this way
the two lateral cords of the ventral nerve-trunk are formed, and in addition
a groove-like invagination, lying in the longitudinal median line (similar
to the medullary tube of vertebrates), takes part in the formation of the
ventral chain of ganglia. HATSCHEK defends the view that the entire
nervous system arises from a single fundament. In this he relies mainly
upon his embryological investigations on *Criodrilus* and *Polygordius*, and
furthermore on the comparative anatomical conditions in *Protodrilus*, in
which Archiannelid the œsophageal connectives are said to remain
throughout life in connection with the body epithelium as ectodermal
thickenings.

In opposition to this theory, KLEINENBERG—with whom GOETTE, SALENSKY, BERGH, and FRAIPONT agree—espouses the view that the nervous system is composed of two separate fundaments. The supra-œsophageal ganglion arises as a preoral ectodermal thickening independently of the two longitudinal thickenings of the ventral side, which represent the fundament of the ventral nerve cord. (A longitudinal furrow corresponding to the medullary tube of the vertebrates does not exist.) Later it puts forth lateral processes, the œsophageal connectives, which unite with the already-formed ventral nerve cord. Such is the condition in *Lumbricus*. The origin of the nervous system in *Lopadorhynchus*, likewise studied by KLEINENBERG, depends upon much more complicated formative processes. *Lopadorhynchus* develops from a monotrochal larva, the posterior portion of which grows out into the worm in the manner already described. A ciliated pit, the so-called apical organ (Fig. 135, p. 293), and the two apical tentacles arise in the vicinity of the apical pole as provisional sense-organs. Behind these the two pairs of permanent antennæ and the olfactory pits are formed, also as ectodermal growths. From these organs, which later degenerate in part, the formation of the supra-œsophageal ganglion proceeds. Ordinary ectodermal cells are metamorphosed into ganglionic cells, which accumulate in the region of these organs, later sink in deeper, and unite to form the supra-œsophageal ganglion. This finally detaches itself from connection with the ectoderm and appears inside the body as an independent organ.

Just as the formation of the supra-œsophageal ganglion, according to KLEINENBERG, starts from the sensory organs, so the origin of the ventral nerve cord is also referred by this investigator in part to the influence of the sensory organs. In the main, however, the impetus to its formation proceeds from the locomotor organs. From the inner [deep] side of the ventral ectoderm, the outer surface of which bears tufts of sensory hairs (Fig. 134 *C*), a plate is separated off, the so-called neural plate, in which a right and left portion can be distinguished (Fig. 134, p. 292). Along this plate arise segmental, paired ingrowths, the setigerous sacs (Fig. 134 *C*). Dorsad and ventrad from these are formed as ectodermal ingrowths the dorsal and ventral cirri. The parts of the neural plate situated nearest to the median plane supply the ventral cord. They approach more and more the middle line, and here fuse with each other.

The union of the ventral nerve cord with the supra-œsophageal ganglion is secondary. It is brought about by the neural plates extending forward and sending out processes to the ring-nerve of the ciliated band. But processes of the supra-œsophageal ganglion also pass into this, and in this way the œsophageal connectives arise, whereas the ring-nerve itself, together with the ciliated band, disappears.

Therefore, according to KLEINENBERG'S description, here reproduced briefly, the brain and ventral cord appear to have a separate origin, the impulse to which comes through sensory and locomotor organs.

The origin of the sensory organs has already been touched upon several times, as, for example, the formation of the auditory vesicles in *Eupomatus* (comp. p. 267). The eyes of the *Alciopidæ* are formed, according to KLEINENBERG, as invaginations of the ectoderm, which are constricted off and unite with the brain, this union constituting the optic nerve. The retina arises as the result of the differentiation of the inner [deep] wall of the vesicle, whereas the outer wall becomes very thin. Within, the lens and, by the activity of certain gland-like cells, the vitreous body are secreted.

MESODERMAL STRUCTURES.

Body Cavity; Musculature; Blood-vessels.—The differentiation of the mesodermal bands, which results in the formation of the segmental cavities, and thereby causes the segmentation of the body, takes place in a simple manner. The mesodermal bands have extended forward and in the anterior part of the body become several rows wide and several layers deep. Then a segmentation begins at their most anterior end, individual parts becoming differentiated in groups, and finally separated from one another by transverse boundaries (Fig. 131, p. 285). These box-like, quadrangular cell-plates, which succeed one another along the course of the mesodermal bands, and therefore lie side by side in two rows, are the primitive segments, the influence of which on the segmentation of the body we have already briefly mentioned in considering the development of *Polygordius* and *Lumbricus* (pp. 268 and 284—286). We saw there also that the development of the primitive segments takes place from in front backwards. When the primitive segments are already well formed in the anterior part of the body, the mesodermal bands are still entirely undifferentiated in their posterior portions, and new cell material continues to be formed here in the vicinity of the primitive mesoderm cells (Fig. 131). A fissure soon makes its appearance in the primitive segments, owing to the fact that the two or more cell-layers out of which they are composed separate from each other at the middle of each primitive segment (Fig. 133 *B* and *C*). Thus the segmental cavity—that is to say, the be-

ginning of the body cavity—is formed in each segment of the
body of the worm. The cavity enlarges while the walls of
the primitive segments are more and more distended and
apply themselves to the body-wall and to the wall of the
intestine as the somatic and splanchnic layers respectively
(Fig. 133 *C*). But of course every two of the segments abut
on each other with their anterior and posterior walls, and
thus arise the septa (dissepiments), which separate the
different segments of the body. Since each segment of the
body requires for its formation a primitive segment on the
right side and one on the left, there are formed a dorsal and a
ventral mesentery (Fig. 133 *C*). These mesenteries dis-
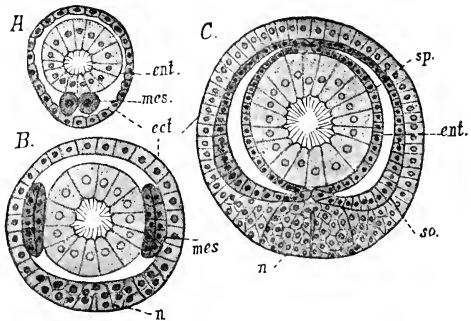
FIG. 133.—*A* to *C*, transverse sections of *Polygordius* larvæ (after HATSCHEK).
A, optical cross-section of the body of an unsegmented larva, immediately in
front of the anus, showing the two primitive mesoderm cells (*mes*); *B*, *C*, two
cross-sections of an older larva, the former from the posterior, the latter from the
anterior, part of the body; *ect*, ectoderm; *ent*, entoderm; *mes*, mesoderm; *n*,
fundament of the nervous system; *so*, somatic, *sp*, splanchnic layer of the meso-
derm.

appear in most of the Chætopods (just as the septa also are
frequently perforated), but they persist in some of the lowest
Annelids, such as *Polygordius* among the Archiannelida and
Saccocirrus among the Chætopoda.

The body musculature arises from the somatic layer of
the primitive segments, the ventral longitudinal muscles
being the first to be formed. By the arrangement of the

musculature its segmental origin can be recognize l even in the fully developed animal. The peritoneal epithelium is also derived from the primitive segments.

The splanchnic layer of the mesoderm produces so much of the wall of the intestine as is not of entodermal or of ectodermal origin, and the walls of the vessels also arise from it. According to SALENSKY, the formation of the blood-vascular system begins (in *Psygmobranchus* and *Terebella*) in the form of canals, which lie between the entoderm and the splanchnic layer, and which are therefore really parts of the segmentation cavity. Later these blood-filled cavities are surrounded with a cellular wall, which comes from the splanchnic layer. According to KOWALEVSKY'S observations also, mesodermal cells, which collect between the ectoderm and splanchnic layer, form the walls of the vessels; more-over, the dorsal vessel (*Lumbricus* and *Criodrilus*, according to VEJDOVSKY) arises from separate paired fundaments. These extend along the boundaries of the mesodermal bands as they grow dorsad, and, advancing with them, finally fuse with each other to form the dorsal vessel. This con-dition is of especial interest from the fact that in *Pleurochæta* (*Megascolex*) the separate fundaments of the dorsal vessel are retained in certain parts of the body throughout life (BEDDARD).

It appears questionable whether the cephalic cavity is formed in the same way as the segmental cavities of the body, or whether it is to be distinguished from these. On the first assumption, the two most anterior primitive segments would unite for its formation, and therefore outgrowths of the mesodermal bands must have crowded forward past the œsophagus even into the head region. The outer wall of the head and the muscula-ture of the œsophagus would then be formed from the somatic and splanchnic layers respectively in the usual way. The conditions were described in this way by KLEINENBERG in his earlier work, and VEJDOVSKY also derives the cephalic cavity from the two "anterior ends" of the mesodermal bands, which he describes as being fused (*Rhynchelmis*). Opposed to this is the view, supported especially by the free-living larvæ, that the cephalic cavity arises by means of a separation of the two primary germ-layers and by an immigration of mesodermal elements from the trunk (HATSCHEK). According to this explanation, the first pair of primitive segments lies behind the head, and the mesoderm of

the head arises from one wall, or from the still undifferentiated mesodermal bands. The absence of the mesenteries in the head of *Polygordius* supports the view that the cephalic cavity is not paired, but unpaired, in its origin (HATSCHEK).

The difference between head cavity and body cavity vanishes when— as is the case, according to KLEINENBERG, in many Annelids, for instance
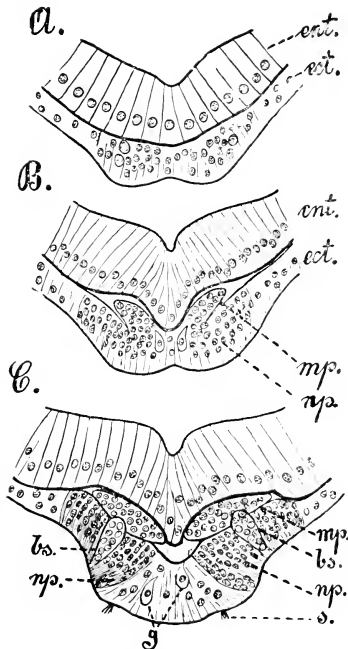
FIG. 134.—*A* to *C*, parts of frontal longitudinal sections of the larva of *Lopadorhynchus*, showing the splitting off of the muscle-plates (after KLEINENBERG). *bs*, fundaments of setigerous sacs; *ect*, ectoderm; *ent*, entoderm; *g*, ganglionic cells of the larval nervous system; *mp*, muscle-plates; *np*, neural plates; *s*, larval sensory organs.

in *Lopadorhynchus*—a regular splitting of the mesoderm into a somatic and a splanchnic layer does not take place, but the investment of the entoderm is effected by separate cells detached from the mesodermal

bands. The body cavity of the trunk in such cases therefore does not represent the cavity between the two layers of the mesoderm, but corresponds to the blastocœle (traversed by mesodermal cells), just as the cephalic cavity does in the case mentioned above. Moreover, in *Lopadorhynchus* this also arises by an immigration of mesoderm cells into the head portion. From this description it follows that the formation of the body cavity does not always take place in so regular a manner as has been described above; in fact, according to KLEINENBERG's statements, the formation of the entire mesoderm may be effected in another manner. It has already been mentioned (p. 286) that in KLEINENBERG's opinion the ectoderm, in addition to the pole cells, takes part in the formation of the mesodermal bands of *Lumbricus trapezoides*. Cells are separated off from the ectoderm and added to the germ bands lying under them. In
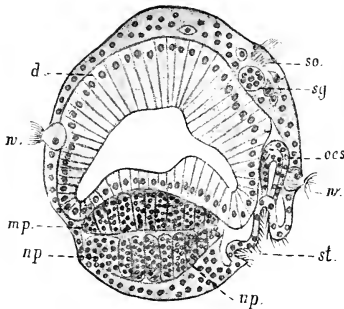
FIG. 135 —Sagittal section of a larva of *Lopadorhynchus* (after KLEINENBERG). *d*, intestine ; *mp*, muscle-plate ; *np*, neural plate ; *œs*, fundament of the (permanent) œsophagus ; *sg*, fundament of the supra-œsophageal ganglion ; *so*, apical organ ; *st*, stomodæum (temporary fore-gut of the larva) ; *w*, preoral band of cilia.

Lopadorhynchus KLEINENBERG derives the entire mesoderm from the ectoderm. According to him, mesoderm does not exist as a separate layer. The musculature of the *Lopadorhynchus* larva arises by means of an emigration of cells from the ectoderm (Fig. 134 *A* to *C*). The so-called muscle-plates (Fig. 135 *mp*) are formed by a splitting of the thickened ventral ectoderm, first at the hind end of the larva and then successively further forwards. The course of this cell growth, leading to the formation of the muscle-plates, is evident from the figures 134 *A* to *C*. The muscle-plates of the two sides are separated by a fold of the entoderm. The segmentation of the muscle-plates takes place after the fundaments of the setigerous sacs have grown in from the neural plates (comp. p. 287 and Fig. 134 *C*). The limits of the segments arise by the

loosening of the texture of the tissue in successive planes at right angles to the long axis of the body (Fig. 135). As was mentioned, individual cells separate from the muscle-plates, in order to apply themselves (like the splanchnic layer) to the intestine, whereas the remaining part of the muscle-plates supplies the musculature and epithelium of the body-wall. Blood-vessels and segmental organs were not observed in *Lopadorhynchus*. According to KLEINENBERG's explanation, with which, as regards the ecto-dermal origin of the mesoderm, SALENSKY also concurs, the primitive mesoderm cells occurring in other Annelids must be looked upon only as early differentiations of ectodermal parts. But when several organs of altogether different kinds, such as the musculature, the blood-vascular and excretory systems, can be referred back to such a common funda-ment, then the theory which considers this fundament as a germ-layer is not unwarranted, even when the fundament at times, as in *Lopad-orhynchus*, makes its appearance in somewhat later stages and in a less primitive manner, namely by the splitting off of a cell-layer from one of the two primary germ-layers.

WILSON's view should also be mentioned here, according to which, in addition to the two pole cells from which the mesodermal bands arise, three other pairs of similar pole cells are present on the ventral side of the embryos of *Lumbricus*. The three large cells mentioned, from each of which a row of cells extends toward the anterior end of the embryo, lie on either side of the middle line somewhat farther forward than the pole cells of the mesoderm and somewhat more superficial, therefore more in the region of the ectoderm. The innermost of these three rows is said to constitute the fundament of the nervous system, and the middle one that of the nephridia, whereas the significance of the outer one re-mained unknown to the author of this theory.[1]

The formation of the mesoderm and body cavity in *Enchytræoides* takes place, according to ROULE, in a very singular manner, as far as can be judged from his brief communication. In the "morula," which re-sults from an irregular cleavage, an outer layer, the ectoderm, is split off from a central mass, while the latter separates by means of a similar process into the centrally situated entoderm and the surrounding meso-derm. The former (entoderm) by the appearance of a cavity in it becomes the intestine, while spaces are formed in the mesoderm, which become confluent, and thus give rise to the body cavity between the two layers

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[1] [The conditions of the mesoderm have been further elucidated by the recent works of WILSON (Appendix to *Literature* on Annelida, Nos. XXIV. and XXV.) and BERGH (No. VII.). The origin of the pole cells and their relations to the organs have been followed out further. As a result more definite relations of those parts which were previously held to be exclu-sively mesodermal have been disclosed. A portion of the body muscula-ture appears to be of ectodermal origin. On this point the papers of BERGH and WILSON should be consulted.—K.]

of the mesoderm. The septa are said to be formed by outgrowths of cells from the somatic layer, which unite with the splanchnic layer!

Head Kidney and Segmental Organs.—In the larva of *Eupomatus* the head kidney arises by the outgrowth of a cell lying in front of each pole cell of the mesodermal bands. Some other mesodermal cells take part in their formation, for they supply the spheroidal cells which rest upon the inner blind end of the head kidney and elongate into the ligament-like threads of attachment of the organ (Fig. 118 *B*, p. 265). In addition to the formation of the head kidney, the few cells of which the mesodermal bands at first consist are further employed for the formation of the larval muscles. Only the two pole cells remain. These, by repeated division, supply the new mesodermal bands, which HATSCHEK designates as secondary in contrast to those primary ones which were early put to use. Later they reach the great development which has already been described.

According to HATSCHEK, the remaining segmental organs originate from the head kidney, for a small ciliated canal (in *Polygordius*), running in the somatic layer of the mesoderm, branches off from each head kidney at the junction of its two arms. The nephridia are said to be given off from this canal, one to each segment (Fig. 136). While the head kidney degenerates, they reach their final development.

HATSCHEK's description has met with little recognition, for it could not be substantiated by subsequent investigators (FRAIPONT). However, the discoveries recently made by E. MEYER on certain Terebellidæ (*Lanice, Loimia*) show the observations of HATSCHEK in a new light. In the two Annelids mentioned the nephridia are united by means of a [longitudinal, blindly ending, common] duct, which extends far backward. The discharge takes place through as many [successive lateral] canals as there are nephridia present, but these canals are connected with the nephridia only indirectly, *i.e.* by means of the common duct. In the *Capitellidæ* also, according to EISIG, connections between the different nephridia exist in the form of ciliated canals. We do not intend to assert that any great importance is to be ascribed to these conditions, for in the first place their development is not known, and then the nephridial system of the Terebellidæ (and Capitellidæ) is shown to be essentially modified.

A connection between all the segmental organs is found by HATSCHEK in *Criodrilus* also, for they are said to arise from a cord-like thickening of the somatic layer, which extends the whole length of the body dorsal to the ventral longitudinal muscles. These cords are then separated segmentally into loop-like parts, the fundaments of the nephridia. The latter acquire lumina, and open into the body cavity in front of the segment to which they belong through the future funnels, and finally fuse at their posterior ends with the ectodermal wall to form the external openings. The funnels and nephridial ducts arise separately. But
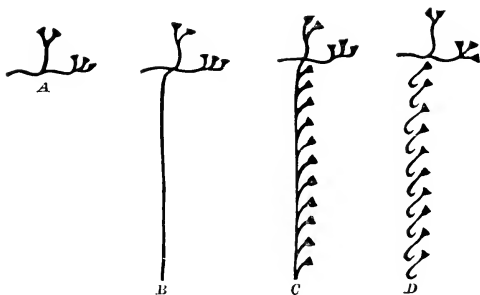
FIG. 136.—Diagram of the development of the excretory system of *Polygordius* (after HATSCHEK, from BALFOUR's *Comparative Embryology*).

these statements of HATSCHEK also find opponents in VEJDOVSKY and BERGH, according to whom the segmental organs of the Oligochæta arise from separate fundaments by the growth of the cells in the somatic layer and in the partition walls of the primitive segments. Fig. 137 *A* shows that at the boundary of the septum and somatic layer there is a considerably enlarged cell (*tz*). It contributes especially to the formation of the funnel. Behind it other cells of the somatic layer arrange themselves into a cord of cells (Fig. 137 *B*), which constitutes the fundament of the nephridial duct. In it, as also in the funnel, a lumen makes its appearance later; the entire structure

becomes covered with peritoneum (Fig. 137 C, pt), and presses its way out towards the ectoderm, in order to fuse with it directly, or with an invagination of it (BERGH, No. 7), which forms the terminal portion of the duct, or collective vesicle, when such is present (VEJDOVSKY, No. 43).

According to the observations of E. MEYER (No. 31), the thoracic nephridia of *Psygmobranchus* are composed of separate parts. The nephridial ducts arise from large mesoderm cells, which are found in the blastocœle of the larva; the funnels, on the contrary, and the peritoneal covering of the nephridia are supplied later by the primitive segments. The ends of the nephridial tubes open to the exterior by means of provisional pores, which later occupy the floor of a ciliated groove, which closes, and represents the unpaired ectodermal efferent duct of these two so peculiarly constituted nephridia of *Psygmobranchus*.

Genital Organs. — The development of the sexual glands is very simple in both the *Polychæta* and *Oligochæta*. They arise as growths of the peritoneal epithelium on the septa, or, as frequently in the *Polychæta*, on the investment of the blood-vessels. The genital gland, which in *Lumbricus* is distinguishable even during cocoon life (BERGH), separates from the peritoneum as the result of a rapid proliferation of the cells, and gradually assumes its permanent form (Fig. 138 A to D, after E. MEYER). The genital products are
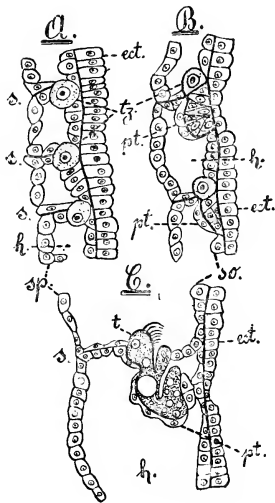
FIG. 137.—A to C, parts of longitudinal sections through embryos of *Criodrilus*, showing the development of the nephridia (after BERGH). *ect*, ectoderm; h, cavity of primitive segment; pt, peritoneum (of the nephridia); s, septa; so, somatic, sp, splanchnic layer of the mesoderm; t, funnel; tz, funnel cell.

liberated one by one (Fig. 138 D), and either undergo their
further development while floating free in the body cavity,
or, as in the case of the testicular cells of the earthworms,
reach special vesicles (vesiculæ seminales), which, according
to BERGH (No. 5), arise on the septa by means of a process
of growth and invagination.

The ducts of the sexual organs are to be looked upon as
more or less modified segmental organs. They arise in the
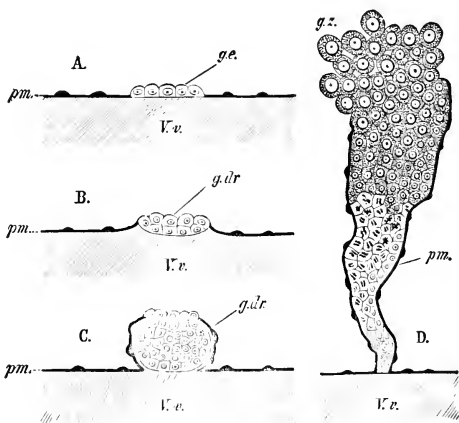
FIG. 138.—A to D, diagrammatic representation of the structure and development
of an ovary of *Amphitrite rubra* (after E. MEYER). *g.dr*, sexual gland; *g.e*, genital
epithelium; *g.z*, genital cells in the act of breaking away; *pm*, peritoneum; *V.v*,
vas ventrale.

same way as the nephridia themselves, except that the
funnel is formed earlier than in the actual segmental organs
(VEJDOVSKY). The entirely independent origin of the efferent
sexual ducts from the nephridia and the simultaneous occur-
rence of both organs in the same segment, as happens in the
earthworms, form no argument against the origin of the
ducts from nephridia, since in some Annelida (*Capitellidæ*,
according to EISIG) several pairs of nephridia occur in the
same segment. In the earthworms especially, many things

seem to suggest that two pairs of nephridia originally belonged to each segment (BENHAM). The metamorphosed segmental organs function in the following manner: the funnel takes up the genital products out of the body cavity, the nephridial ducts pass them onward, and the part distended into a terminal vesicle serves as a genital atrium. But the terminal portion in the male apparatus of the Oligochæta may be metamorphosed into an evertible copulatory organ (thus in *Stylodrilus*, No. 43).

The receptacula seminis have also been traced to nephridia, of which only the ectodermal vesicular end portion is assumed to develop; but BERGH prefers to consider them metamorphosed dermal glands. They arise as tubular invaginations of the epidermis into the interior of the body cavity, and are surrounded by the other layers of the body-wall (VEJDOVSKY, No. 43; BERGH, No. 5).

ENTODERMAL STRUCTURES.

Intestinal Canal.—In the Polychæta and Oligochæta we saw that the intestine arises from portions of all three germ-layers. The permanent mouth is generally found at the place of the blastopore, a depression of the ectoderm taking place here, so that the fore-gut (just like the hind-gut, which arises later) is an ectodermal structure. In those cases in which the larva arises from an epibolic gastrula, and the blastopore does not become the mouth, as in Rhynchelmis and Psygmobranchus, the fundament of the intestine at first consists of a solid entodermal mass rich in yolk (Fig. 128 *A* and *B*, p. 280). The entodermal wall of the mid-gut, by means of which the yolk-mass that still remains is absorbed, arises by the disintegration of the more central cells, while smaller cells at the periphery with less food-yolk are separated from the rest of the mass and form an epithelium. In this condition the intestine consists of a sac closed on all sides. The fore- and hind-guts are formed by its union with the ectoderm in front and behind.

The share which the two ectodermal invaginations take in the formation of the fore- and hind-guts is said to be very variable in the different

Annelida (SALENSKY). Thus the œsophagus may be formed of ectoderm (*Pileolaria*, *Lumbricus*), but it is maintained that it may also be for the greater part of entodermal origin (*Psyqmobranchus*, *Rhynchelmis*). The conditions in *Lopadorhynchus* are peculiar; here the wide ciliated stomodæum (the larval fore-gut) is not directly converted into the œsophagus, but constitutes a transitory structure. On the wall of the stomodæum two cushion-like thickenings make their appearance, which become hollow, and form two small sacs (Figs. 139 and 135 *œs*). These become considerably enlarged, surround the stomodæum, and finally grow together, after the stomodæum has closed and separated from the ectoderm. The detached stomodæum is now seen as a ciliated sac, surrounded by the likewise saccular œsophagus. This finally unites permanently with the ectoderm and entoderm (KLEINENBERG).
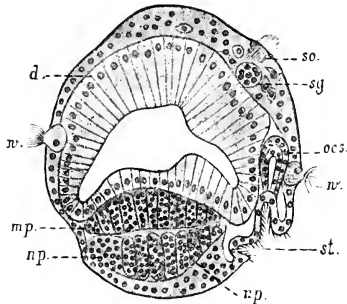
Fig. 139(135).—Sagittal section of a larva of *Lopadorhynchus* (after KLEINENBERG). *d*, intestine; *mp*, muscle-plate; *np*, neural plate; *œs*, fundament of the supra-œsophageal ganglion; *so*, apical organ; *st*, stomodæum (fore-gut of the larva); *w*, preoral ciliated band.

The musculature and peritoneal covering of the intestine are supplied by the splanchnic layer of the mesoderm. The chlorogogenous cells which surround the intestine are considered as excretory organs, and have the same origin and significance as the so-called pericardial glands occurring on the blood-vascular system, and are also outgrowths of the same layer (GROBBEN). In the Lumbricidæ the *typhlosole* arises in the dorsal median line of the intestine as a more or less deep groove-like infolding of its entire wall.

4. Non-sexual Reproduction; Alternation of Generations.

The Chætopoda possess to a high degree the power of restoring parts of the body that have been lost; not only the less important parts of the body, but also the more important ones, such as the head region, including mouth and brain, can be formed anew by them. This power of regeneration passes into a kind of non-sexual reproduction (*schizogeny*), when the body, as in *Lumbriculus*, separates spontaneously into several pieces, each of which is able to regenerate itself into a perfect worm. Approaching closely to this is the reproduction of one of the marine Annelida, closely allied to the Oligochæta, which is found actively multiplying throughout the year, without at any time developing genital organs (*Ctenodrilus monostylos*, according to Count ZEPPELIN). This worm reproduces in the most primitive way: a constriction is formed on the body immediately behind a septum, and becomes deeper and deeper until the worm falls into two parts (Fig. 140 *A*). Of the two resulting parts the anterior is thus without an anus, the posterior without a head. This primitive kind of division may go so far that parts arise which are destitute of both head and anus, and at times consist of only a single segment (Fig. 140 *B*). Head and terminal parts are formed by the thickening of the integument (hypodermis), which sends inward plug-like ingrowths that unite with the intestine. In this way the mouth and anus arise. The new segments that are to be formed are interpolated between the newly formed anus and the preceding segment.

FIG. 140.—*A, Ctenodrilus monostylos* dividing transversely (after Count ZEPPELIN). *B*, a portion of the same worm consisting of only a single segment; *c*, cirrus; *d*, intestine. *C, Ctenodrilus pardalis* (after v. KENNEL); *kn*, budding zone, where the worm later separates into the different parts; *d*, intestine.

Less primitive is the condition in another worm belonging to the same genus, *Ctenodrilus pardalis*, which likewise was found only in a state of non-sexual reproduction (v. KENNEL). In this case thickened zones, corresponding to the anterior and posterior ends of the worms about to be produced (Fig. 140 *C*), are formed—even here in a simple way, it is true—before the division; that is to say, a so-called budding zone is

found at this point, where the division is about to take place. In *Ctenodrilus pardalis* each portion includes only one segment, and thus the budding zones are seen to be repeated segmentally. While they still remain united to one another, the cephalic lobe [prostomium] and the brain, as well as the oral and anal invaginations, are developed on the several portions. The degree of development in which the zones are found increases from behind forwards (Fig. 140 C).

Some Polychæta and those Oligochæta in which non-sexual reproduction is known are like Ctenodrilus in so far as they also divide in a condition in which no genital organs are present. In the *Protula* described by HUXLEY a budding zone arises between the sixteenth and seventeenth segments; then follows the formation of the prostomium of a new individual in the seventeenth segment. In this case, however, after the separation both individuals become sexually mature. The conditions are similar in the *Naididæ*, in which they were thoroughly studied by SEMPER. These worms also reproduce by division in the sexually immature condition only. The body of the worm may be first separated by a budding zone into two regions; then new budding zones are interpolated; that is to say, fundaments of younger animals arise in the individuals already established. This process is kept up, not, however, serially from in front backwards, but in such a way that individuals of quite different ages come to lie one behind another. When the chain has reached a certain stage of development, it separates into the different individuals, which now reach their final shape by growing considerably, by increasing the number of their segments, and by maturing their sexual organs.

The cases last considered were, it is true, those of animals without sexual organs, which multiplied non-sexually; finally, however, all individuals acquire sexual maturity, and are not distinguishable from one another in shape. The conditions are different in those Polychæta in which new individuals, which become sexually mature, are continually being separated off from the hinder part of the body of an individual that remains [sexually] sterile, a process that is to be placed alongside that of strobilization in the Scyphomedusæ. Thus in *Autolytus* (according to KROHN and AGASSIZ) there are formed, by the budding of the parent, male and female animals, which lie in a chain one behind the other; of these the most anterior, the one lying nearest to the parent animal, is the youngest. They separate from the chain according to their ages. The sexually mature animals are essentially different in shape from the budding forms, so that the two were formerly assigned to different species. The sexual animals appear to copulate; for in a brood-pouch of the female the eggs develop into the worm which subsequently reproduces by budding. This is therefore a genuine *alternation of generations.*

Similar conditions of reproduction are found in some *Syllidæ*, from the budding individuals of which are detached sexual animals, which, by the great development of their parapodia and setæ and by their well-

developed orienting apparatus, are especially well adapted to a free life. They swarm about and secure the necessary distribution of the sexual products, whereas the less active budding form remains at the bottom of the sea. The extensive development of the parapodia is completed even while the buds are still connected with the parent. This recalls the condition of certain *Nereidæ*, in which new setæ, better adapted to swimming, make their appearance on the posterior part of the body at
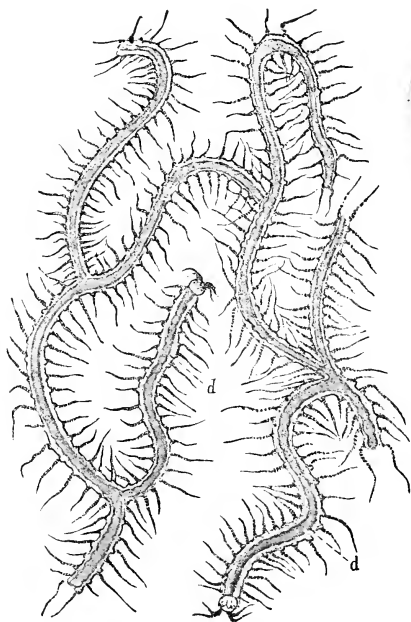
Fig. 141.—Part of a stock of *Syllis ramosa* (somewhat diagrammatic, after McIntosh, and from a preparation of the *Challenger* material). *d*, intestine, which branches throughout the entire stock. The stock is injured in some places.

the time of sexual maturity (*epitokal form*); these give to the sexually mature animals an entirely different appearance from that of the young form (so-called *atokal form*), so that here also the sexually mature and the young forms were assigned to different species and genera. In the

Nereidæ, however, the hinder part of the body, thus equipped, does not become detached, but its better equipment serves only to facilitate the locomotion of the sexually mature animal (EHLERS). But in any event the conditions existing in the *Nereidæ* and *Syllidæ* are comparable with each other.

Under the influence of special conditions of life the reproduction of the *Syllidæ* may assume a very peculiar form. In the sponge, *Aulochone*, and other Hexactinellidæ a *Syllis* has been found (MCINTOSH), on which new individuals arise, not only one after another, but also by lateral budding (*Syllis ramosa*, Fig. 141). A genuine stock is formed in this instance, the branches of which extend without limit in the canal system of the sponge, for the branches in turn have the power of producing new buds. These detach themselves from the stock as male and female sexual animals (Fig. 142); and since they are provided with better swimming apparatus, and with especially well developed eyes, one can readily assume that they abandon the sponge, and, swarming about free in the sea, secure a wider distribution of the sexual products. Their descendants, which they produce by sexual means, then migrate back, it is to be assumed, into sponges. In this interesting case the *alternation of generations combined with stock-formation* is particularly evident.

FIG. 142.—Anterior part of a female individual, such as is found in the sponge stocks inhabited by *Syllis ramosa*. The animal is filled with eggs. The large eyes can be recognized on the head (after MCINTOSH).

II. ECHIURIDÆ.

Echinrus; Thalassema; Bonellia.

While *Bonellia viridis* lays its eggs in the form of a thick, tortuous cord, consisting of a gelatinous mass, in which the eggs lie in several rows (SPENGEL), the *Thalassema mellita* observed by CONN discharges its eggs and spermatozoa free in the sea, so that with this animal artificial fertilization could be undertaken.

1. Cleavage and Formation of the Germ-layers.

The cleavage of the egg was closely studied by SPENGEL in *Bonellia*. An animal portion of the egg, consisting of finely

granular protoplasm, can be distinguished from a yolk-laden vegetative pole. The cleavage corresponds with this condition. At first the egg is divided into four large spheres by cleavage along two meridional planes, but then four small blastomeres are constricted off from these at the animal pole. By division of the latter and the formation of new micromeres from the macromeres, the number of the small cleavage spheres rapidly increases ; they spread out over the four large spheres, and finally envelop them completely, producing an epibolic gastrula (Fig. 143 *A*). The small cells that are now being constricted off from the macromeres no longer reach the surface, but remain lying under the layer of micromeres. They form the entoderm. Inside of these the four macromeres are still retained for a while. In the region of the
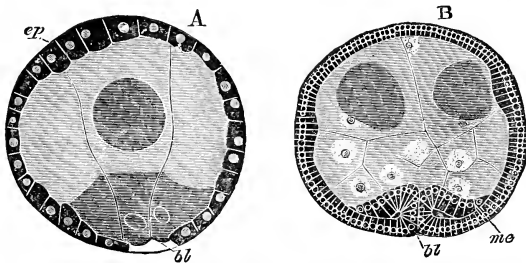
FIG. 143.—*A* and *B*, embryos of *Bonellia* (after SPENGEL, from BALFOUR'S *Comparative Embryology*). *A*, epibolic gastrula ; *B*, formation of the mesoderm ; *bl*, blastopore ; *ep*, ectoderm ; *me*, mesoderm.

blastopore there appears a layer of cells (Fig. 143 *B*), which surrounds the blastopore in the form of a circle. SPENGEL believes this to have arisen by a migration inward of the micromere layer. He interprets it as the fundament of the mesoderm (Fig. 143 *B*, *me*).

Cleavage and the formation of the germ-layers in *Thalassema* (KOWALEVSKY, CONN) do not take place in the same manner as in *Bonellia*. In *Thalassema* cleavage is equal, and its result is a blastula from which an invagination gastrula arises. To be sure, the latter is not altogether typically expressed in *Thalassema mellita*, for the invagination merges

into an ingrowth of cells (Fig. 144 *A*). As in the later stages
of the epibolic gastrula of *Bonellia*, here also the entoderm
consists of a solid mass with an outer differentiated cell-layer
and an inner yolk-mass (Fig. 144 *A*).

2. Larval Form and Metamorphosis of Echiurus and Thalassema.

The Echiuridæ possess free-swimming larvæ, which exhibit
more or less clearly the form of the *Trochophore*. The
development of the gastrula into the Trochophore takes place
in *Thalassema* by the appearance of a thickening of the ecto-
derm at the upper pole, the fundament of the apical plate.
This place becomes covered with a tuft of cilia in the same
way as in the larvæ of the Polychæta. At an early stage
cilia make their appearance on the outer surface of the
embryo, and these are said to traverse, as in *Eupomatus*, the
egg-membrane, so that the latter would become the cuticula
of the larva (CONN). Even during the gastrula stage a circle
of long cilia makes its appearance at the equatorial circum-
ference of the larva (Fig. 144 *A*). Below it lies the blasto-
pore. The cavity of the intestine arises as the result of the
absorption of the central yolk-mass by the rapidly multiply-
ing entoderm cells. It becomes connected with the outside
world by means of the mouth, which is formed at the place of
the blastopore. By the outgrowth of the hinder part of the
larva the mouth comes to lie more on one side (on the future
ventral surface) immediately under the band of cilia. The
latter is then differentiated into a row of cilia lying in front
of the mouth and one lying behind it (Fig. 144 *B*). In addi-
tion a ciliation makes its appearance in the middle line of the
ventral surface. The intestine grows so much in length that
it lies in loops. This is particularly true of the anterior part.
The terminal portion fuses at the hind end of the larva with
the ectoderm, thereby giving rise to the anus (Fig. 144 *B*).
Fore- and hind-guts, according to CONN, are entodermal
formations (?). Mesenchymatous muscle-cells extend be-
tween the ectoderm and entoderm of the larva, and at the
hind end lie two band-like cell complexes, the mesodermal

bands (Fig. 144 *B*, *mes*). Consequently the larva of *Thalas-sema* possesses the greatest similarity to the *Trochophore* of the other Annelida. The same applies to the larva of *Echiurus* (Figs. 145 and 146), the structure and meta-morphosis of which were thoroughly studied by HATSCHEK, who established the presence of a head kidney. This paired organ consists at first of a simple canal, which opens to the exterior on the ventral side at the anterior end of the mesodermal bands. Later there is added to this primary head kidney a secondary branch, which is much ramified (Fig. 145). Altogether the larva undergoes a number of changes, until it arrives at the height of its develop-ment, and the larval organs begin to degenerate. This is true of some other meso-dermal structures as well as of the head kidney. In addition to the muscles characteristic of Annelid larvæ, which extend through the blastocœle, there appears in *Echiurus* under the ectoderm a fine membrane, which arose by the union of branched mesodermal cells and is characteristic for this larva. The mesodermal bands are developed in the

FIG. 144.—*A* and *B*, gastrula stage and Trochophore larva of *Thalassema mellita* (after CONN). *a*, anus; *d*, intestine; *m*, mouth; *mes*, mesodermal bands; *œs*, œsophagus; *sp*, apical plate.

manner typical for the Annelida. The pole cells lie at their posterior ends, whereas the differentiation begins at the anterior end. It is here that they are first many-layered, and that they separate into the primitive segments. The

latter acquire cavities and enlarge in the well-known manner. Just as in the other Annelida, so in the *Echiuridæ* (Fig. 145), there is established an internal segmentation, corresponding to which there is an outer one, in so far as a large number of segmental ciliated bands make their appearance on the posterior part of the Echiurus larva. But this segmentation is only temporary, for, like the bands of cilia, the septa between the cavities of the segments also degenerate. Of the fifteen primitive segments which were begun, only the somatic and splanchnic layers remain, and, as the result of the disappearance of the septa, the secondary body cavity of

the trunk unites with the primitive head cavity. Like the cavity of the trunk, the head cavity is also traversed by branched cells (Fig. 146), and since these are in part applied to the ectoderm, the dermo-muscular sac, which was established in the trunk at an earlier period, is also developed in the head region.

The nervous system is also established in the larva. On either side of the ventral ciliated groove arise thickenings of the ectoderm, from which small nodular processes grow inward, and unite segmentally into large masses of cells, the ventral

Fig. 145.—*Trochophore* larva of *Echiurus* (after HATSCHEK). *a*, anus; *ab*, anal vesicle; *d*, intestine; *kn*, head kidney; *m*, mouth; *mes*, mesodermal bands; *n*, ventral chain of ganglia; *sc*, œsophageal connective; *sp*, apical plate. The ciliated bands of the posterior part of the body are indicated by the cilia at the margins only.

ganglia (Figs. 145 and 146). In this way the lateral cords arise, to which a middle cord is added. The latter separates from the ectoderm of the ciliated groove. At first the entire ventral cord is still intimately united with the ectoderm, but the latter gradually detaches itself, and the ventral cord thereby acquires a deeper position. The fundament of the supra-œsophageal ganglion, which is small in the

fully formed animal, we have already identified as the apical plate. From it two cords extend backwards, embrace the mouth-opening, and unite with the ventral cord. In this way are formed the œsophageal connectives, which are unusually large in the *Echiuridæ* (Figs. 145 and 146 *sc*).

The anal vesicles, which open to the exterior along with the intestine (Figs. 145 and 146), do not arise, as was supposed, from the intestine, but are formed in the somatic layer of the mesoderm. They lie here in the terminal segment of the body as two compact cylindrical structures, which later become hollow and unite with the ectoderm on either side of the anus. At the same time they grow inward. Their middle part is distended, and the inner end opens free into the body cavity by means of a ciliated funnel (Fig. 146 *ab*). Their entire mode of origin proclaims the anal vesicles to be nephridia, which only secondarily entered into connection with the hindgut.

FIG. 146.—Larva of *Echiurus* (after HATSCHEK). *a*, anus; *ab*, anal vesicle; *b*, circle of setæ at the hind end of the body; *d*, intestine; *m*, mouth; *n*, ventral chain of ganglia; *sc*, œsophageal connective; *sp*, apical plate; *vb*, ventral or uncinate setæ.

The intestine is no longer so wide in comparison with the entire body, as is to be seen in Fig. 146; on the contrary, it has grown more in length and makes several turns, which subsequently are still more emphasized. In the meantime the larva has also altered externally, in that its transverse diameter has decreased in proportion to its longitudinal diameter (Figs. 145 and 146). On the surface the rows of dermal papillæ become noticeable, and, just as in the Chætopoda, the uncinate setæ which are formed in the setigerous sacs (immediately under the ectoderm) break through to the outside (Fig. 146). The further development consists first of all in an active growth of the hinder portion

of the body, which thus approaches the form of the adult worm, as can be seen from the larval stage of *Thalassema* shown in Fig. 147. Even in this stage the ciliated bands are still present. With the gradual reduction of these, which soon takes place, the larva approaches more and more the shape of the adult animal. The oral and preoral parts of the larva are transformed into the prostomium, whereas the hind part still grows in length.

3. Larval Form and Metamorphosis of Bonellia.

The larva of *Bonellia* resembles the *Trochophore* less than do the larvæ of *Echiurus* and *Thalassema*, although it also can be referred to the *Trochophore*. Evidently it is much modified, as is proved by its internal organization, which is less adapted to a free life. We follow SPENGEL in describing the development of *Bonellia*.
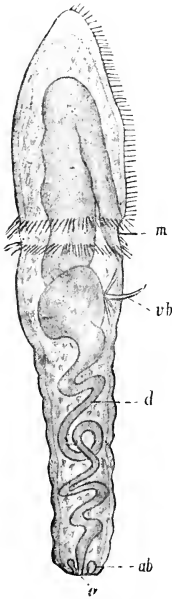
FIG. 117.—Late larval stage of *Thalassema mellita* (after CONN). *a,* anus; *ab,* anal vesicle; *d,* intestine; *m,* mouth; *vb,* ventral or uncinate setæ.

The larva of *Bonellia*, which is at first spherical, possesses, in addition to the anterior band of cilia, a posterior one (Fig. 148 *A*). The anterior to all appearances corresponds to the anterior ciliated band of the larva of *Thalassema* and *Echiurus*, especially since in the latter a band of cilia is also found in the region of the anus. Anteriorly two eye-spots make their appearance (Fig. 148 *A* and *B*). The intestine is not yet differentiated as such, but is developed later. The larva increases in length, becomes flattened dorso-ventrally and covered with cilia (Fig. 148 *B*). It now has more the appearance of a Turbellarian, and, as its shape indicates, it moves by creeping.

The further development of the larva affects first its internal organization. The supra-œsophageal ganglion has become differentiated from the ectoderm, and later the œsophageal connectives and the ventral nerve cord begin to develop. The entoderm has become a single layer

of cells, which surrounds the central yolk-mass like a sac. On the front end of this fundament of the intestine a conical appendage becomes noticeable, the first indication of the œsophagus, which subsequently breaks through to the exterior in the region of the anterior ciliated band (probably behind it). Lying between ectoderm and entoderm is the mesoderm, which has split into a somatic and a splanchnic layer in most parts of the body, whereas in the head region it has the form of a compact mass of vesicular cells. Besides the mesodermal elements which are transformed into musculature and peritoneum, there exist still others, which lie in the body cavity. These are transformed into structures like blood cells, which float in the body fluid. It is only at this time that the formation of the spacious body cavity is accomplished. The vessels arise from the peritoneal lining of the body cavity.
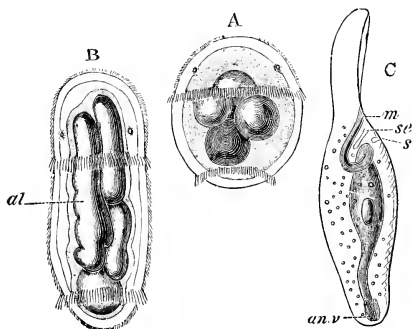
Fig. 148.—Stages of development of *Bonellia* (after Spengel, from Balfour's *Comparative Embryology*). *A* and *B*, larvæ with anterior and posterior bands of cilia. *C*, young Bonellia. *al*, intestinal canal; *an.v*, anal vesicle; *m*, mouth; *s*, fundament of the ventral hook; *se*, excretory organs.

At the same time with the internal processes of development described, an external change of form takes place. The ciliation of the body disappears for the most part; the anterior portion of the body grows considerably in length, and its ventral side, which is still ciliated, becomes depressed, in this way acquiring a spoon-like form (Fig. 148 *C*), and thereby realizing a stage like that in *Echiurus*. Later, projections are formed on the prostomium where the eye-spots are situated. By their further growth is brought about the bifurcation of the prostomium which characterizes the female of *Bonellia*.

Of the internal changes, there is still to be considered the further development of the intestine, whose central yolk-mass becomes absorbed. The mouth-opening breaks through the base of the prostomium, while

the anus is formed at the posterior end of the ventral side. The anal vesicles are said by SPENGEL to arise as evaginations of the hind-gut (Fig. 148 C). We saw that in Echiurus their origin was described differently, and that therefore they are preferably to be considered as nephridia (p. 309).—A pair of tubes which make their appearance behind the mouth are considered by SPENGEL to be the provisional excretory organs (Fig. 148 C). Immediately behind these the ventral setæ are formed (Fig. 148 C).

The earliest fundament of the ovary was also observed by SPENGEL. It is formed, in the same way as in other Annelids, from the peritoneal covering of the blood-vessels, in this case on the posterior part of the ventral vessel. The duct for the sexual products is a tube, which is to be looked upon as a nephridium, although it is not quite evident whether it is connected, and if so by what means, with the provisional excretory organs observed by SPENGEL.

The description of the development of *Bonellia* up to this point applies to the female only. The development of the small male, living in the uterus, is much simpler, since it remains in the state of the ciliated larva. The larvæ which develop into males seek the ciliated groove on the prostomium of the female, and there attach themselves. They lose the two ciliated bands, but retain the uniform coat of cilia. Their internal organization corresponds on the whole to that of the female, only certain simplifications arise ; thus, for example, the mouth and anus are wanting. In the male also the genital products arise from the cells of the peritoneum. Balls of spermatic cells are detached from this and fall into the body cavity, subsequently to be taken up by the funnels of the spermatic duct. After the males have remained for a short time on the prostomium of the female, they migrate into the œsophagus, in order to complete there their metamorphosis. SPENGEL found as many as eighteen males in the œsophagus. Subsequently they abandon the œsophagus and repair to the uterus, where ordinarily six, eight, or more males are found.

General Considerations.—As regards the position of the *Echiuridæ*, we agree with HATSCHEK's view (No. 51) ; he sees in them a division of the Annelida, and brings them into relation with the Chætopoda. The form and internal organization of the larva, as well as the mode of origin of the setæ, seem fully to substantiate this view. Even though a segmentation [metamerism] no longer exists in the adult animal, it was nevertheless established in the larva, just as in the *Chætopoda* and *Archiannelida*. The loss of the segmentation and the reduction of the setæ, as well as the enormous extension of the prostomium, or so-called proboscis, make the *Echiuridæ* appear as somewhat modified forms.

III. DINOPHILUS.

Although the development of *Dinophilus* is not yet known in detail, we include this aberrant form in the course of our present account, because the adult animal itself remains to a certain extent at the stage of an Annelid larva.

In its outward shape (Fig. 149) *Dinophilus* presents a striking resemblance to certain polytrochal Annelid larvæ, *e.g.*, to those of *Ophryotrocha* and a larval *Syllis* not yet described, which we observed in the "tow" at Trieste. This applies not only to the ciliated bands, the distribution of the sensory hairs, and the ventral tail-like appendage, but more especially to the entire habit of the worm. The caudal appendage of *Dinophilus*, like that of the Annelid larva in question (*Ophryotrocha* sp.), is segmented. For this reason, as also on account of its ventral position, it recalls the foot of the Rotatoria, a comparison which indeed does not appear altogether without foundation when one considers the similarity in the organization of Trochophore larva to that of the Rotatoria, which has already been emphasized (p. 259). Should the statement prove to be correct that the five pairs of nephridia possessed by *Dinophilus* (Fig. 149) end blindly
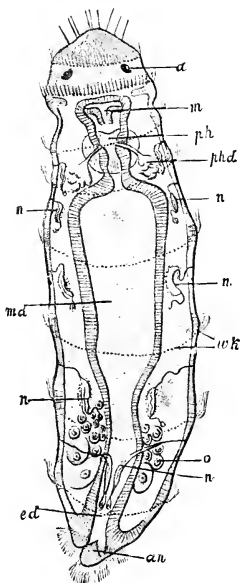
FIG. 149.—Female of *Dinophilus gyrociliatus* (after E. MEYER, from LANG's *Lehrbuch*). *a*, eye; *an*, anus; *ed*, hind-gut; *m*, mouth; *md*, mid-gut; *n*, nephridia; *o*, ovary; *ph*, pharynx; *phd*, pharyngeal glands; *wk*, ciliated band.

in the body cavity (E. MEYER), there would exist in this particular also conditions such as are found in the Annelid

larva and in the Rotatoria. As regards the rest of the organization—for example, the structure of the nervous system—*Dinophilus* has been compared directly to the Archiannelida.

Dinophilus lays its eggs, several united, in transparent gelatinous capsules. In *Dinophilus apatris (gyrociliatus)* there are found in the capsules, in addition to the large oval eggs, spherical ones, which are several times smaller; the number of the former compared to the latter is about as two to one. From the larger eggs arise the females, from the smaller the males, when, as in *D. apatris (gyrociliatus)*, there is a great difference in the size and form of the two sexes (KORSCHELT).

Cleavage is unequal in both kinds of eggs, and, according to KORSCHELT's statements, which are corroborated by HARMER, leads to the formation of an epibolic gastrula. REPIACHOFF, on the contrary, describes the occurrence of an invagination gastrula for the large eggs of *D. gyrociliatus*, which arose from a blastula thickened on one side. The blastopore appears to become the mouth. Two large cells are differentiated near it, which, according to REPIACHOFF's observations, move into the blastocœle, and there, as in other Annelida, produce the two mesodermal bands. The supra-œsophageal ganglion is to be seen lying close to the ectoderm.

However, the accounts last mentioned do not seem to be well established; but what is known of the development of *Dinophilus* harmonizes with Annelid development, and the entire organization of the worm points to relationships with the Annelida.

From the fact that a most striking sexual dimorphism exists in *Dinophilus*,—in so far as the males are much smaller and more simply organized than the females, lacking the intestine, the eyes, and the segmental bands of cilia (KORSCHELT),—relationships of this genus with the *Rotatoria* have also been contended for; but these conclusions do not appear to be justified when one reflects that, while sexual dimorphism makes its appearance in certain species (*D. apatris*, *i.e.*, *D. gyrociliatus*), in very similar species, such as *D. vorticoides*, *gigas*, and *tœniatus* (according to O. SCHMIDT, WELDON,

and HARMER), the males, apart from the sexual characters proper, are formed just like the females.

IV. MYZOSTOMA.

Myzostoma, the discoid parasite of the Crinoids, provided with hook-bearing parapodia arranged in pairs, deposits its eggs in large masses without bestowing on them any special care. The eggs, which are enclosed in a structureless membrane, are fertilized outside the parent, after the formation of the two polar cells. The fertilized eggs sink to the bottom. Their development was studied by METSCHNIKOFF in *Myzostoma cirriferum*, and afterwards somewhat more fully by BEARD in *Myzostomum glabrum*. The unequal cleavage leads to the formation of an epibolic gastrula, of whose six inner cells the two lying nearest to the blastopore are said to give evidence by their darker appearance of being mesodermal cells. Tufts of cilia soon afterwards make their appearance on the ectoderm cells all around the ovate embryo, which now breaks through the egg-shell. Its shape soon becomes pyriform. An ectodermal invagination, the fundament of the mouth and fore-gut, makes its appearance in the region of the blastopore. It grows inward and unites with the stomach, which in the meantime has been formed out of the entoderm cells, which have increased greatly in number. The anus arises at the posterior pointed end of the larva. It is not easy to determine whether it also is formed by an ectodermal invagination or merely by a fusion of ectoderm and entoderm. In front of the anus there appears a papilla [on the ventral side], which subsequently becomes quite large and constitutes the end of the body, the anal opening thus becoming displaced dorsad (Fig. 150). The subsequent stages are characterized by the fact that the cilia distributed over the entire body become restricted to certain regions. These are, first the anterior end of the preoral part of the body, which constitutes the apical area and bears a tuft of rigid cilia (Fig. 150), then a band of cilia lying immediately behind the mouth and a second one in the region of the anus, and finally a bundle of rigid cilia at the tip of the caudal appendage (Fig. 150). At the same time with the changes in

the ciliation, there appear on both sides of the head, behind the post oral band of cilia, the fundaments of setæ, which soon elongate considerably, and finally reach approximately the length of the entire larva.

It is not to be denied that this *Myzostoma* larva possesses a very great resemblance to the larvæ of Annelids, even though the absence of the preoral band of cilia, which could not be found by BEARD, interferes with a complete resemblance to the *Trochophore*. The thickened apical area, the two bands of cilia, the sensory hairs at the anterior and posterior ends, as well as the internal organization of the larva are quite Annelid-like. A caudal appendage, covered in the same way with tactile hairs and constituting a prolongation of the ventral surface, is found in the larvæ of *Telepsavus* and *Ophryotrocha*. In the same way the provisional setæ of the Myzostoma larva, which probably arise in ectodermal sacs, point to the corresponding structures of certain Annelid larvæ (comp., for example, the drawing of *Mitraria*, Fig. 124, p. 276). In any event the similar characters in the larvæ of *Myzostoma* and other *Annelids* are very many, and the further development also presents other common features, *e.g.*, the formation of the parapodia and their bristle- or hook-bearing, stumplike processes.

FIG. 150 —Larva of *Myzostoma glabrum* (after BEARD). *a*, anus; *b*, setæ; *m*, mouth; *s*, caudal appendage; *sp*, apical plate.

After the larvæ have moved about free at the bottom of the aquarium for some seven days, they cast off the provisional setæ and betake themselves to an Antedon, on which they are found crawling about like worms, for the larval

ciliation meanwhile has degenerated. The further develop-
ment of the larva is quite simple. The body, which up
to this time was broad in front and narrow behind (Fig.
150), changes its shape to such an extent that it becomes
broader behind than in front. The principal changes in
the shape of the larva are brought about by the develop-
ment of parapodia, which takes place from in front back-
wards, as in the Polychæta. Like the setæ in Polychæta, the
hooks in Myzostoma are said to arise in ectodermal sacs.
A segmental differentiation of the compact mesodermal mass
lying between the integument and the intestine, a differen-
tiation which proceeds from in front backwards, might be
compared with the segmentation of the mesodermal bands in
the Annelida. A large part of these mesoderm cells become
connected with the parapodia as musculature. Others are
applied to the mid- and fore-guts. The latter effect the
formation of the evertible proboscis. Up to this time the
intestinal canal has retained its simple character; but by
the time the development of the parapodia is completed
evaginations are seen in it, and in this way its branched
character takes its origin. As regards the formation of the
nervous system, the apical plate, which is to be looked upon
as a larval central organ, is said by BEARD to degenerate ;
but since this author did not recognize the presence of a
supra-œsophageal ganglion and œsophageal ring, which
nevertheless are present, it is quite possible that the former
arises from the apical plate, and that, as in other Annelids,
a union with the ventral cord, which arises as an ectodermal
thickening, also occurs in the development. The ventral
cord, which exhibits, according to NANSEN and v. WAGNER,
the usual form of a chain of ganglia with transverse com-
missures, has thus a segmental arrangement.

The statements concerning the origin of the mesodermal
structures are less certain. A true body cavity is not present,
but its place is occupied by parenchymatous tissue, which is
traversed by muscle fibres, and yet the authors (NANSEN,
BEARD) speak of an epithelium of the body cavity, from which
the sexual products arise. It appears, then, as if the hollow
spaces which contain the sexual products constitute remnants

of the body cavity.   Segmental organs have not been
identified, though the oviducts were held by BEARD to be
remnants of such, and NANSEN believed the same of the
paired ciliated depressions of the outer surface of the body
formerly called sucking discs ; but up to the present time
sufficient grounds for this view have not been produced.   The
sexual organs in *Myzostoma* are not always developed in the
same way.   In addition to the hermaphroditic individuals,
there are living on them very much smaller male animals
(*complemental males*).   The fact that oviducts were also
found in these (NANSEN) indicates that we have to do, not
with individuals of really separate sexes (BEARD), but only
with incompletely developed hermaphrodites.

The place which we assign to the genus *Myzostoma* appears
to be justified by the manner of its development.   This
characterizes it as a branch of the Annelid stem, which, to
be sure, is rather aberrant, and has suffered great changes,
probably as the result of the parasitic mode of life.   The
place previously ascribed to it, supplementary to the class of
Arthropods, was necessarily given up when the development
became better known.   The form and internal organization
of the larva, as well as its ciliation, which is also a feature
of the adult animal, separate it sharply from the Arthro-
poda.

V. HIRUDINEA.

The Hirudinea, like the *Oligochæta*, lay their eggs in
cocoons, which are formed in the same way in the two
cases, namely, by a secretion from dermal glands, which
hardens.   The cocoons themselves are of various sizes,
according to the size of the animal.   In the medicinal leech
they become more than 2 cm. in length.   Their shape also
varies in different species and genera.   Those of *Hirudo* and
Aulastoma are ellipsoidal, and exhibit outside the shell
proper a layer of spongy substance, which probably serves to
protect them against desiccation (LEUCKART).   They are
deposited in the earth.   The flattened cocoons of *Clepsine*
and *Nephelis* are found in water, firmly glued to some fixed
object.   *Clepsine* covers the cocoon with its body, and

further cares for the brood by carrying about with it, attached to its ventral side, the young after they have hatched from the cocoon. The cocoon ordinarily contains a large number of eggs, as many as twenty in the medicinal leech. The Gnathobdellidæ and Rhynchobdellidæ are distinguishable by the fact that the cocoon of the former is filled with albumen, in which the eggs are found embedded, whereas in the Rhynchobdellidæ the cocoons lack the albumen, and the much larger eggs lie in rows and in layers alongside and above one another in great numbers, in *Clepsine*, for example, as many as 200. Correspondingly the eggs of the Gnathobdellidæ are small, and contain little yolk ; the embryos leave the eggs at an early stage of development, and, like the Oligochæta, float as larval forms in the albumen of the cocoon, by means of which they are nourished. Only after several weeks do they quit the cocoon. The Rhynchobdellidæ, on the contrary, whose large, richly yolk-laden eggs furnish to the embryos sufficient nourishment, do not break through the egg-membrane until a much more advanced stage of development and soon after also abandon the cocoon.

1. Cleavage, Formation of the Germ-layers, and Development of the Outward Form of the Body.

A. RHYNCHOBDELLIDÆ.

The *process of cleavage* can best be followed in the *Rhynchobdellidæ*, on account of the larger size of the eggs, and has been repeatedly studied in *Clepsine*. According to WHITMAN, three small blastomeres and a single larger one are first produced by the formation of two vertical cleavage planes, whose position indicates the subsequent orientation of the body of the worm. The three smaller ones mark the anterior end, the larger one the posterior end, of the worm. Then four small blastomeres bud out at the animal pole from the four large ones, whereby the familiar stage of four macromeres and four micromeres is reached (Fig. 151 A). The further metamorphosis consists in the separation of the posterior large blastomere into two of nearly the

same size (Fig. 151 *B*), one of which WHITMAN designates as neuronephroblast, and the other as mesoblast, in accordance with their subsequent fate. The mesoblast soon divides into two cells, which at first do not occupy bilaterally symmetrical positions, as would be expected of the primitive cells of the mesoderm. One of them lies more behind, the other more in front beneath the micromeres, the number of which soon increases, first at the expense apparently of the
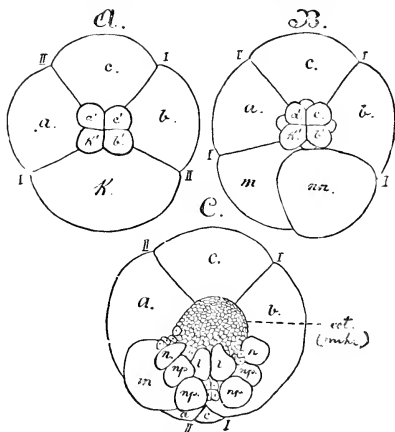
Fig. 151.—*A* to *C*, cleavage stages of *Clepsine*, diagrammatic (after WHITMAN). *I.* and *II.* indicate the direction of the first and second planes of division; *a*, *b*, *c*, the macromeres which become entoblasts; *k*, the macromere which supplies the germ bands; *a'*, *b'*, *c'*, *k'*, micromeres which arise from the macromeres *a*, *b*, *c*, and *k*; *m*, mesoblast; *nn*, neuronephroblast; *n*, neuroblast; *np*, nephroblasts; *l*, pole cells of the lateral cell-row of the germ bands, *ect* (*mkr*.), which are descendants of the micromeres.

macromeres (Fig. 151 *B*). With the exception of this production of micromeres at the animal pole, the anterior three macromeres take no further part in the subsequent cleavage. They contain the nutritive yolk of the egg, and later supply the cell material for the formation of the mid-gut; they are therefore to be designated as entoblasts. At the time when the neuronephroblast divides into eight cells symmetrically

placed at the posterior pole (Fig. 151 *C*), additional nuclei make their appearance in the entoblasts without any corresponding division of the entoblasts. In addition, however, certain cells that are from the beginning distinct are constricted off from the entoblasts; they lie under the layer of micromeres, and are to be looked upon as the earliest entoderm cells. Later, cells that have been differentiated within the entoblasts are added to them, so that a distinction between the two kinds can no longer be made.

The embryo, up to the stage to which we have followed it, consists of a solid mass of cells formed of the three macromeres (entoblasts), which become partly covered over by the disc of micromeres, which have now become very numerous (Fig. 151 *C*). Under the latter, consequently between them and the entoblasts, there already lie a number of entoderm cells, while the nuclei that appear within the entoblasts provide for the formation of further cell material to be added to the entoderm. At the posterior pole appear the two symmetrical groups of neuronephroblasts, each composed of four large cells (Fig. 151 *C*), and below them, sunk somewhat deeper, lie the two mesoblasts; these, too, are now almost symmetrically arranged, although that relation cannot be recognized in a surface view, such as Fig. 151 *C*.

The two groups of five cells each at the posterior end are of great importance from the fact that the greater part of the body of the leech arises from them. Since in their origin they can be traced back to the hindermost of the four original macromeres, it follows that this is the one which is responsible for the development of by far the largest part of the body. These two groups of cells undergo the following change : from the anterior face of each of the ten cells new cells are constricted off by repeated cell division, a process which can be compared with the multiplication of the pole cells of the mesoderm in the Chætopoda, and also leads to the same result. On each side, then, there arise four adjacent rows of cells, those of the neuronephroblasts, and one lying somewhat deeper, that of the mesoblasts. All of them together constitute the two germ bands, which, how-

ever, as will be shown later, are not directly comparable to
the mesodermal bands of the Chætopoda.

As a result of the rapid cell-proliferation, the germ bands
grow forward, and the layer of micromeres, which have in
the meanwhile increased considerably in numbers, advancing
at the same time with them, covers a greater extent. Thus
the entoblasts gradually become overgrown by the germ
bands and the descendants of the micromeres. Whereas the
two germ bands at first diverge, their ends subsequently
unite at the anterior part of the embryo (Fig. 152 *A*). They
now elongate to such an extent that they occupy approxi-
mately the greatest periphery of the egg (Fig. 152 *B*). Their
further change in position takes place in such a way that
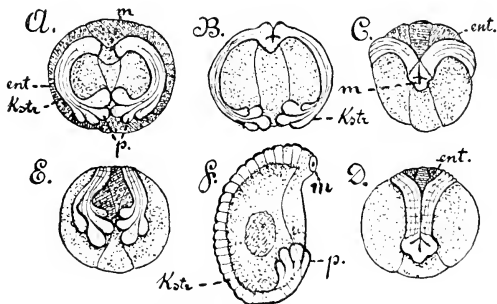
Fig. 152.—Embryos of *Clepsine*, elucidating the development of the germ bands
(after WHITMAN). Between the germ bands (*kstr*) the portion already overgrown
by ectoderm is dotted ; the entoblasts (*ent*) are shaded by parallel lines. *m*, region
of the mouth ; *p*, pole cells of the cell-rows constituting the germ bands.

their anterior and posterior ends appear to be fixed, but they
themselves move down toward the ventral side, and thus
approach each other, so as finally to unite in the ventral
middle line (Fig. 152 *F*). Fig. 152 *C*, which is a view at an
angle of ninety degrees with that of Fig. 152 *B*, shows the
beginning of this process, whereas in Fig. 152 *D* the fusion
of the germ bands, which takes place from in front back-
wards, has progressed still farther. Fig. 152 *E* exhibits the
other hemisphere, and shows that here the germ bands are

not yet completely united.   This has occurred, however, in
Fig. 152 *F*, which shows the embryo in profile.

Since the layer of small cells arising from the micromeres
follows the growth of the germ bands, the embryo becomes
surrounded by a superficial cell-layer, which, according to
WHITMAN, produces the epidermis.   Furthermore, the head
portion of the worm is said to arise from these cells, and
perhaps in the same way as the trunk is formed from the
germ bands, for the trunk alone owes its origin to these
bands (WHITMAN, BERGH).

During the processes described certain changes, which
give rise to the formation of the mid-gut, have also taken
place in the entoderm.   Even at an earlier stage certain
cells had separated from the upper part of the entoblasts.
Others succeed these, for the nuclei move out to the surface
of the entoblasts, surround themselves with plasma, and in
the form of an epithelium—the cells of which at first are
flat, but later become cubical—are added to the cells
already present.   The formation of the mid-gut begins at
the anterior end, and progresses from there backward on the
ventral side with unusual rapidity.   Finally the completely
formed mid-gut surrounds the entoblasts, which have now
sunk to the value of mere food-yolk.   At the anterior end
the pharynx, which has arisen as an ectodermal invagina-
tion, unites with the mesenteron.   A shallow depression
makes its appearance at a very early period in the region of
the ectoderm cells which are first formed (micromeres) ; in
later stages this comes to lie at that point where the two
germ bands meet (Fig. 152 *m*).   This depression indicates
the future pharyngeal invagination.   The latter makes its
appearance as a solid growth of the ectoderm, which lies in
the depression.   Later it becomes hollow and fuses with the
entoderm.   This (entoderm) lines a part of the proboscis.
whereas the remaining part of the proboscis and the pro-
boscis-sheath are formed of ectoderm.   The anus does not
arise until later.

When the embryo has developed thus far—that is, when
the circumcrescence is completed, and its surface is entirely
closed—it abandons the egg and soon afterwards the cocoon

also to undergo its further development while attached to
the ventral surface of the parent. As regards the external
form of the body, a segmentation [metamerism] can be recog-
nized, which is to be referred to that of the germ bands
(Fig. 152 *F*). This segmentation makes its appearance in
the same way as in the Chætopoda, namely, progressing
from in front backwards.[1] Furthermore the shape changes,
in that the body, which was first flat on the dorsal and
strongly curved on the ventral
surface (Figs. 152 *F* and 153),
becomes straight and flat on
the ventral surface, while its
dorsal side assumes the fami-
liar arching owing to the more
active growth of that part.
At this stage the body consists
of thirty-three segments, the
posterior eight of which unite
to form the posterior sucker
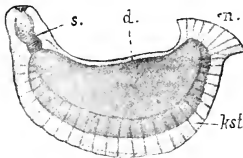
Fig. 153.—Embryo of Clepsine (after
Rathke and Whitman). *d*, intestine;
kst, germ bands; *s*, pharynx; *sn*,
sucker.

(Fig. 153). The anus arises dorsad of this by the fusion of
the entoderm and ectoderm.

It is a question how the formation of the germ-layers is to be ex-
plained. Whitman assigns to the ectoderm the cells that have arisen by

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[1] [Whitman (No. XXII., Appendix to *Literature* on Annelida) has
recently investigated the metamerism of the Hirudinea and its origin.
He endeavors to explain the segmentation of the adult animal by
means of embryological facts, and further supports his opinion by the
anatomical conditions, especially that of the nervous system. The
principal question concerns the interpretation of the head, which is
composed of the primary head segment and several trunk segments
united with it, a condition similar to that which is also assumed for
the Chætopoda. The mouth may be placed as far back as the fourth
segment.

The segmented body is derived from an unsegmented. The origin of
the segmentation is to be sought in the reproduction by division of the
originally unsegmented worm. The individual segments therefore really
correspond to separate individuals. The increase in the number of
segments is caused by the method of life, which necessitates such an
increase. (Comp. in this connection the statements made under "General
Considerations regarding Annelida," p. 348.)—K.]

the division of the neuronephroblast (Fig. 151 *B, C*) ; in that case the circumcrescence of the macromeres by the layer of small cells and the germ bands would seem to produce an epibolic gastrula, an interpretation that was in fact given by BALFOUR. The deep layer of the germ bands arising from the mesoblasts would then be the mesoderm, though its superficial layer also, by becoming overgrown with the small cells, soon comes to lie inside. These processes recall to a certain extent those in *Rhynchelmis*, in which Oligochæte the mesomeres at first lie in the region of the ectoderm and give off to it products of their division. Perhaps more detailed observations on this point will yield greater evidence of agreement. At present the germ bands of the Hirudinea and the meso-dermal bands of the *Oligochæta* are not to be looked upon as homologous structures, for they are composed of different kinds of elements. How-ever, KLEINENBERG argues for a participation of the ectoderm in the formation of the mesodermal bands, and WILSON likewise finds these same bands of cells, which form the germ bands of the Hirudinea, even in the Oligochæta (comp. *supra*, p. 294).

If such stages of the embryos of *Clepsine* and *Lumbricus* as are shown in Fig. 153 (p. 324) and Fig. 132 (p. 286) are compared, the conclusion is natural that processes which led to such similar structures must have been at the beginning of like nature, even though they are now changed in their details.

B.   GNATHOBDELLIDÆ.

A detailed investigation of the cleavage of the egg of *Nephelis* has been given by BÜTSCHLI. Nevertheless, owing to the small size of the egg, we are not as accurately informed about the cleavage and formation of the germ-layers in the *Gnathobdellidæ* as about the corresponding processes in the *Rhynchobdellidæ*. At all events, certain differences between the groups seem to exist.

In *Nephelis* there also occurs a cleavage stage of four *macromeres* and four micromeres, though the latter are said not to arise from all four, but from only three, of the macromeres, whereas the fourth, posterior blastomere remains for a time passive. These three macromeres then again give rise to three small cells, which are arranged, as in *Clepsine*, under the micromeres first formed, and constitute the first entoderm cells. The fourth of the four macromeres now divides into two large blastomeres, which WHITMAN interprets as corresponding to the neurone-phroblast and mesoblast in Clepsine. According to this view, to which BERGH also inclines, the superficial layer of the germ bands would be derived from the former, the lower layer, on the contrary, from the latter. The fact that the "neuronephroblast" is said to form two

additional small cells, which are added to the four ectoderm cells already
present, does not agree with the processes in Clepsine. The "neurone-
phroblast" and the "mesoblast" each divide into two cells, which are
placed symmetrically in respect to the middle line. The edges of the
macromeres arch up more or less over the small blastomeres, so that
these at times appear to be embedded in them, a process that also takes
place in like manner in Clepsine. The fate of the different blastomeres
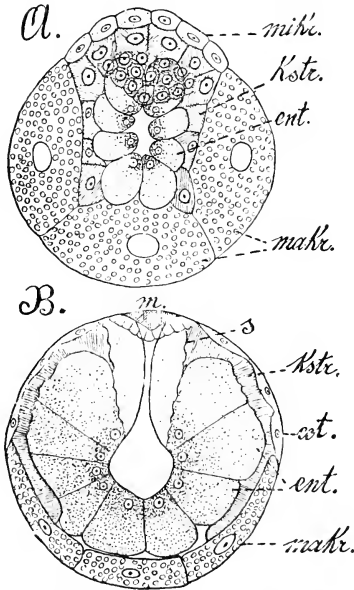
Fig. 154.—*A* and *B*, cleavage stage and an embryo at the time of hatching of
Nephelis vulgaris (after Bütschli). *ect*, ectoderm; *ent*, entoderm; *kstr*, germ
bands; *makr*, macromeres; *mikr*, micromeres; *m*, mouth-opening; *s*, pharynx.

could not be followed farther than this, though it is to be assumed
that the further differentiation is the same as in Clepsine. At all events,
two "germ bands" are also formed here (Fig. 154), which extend from
behind forwards and there (in the region of the future mouth) unite.
The metamorphosis of the entoderm is important, and in determining
the entire shape of the animal, significant. To the entoderm cells first

formed from the three macromeres have been added others, which like-
wise have probably been furnished from the same source. The entoderm
now lies in the form of two rows of cells upon the macromeres (Fig. 154
A), which now represent a kind of food-yolk. They are surrounded and
partly covered in by the germ bands, while the ectoderm, now increasing
more rapidly, covers over the anterior part of the embryo. A central
fissure (the fundament of the cavity of the mesenteron) soon arises be-
tween the entoderm cells, which enlarge at the expense of the yolk-cells
[macromeres] (Fig. 154 *A*). The latter are forced more toward the hind
end of the embryo, and are finally overgrown by the ectoderm, which
also spreads out backwards (Figs. 154 *B*, 156). In this case, there-
fore, the macromeres are not taken into the intestine, as in Clepsine,
but remain outside of it; but in this position they too are gradually
absorbed. The mouth and pharynx finally arise at the anterior end of
the embryo in the form of an ectodermal invagination, which unites with
the intestine (Fig. 154 *B*).

2. The Larvæ of the Gnathobdellidæ.

The embryos of the Gnathobdellidæ break through the
egg-membrane at a stage in which they are spherical or oval
and have attained about the condition represented in Fig.
154 *B*. The pharynx, still very simple in structure, leads
into the intestine, which now begins to enlarge. The ecto-
derm has not yet quite grown over the macromeres. The
" germ bands " lie between it and the entoderm. It is seen
that the development is not so far advanced as that of
the hatching embryo of Clepsine. Whereas the latter is
converted directly into the worm, the embryo of the
Gnathobdellidæ undergoes a protracted larval existence.
Like the larvæ of the *Oligochæta*, those of the Gnathobdel-
lidæ float in the albumen of the cocoon, and take this into
the intestine by means of deglutitory movements. For this
purpose a provisional pharynx (Figs. 154 *B* and 156 *s*) is
developed, which is provided with a powerful musculature.
The larva possesses still other provisional structures which
are entirely wanting in Clepsine. In Nephelis a cephalic
process is developed, which is thickly covered with cilia (Fig.
156). This ciliation recalls that which occurs in the larvæ
of the Oligochæta, especially since, as in *Lumbricus trape-
zoides*, it extends on to the ventral side, where it is found in

the median line of the entire ventral surface (ROBIN). The larvæ of the *Gnathobdellidæ* also possess provisional excretory organs which are comparable to those of the *Oligochæta*, even though in number and form they are different. In *Nephelis* there are two (Fig. 156 un_1 and un_2), in *Hirudo* three, and in *Aulastoma* four pairs of provisional kidneys. In the last form they are found lying on the ventral surface of the larva, on either side of the germ bands from which, according to BERGH, they take their origin as cell-growths, composed at first of one, then of several rows of cells (Fig. 155). Subsequently they separate from the germ bands, and then consist of structures somewhat annular in shape and composed of two rows of cells (Fig. 156 un_1). These two cell-rows subsequently differentiate in such a way that they consist
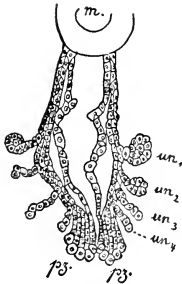
FIG. 155.—Origin of the primitive kidneys (un_1 to un_4) from the germ bands (*Rumpfkeim*) of *Aulastoma gulo* (after BERGH). m, mouth; pz, pole cells terminating the cell-rows of the germ bands.

of two adjacent canals; one of them becomes the stouter, chief canal, and the other one winds several times about it (Fig. 156 un_1). At the turning point the two are continuous with each other, and therefore really constitute only *one* canal. A ciliation has not been observed in the canals. Not only is there in *Nephelis* the ring-like canal, which is wound about itself, but this is prolonged into a duct, which to a certain extent constitutes the efferent duct of the organ, and has been compared to such by BERGH, in the sense that the two primitive kidneys would correspond to the two arms of the primitive kidney of Polygordius, and that the duct would lead to the point of union of the two. As has been stated, there are in *Hirudo* three and in *Aulastoma* four pairs of primitive kidneys, and LEUCKART even describes in the medicinal leech their opening to the exterior. BERGH, however, could not confirm this.

The primitive kidneys of the Hirudinea are said by BERGH to have nothing to do with the permanent excretory

organs, for these are not formed in the germ bands until the primitive kidneys have already separated from them (comp. also p. 332).

Like the primitive kidneys, other organs of the larva also degenerate during its metamorphosis into the adult worm. A musculature consisting of longitudinal and circular fibres, which in the region of the mouth enlarges into a powerful circular muscle, is found under the epidermis of the larva. Between the muscle fibres BERGH finds spindle-like and branched cells, which he takes to be of a nervous nature. This entire larval skin is said by BERGH to be cast off in the metamorphosis, and the whole body of the leech, with the single exception of the mid-gut, arises from the so-called trunk and head germs (*Rumpf- und Kopfkeime*), of which more will be said later. At this time the mouth closes. The provisional pharynx of the larva is replaced by a permanent one. Details about these processes will be given in considering the formation of the organs.

3. The Further Development of the Body; Formation of the Head and Trunk.

A distinction between head and trunk was apparent even in the *Chætopoda*; it was recognizable by the condition of the mesoderm, and also probably found expression in the mode in which the nervous system was formed. In the *Hirudinea* this contrast is still more decided, for the fundaments of the nervous system of the head and trunk are separate, and the so-called germ bands probably take no part whatever in the formation of the head. According to the investigations of BERGH, which to a certain degree confirm and extend the earlier discoveries of LEUCKART and SEMPER, there are two so-called *head germs* (*Kopfkeime*) in addition to the germ bands, which we have already learned about, and which are designated by BERGH as *trunk germs* (*Rumpfkeime*). These head germs, the origin of which is still obscure, lie between the pharynx and epidermis as two cell-masses, which become united by a connecting cord

of cells, extending over from one to the other (Fig. 156).
From these head germs the whole head portion is said to be
formed, including even the epidermis, for the epidermis
which is now present (Fig. 156 ep) is of only a provisional
nature. In like manner the entire trunk portion (with the
exception of the mid-gut) is said to arise from the trunk
germs. The head germs and trunk germs unite in the region
of the mouth. Thus in the formation of the body a decided
difference would exist between head and trunk.
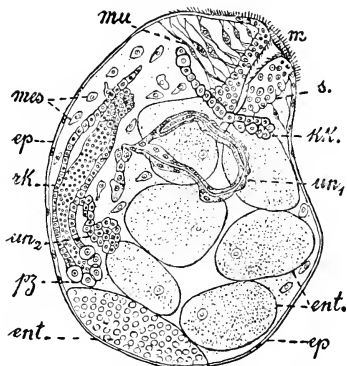
Fig. 156.—Longitudinal section of a larva of *Nephelis* (after BERGH). *ent*, ento-
dermal elements; *ep*, provisional epidermis; *kk*, head germ (*Kopfkeim*); *m*,
mouth-opening; *mes*, individual mesoderm cells; *mu*, muscle cells; *pz*, pole cells
of the germ band (*i.e.* trunk germ); *rk*, trunk germ (*Rumpfkeim*); *s*, provisional
pharynx; *un₁* and *un₂*, primitive kidneys or their fundaments.

WHITMAN also assumes a fundamental distinction between head and
trunk portions, and is inclined to refer the origin of the former to the
four micromeres first formed. However, the difference in the Clepsine
observed by WHITMAN is not so striking as here, for in that case the
epidermis is not cast off.

If the permanent body of the medicinal leech is really formed from
four fundaments, then the comparison with the formation of the
Nemertean from the *Pilidium*, which was attempted by BERGH, is a natural
one. In *Pilidium* also the larval skin is cast off, and the body arises
from several separate fundaments, of which the mesodermal are four in
number (two in the head and two in the trunk portion) (comp. p. 223).
Yet these processes, as far as they are known, appear to take place in

the *Nemertini* and *Hirudinea* in a manner that is too inharmonious to warrant a comparison.[1] Also the further development of the "head germs and trunk germs," which in the Nemertini takes place by means of ectodermal invaginations and additions of mesenchyma cells, but in the Hirudinea as early differentiations of embryonal cells, shows little similarity, apart from the fact that the Annelidan and Nemertean larvæ themselves have only a very slight resemblance to each other.

4. Formation of the Organs.

The Body-covering.—At an early stage of embryonic development the layer of small cells grows over the germ bands and macromeres, and thus forms the epidermis.   This epidermis, beneath which muscles have already been developed, probably from the germ bands, becomes in Clepsine the epidermis of the adult worm, whereas in the Gnathobdellidæ it, together with its musculature, is said gradually to disintegrate, and to be replaced by a new epithelium, which is formed from the superficial layer of the "head germs and trunk germs."   These have united in the region of the mouth, and thus the entire body is covered by the new epidermis.   At the same time the body musculature is formed from the head germs and trunk germs.   The remnants of the larval skin are finally cast off.

According to the description given by WHITMAN for *Clepsine*, and by BERGH for *Aulastoma* and *Nephelis*, the epidermis does not appear to be homologous in the two groups, which differ from each other to the extent that the larval skin in one group is directly transmitted to the adult animal, but in the other is cast off, being replaced by a layer of different origin.   However, an intermediate condition is said to exist in *Clepsine*, for, according to WHITMAN, two cells of the germ bands take part in the formation of the epidermis, though WHITMAN explicitly denies that it arises from these alone.

In *Clepsine* there is developed out of the epidermis, between it and the ganglion underlying the pharynx, a mass composed of numerous large gland-cells, whose secretion serves to attach to the mother the newly hatched young until their suckers are developed (WHITMAN).

The Nervous System.—In the development of the Hirudinea it is difficult to separate ectodermal and mesodermal ele-

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[1] It should be added that BERGH himself afterwards ceased to place any value on this quite natural comparison.

ments from each other. Thus the germ bands can be in-
terpreted as being formed of both kinds of elements
(WHITMAN). As we have seen, each germ band is composed
of four superficial rows of cells and a more deeply located
one (Fig. 151 C). The ventral chain of ganglia arises from
the innermost row of each germ band. The cells multiply,
and in this way a cord of cells consisting of several layers is
formed from the single row. A segmentation takes place in
this from in front backwards. In addition, median and
lateral parts are differentiated in the separate cell-masses,
and both cords unite in the middle line. In this way arise
the ganglia and the commissures.

BERGH, like WHITMAN, also derives the ventral chain of ganglia from
the germ bands, but, according to him, the permanent epidermis arises
from the same source, and consequently the nervous system takes its
origin beneath this.

NUSBAUM'S (No. 75) theory of the origin of the nervous system differs
from that described. He derives the ventral chain of ganglia, as well as
the brain, from a thickening of the ectoderm—that is to say, from the
primitive epidermis—and thus adopts an interpretation that (more in
harmony with theoretical considerations) was also espoused by KOWA-
LEVSKY and BALFOUR. The statements of NUSBAUM on this and other
developmental processes of the Hirudinea harmonize so little with the
statements of the other authors on this subject that any further con-
sideration of them must be omitted.

The development of the supra-œsophageal ganglion is
initiated in the head germs, underneath the layer which
supplies the epidermis, by the segregation of a compact
mass of cells, in which the *Punktsubstanz* can soon be
recognized (BERGH). The fundaments of the brain and
ventral chain of ganglia would then be distinct, and not
until after the concrescence of the head germs and trunk
germs would they be united by the development of the œso-
phageal connectives.

The Nephridia.—According to WHITMAN, the nephridia
arise from the two middle cell-rows of each germ band,[1] and,
in fact, WHITMAN, in opposition to BERGH (comp. *supra*, p.

[1] The fate of the fourth, outer row of cells remained unknown to
WHITMAN.

328), finds a certain resemblance between the primitive kidneys and the permanent nephridia, in that both of them arise from the same parts, *i.e.* from the middle rows of the germ bands. However, in the Rhyncobdellidæ themselves, which Whitman studied, primitive kidneys are not present. The origin of the nephridia from a continuous cord of cells, which, moreover, is described by Wilson in the same way for Lumbricus, recalls the theory advanced by Hatschek that in Criodrilus the permanent nephridia arise from a cord of cells in the somatic layer of the mesoderm (comp. *supra*, p. 296).

The development of the nephridia takes place from in front backwards by the cord of cells becoming many-layered and undergoing a segmental division. How the nephridia arise from the cell-masses thus produced has not yet been accurately determined. A pair of nephridia is begun in each segment, though all of them do not develop, for in the adult worm there are only sixteen pairs.[1]

The Body-cavity and its Lining ; Musculature ; Blood-vessels. —The peritoneal lining of the body cavity and the somatic and intestinal musculature arise from the two more deeply located cell-rows of the germ band, the pole cells of which we have learned to designate as the mesoblasts. The two cell-rows have changed into voluminous cords of cells by the rapid multiplication of their elements. These cords undergo a segmentation from in front backwards. The primitive segments thus produced extend out dorsally, and cavities make their appearance in them. The latter correspond to the segmental (metameric) cavities of the Chætopoda. After growing completely around the intestine, they are said to become confluent, and to form the marginal sinus, which belongs to the lacunar portion of the blood-vascular

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[1] [The formation and differentiation of the rows of cells produced by the teloblasts has been again traced by Bergh and by Apathy, as well as in the works of Whitman (see Appendix to *Literature* on Annelida). The subjects involved are the formation of the nervous system, the body musculature, and the nephridia. These organs have been traced back to definite parts of the so-called germ band, though as yet complete agreement on the part of the authors has not been reached.—K.]

system (WHITMAN). According to another view, however,
the two remain separate, and constitute the lateral sinuses of
the two sides. The other processes—the formation of the
septa and that of the intestinal and body musculature—
appear to take place in the same way as in the Chætopoda.
By the growth of the mesodermal elements, the body cavity
may undergo a greater or less reduction. In the Rhyn-
chobdellidæ the body cavity is still well developed, and is
provided with a distinct peritoneal epithelium, whereas in
the Gnathobdellidæ it is almost entirely suppressed (BOURNE).
It has already been mentioned that portions of the body
cavity are metamorphosed into parts of the blood-vascular
system. It has been stated that the dorsal and ventral
trunks of the blood-vessels take their origin from the
splanchnic layer, owing to a splitting of it.[1]

The Genital Organs are doubtless of mesodermal origin,
though the statements which are made concerning their
formation are little to be trusted.[2]

The Intestinal Canal.—In both the Rhynchobdellidæ and
the Gnathobdellidæ we have already become acquainted
with the origin of the mesenteron from the three entoblasts.
These give rise to a vesicle composed of large cells, which
gradually resorbs the entoblasts whether enclosed within or
lying outside it, and becomes connected with the outer
world by means of an ectodermal invagination (comp. pp.
323 and 327). The pharynx which is formed in this way
presents different conditions, according as the development
is direct or indirect. In the first case the pharnyx, pro-
duced by the collaboration of entodermal, ectodermal, and

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[1] [BÜRGER (Appendix to *Literature* on Annelida) has made an ex-
tensive investigation of the formation of the body cavity, the blood-
vascular system, and the nephridia. He traced the establishment of the
cœlom, its differentiation, and its relation to the circulatory system.
In regard to the nephridia, considerable agreement with the Oligochæta
has been found.—K.]

[However, BÜRGER (Appendix to *Literature* on Annelida) has re-
cently given a detailed account of their origin, according to which they
are referable on the whole to proliferations of the peritoneal epithelium.
Not only the sexual glands, but also the efferent ducts, arise in this
way.—K.]

probably mesodermal parts, is converted directly into the
œsophagus, pharynx, and proboscis-sheath of the adult
animal. The intestinal canal attains its final shape as the
result of the ingrowth toward it of the dissepiments,
which thus cause the cæcal diverticula of the intestine. At
the same time the intestine is provided with its musculature.
In *Clepsine* there are six pairs of such diverticula; the
seventh pair grows backward through five segments, and
consequently acquires constrictions similar to those of the
intestine itself. The terminal portion of the intestine
extends straight backwards and unites with the ectoderm to
form the anus.

The conditions are not so simple in the Gnathobdellidæ.
Here the pharynx first formed is of a provisional nature, and
functions only in the reception of the albuminous nourish-
ment. After this office is discharged it degenerates; the
mouth closes as the result of the concrescence of the head
germ and trunk germ (BERGH). At the same point there is
formed an invagination of the united head and trunk
germs, the fundament of the permanent pharynx, which
grows into the larval pharynx and unites with the entoderm,
while the tissue of the old pharynx is gradually absorbed.
The jaws arise in the pharynx as fold-like elevations covered
by a firm cuticula (LEUCKART). The oral sucker is formed
as a circular elevation of the superficial layer of the body.
The development of the mid-gut takes place in a manner
similar to that already described above for Clepsine. On
the other hand, according to BERGH's observations, the hind-
gut is formed as a solid outgrowth of the tissue of the
" trunk germ," which subsequently becomes hollow, and
unites with the entoderm. Such a mode of origin agrees
with BERGH's entire theory, according to which the whole
body of the leech, with the single exception of the mid-gut,
is formed from the so-called head and trunk germs.

The degeneration and regeneration of the pharynx in the Gnathob-
dellidæ recall the replacement of the larval stomodæum by a permanent
pharynx in Lopadorhynchus as described by KLEINENBERG, even though
the metamorphosis takes place there in a different way.

General Considerations.—The development of the Hirudinea doubtless points to the fact that in dealing with them one has to do with Annelida. Although differing in details, the entire process of development is similar to that of the Chætopoda, and especially of the Oligochæta. The so-called germ bands of the Hirudinea and the mesodermal bands of the Chætopoda, it is true, do not appear to be homologous structures, but the entire manner of their formation and their relation to the embryonic body in general, as well as their subsequent development, indicate that both are to be referred to like structures, and that in the Hirudinea a modification has appeared only in so far as the more simple mesodermal bands have there acquired a more complicated structure by the addition of ectodermal parts. In their mode of development the Hirudinea appear to be less primitive forms than the Chætopoda.

Just as the mode of origin of the individual organs, especially the body cavity, the nervous system, and the excretory system, shows the leech to be an Annelid, so, too, does its anatomical structure. This is mentioned only for the reason that direct relationships between the Hirudinea and Platyhelminthes have been sought for in various directions. In this connection it is only the structure of the genital organs and their resemblance to those of the dendrocœlous Turbellarians that appear to be remarkable. It would be desirable to know more than we do at present regarding this point.

In brief it must be said that, as compared with the Chætopoda, the Hirudinea show themselves to be in structure and development higher forms, which exhibit. many secondary modifications.

VI. BRANCHIOBDELLA.

The systematic position of *Branchiobdella* is not yet established. There are anatomical grounds for the view that this worm is to be assigned to the Oligochæta, and that it is only in consequence of its parasitic mode of life that it has acquired certain characters—for example, the posterior

sucker—which cause it to resemble the Hirudinea (Voigt, Vejdovsky). The development exhibits in some features a resemblance to that of the Hirudinea, but otherwise it is so peculiar—provided we can rely on the statement of Salensky—that the relationship of Branchiobdella to either branch of the Annelida cannot be inferred from it.

Branchiobdella lays its eggs, each surrounded by a firm envelope, on the gills of the crayfish, where they are attached by means of a stalk, a prolongation of the envelope. A cocoon proper, as in the Oligochæta and Hirudinea, does not exist, although the egg is surrounded, as in these, by a special envelope; perhaps therefore the outer envelope is equivalent to a cocoon.

In the cleavage and the formation of the germ-layers, conditions are exhibited which do not resemble those of the Hirudinea or Oligochæta, but can perhaps be referred more readily to the latter. We begin with the stage in which one large and three small blastomeres are formed. All four are to be called macromeres, for soon four micromeres are abstricted from them. By division of the micromeres and the formation of new ones on the part of the macromeres, a rapid increase of these small (ectoderm) cells takes place. They soon form an irregularly defined cell-plate, the sides of which grow out and overlie the macromeres in the form of a cap. The striking thing in this is that the micromeres are said to correspond to the ventral side of the worm ; however, it is also stated that for *Clepsine* the mouth breaks through in the region of the first four micromeres, and it has a similar position in *Nephelis* (comp. Fig. 154, p. 326). A rather small cleavage cavity makes its appearance between the micromeres and macromeres; it is subsequently forced away from the macromeres by the production of new cells. The macromeres have likewise divided and arranged themselves as two pairs of large cells at the posterior end (Fig. 157 *A*). A cord of ectoderm cells forces its way between the two pairs. The double-row arrangement of the macromeres persists even when they divide further (Fig. 157 *B*).

These wo rows of macromeres have been compared to the macromeres of the Hirudinea, though, as far as can now be seen, this comparison is not warranted, for the macromeres in Branchiobdella are said to continue dividing, and to give rise to the mesoderm and entoderm. But in both the Hirudinea and the Oligochæta the separation of the two germ-layers takes place much earlier.

The division of the macromeres advances steadily from behind forwards. In this way two different groups of cells arise, one of which lies next to the ectoderm, and constitutes the mesoderm, while the other, lying next to the macromeres, is the entoderm. What is left of the macromeres themselves divides uninterruptedly, so that the cells arising in this way become like the ectoderm. They cover the posterior part of the embryo (Fig. 157 *D*).

Even before the macromeres separated into the different elements in the manner described, a depression of the ectoderm (Fig. 157 *A*), which does not persist long, and perhaps represents the fundament of the supra-œsophageal ganglion, makes its appearance in front of them, and therefore on the dorsal side of the embryo. This originates independently of the ventral chain of ganglia. The latter arises, according to SALENSKY, in the form of an extensive groove on the ventral side (Fig. 157 *C*). The groove is very broad at the posterior end of the embryo. It is bounded here by the large cells still remaining, which, continuing to divide, contribute to the formation of the margins of the groove. The groove becomes narrower anteriorly, extends on to the dorsal side of the embryo, and here bifurcates (Fig. 157 *D*). The part of the ectoderm which is encircled by the two branches probably corresponds to the above-mentioned ectodermal depression, and produces the supra-œsophageal ganglion, which secondarily unites with the two processes of the ventral chain of ganglia by means of two ridge-like processes, the œsophageal connectives. The ventral cord itself is said to originate in a manner quite like that of the medullary tube of vertebrates. The groove becomes closed by the bending together of its upper edges (in this case, however, from in front backwards), and in this way forms a tube, which finally separates from the overlying ectoderm, loses

its lumen, and lies as a cellular cord in the ventral median line of the embryo.

On each side of the nerve cord lies a ribbon-like cord of cells, the mesodermal band. The two mesodermal bands are united to each other by a median part. They have arisen from the common ento-mesodermal mass, the origin of which we have previously traced, by the separation of a ventral layer, the mesoderm, from the dorsal layer, the entoderm.

A segmentation, like that in the ventral cord, also makes its appearance in the mesodermal bands, which separate into the primitive segments. The processes thus effected, as well as the formation of the body cavity and the septa, take place in a manner similar to that described for the other Annelida. The internal segmentation is late in finding expression on the exterior of the body, and is suppressed in its anterior and posterior parts, where the primitive segments for the present acquire no cavities, and therefore remain in an embryonic condition. Each segment exhibits externally a division into
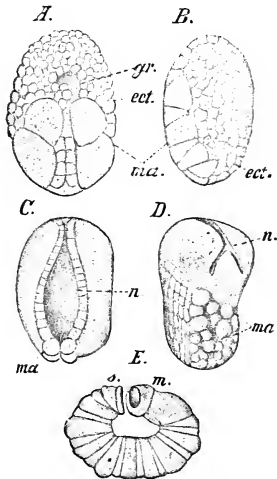
FIG. 157.—*A* to *E*, embryos of *Branchio-bdella* in various stages (after SALENSKY). *ect*, ectoderm ; *gr*, pit in the ectoderm on the dorsal side ; *ma*, macromeres ; *m*, mouth-opening ; *n*, neural groove ; *s*, sucker.

a broader and a narrower portion (Fig. 157 *E*). The former corresponds to a ganglion, the latter to a septum. In front of the anterior end of the ganglionic chain lies a part of the mesoderm, which forms the head cavity ; but regarding this, SALENSKY could not determine whether it likewise arose from the mesodermal bands.

At the time of the appearance of the outer segmentation a peculiar change in the position of the embryo occurs. Up to this time its ventral side was greatly curved, for both the anterior and the posterior ends grew toward the dorsal side. Later it assumes the reverse position. This is effected by a rotation of the embryo on its own axis. The movement begins at the anterior and at the posterior parts of the embryo, and gradually extends to the middle portion. Whereas the ganglion chain at first lay on the convex side of the embryo, it is now found on its concave surface. In the course of this process the anterior and posterior parts of the body assume their permanent shape (Fig. 157 *E*). The posterior end is abruptly truncated. A depression on it, which soon makes its appearance, represents the fundament of the sucker. The absence of segmentation at the anterior end is noticeable; the head, however, is distinct from the anterior part of the body (Fig. 157 *E*). The mouth-opening makes its appearance as a shallow depression of the ectoderm far in front, and probably at the place where the medullary groove bifurcated. It unites with the fore-gut, which, as well as the hind-gut, is said to arise from the entoderm. The entoderm for a long time consists of a compact mass of cells, which increases in length with the growth of the embryo. In the formation of the epithelium, the cells withdraw to the periphery of the mass; and the nutritive material, which is surrounded by them, remains at the centre just as in the formation of the intestine in *Rhynchelmis*. The fore- and hind-guts are the first to be hollowed out. The latter unites with the very short tube which forms the anal invagination located on the dorsal side of the sucker. The entire œsophagus, even the jaws, are said by SALENSKY to be of entodermal nature; and only the lips, with their internal lining, are formed of ectoderm. Last of all follows the development of the mid-gut. Even in the hatching embryos, which have approximately the development described (Fig. 157 *E*), the mid-gut is still filled with an undigested yolk-mass.

To enumerate once more the chief points in the development of this unique group, which it has hitherto been im-

possible to unite satisfactorily either with the Oligochæta or Hirudinea, the following points, in addition to the altogether aberrant cleavage phenomena, are remarkable: the formation of the mesodermal bands and the very peculiar manner in which the nervous system is formed. A germ band in the sense of the Hirudinea is not present, but, on the other hand, the fundament of the nervous system differs from that of the Chætopoda. To be sure, the origin of the chain of ganglia from a ventral ectodermal invagination has been repeatedly described for the Annelida, but this conclusion has not gained currency. At all events, the origin of the nervous system and mesodermal bands of *Branchiobdella* merits renewed investigation.

General Considerations regarding Annelida.

The embryology of the Annelida affords us some hints regarding the phylogenetic derivation of the Annelid stem and its genetic relationships to other groups of animals, and also regarding the origin of metameric segmentation. These suggestions are significant, even though they do not as yet furnish a foundation of positive knowledge, but serve only to support theories of greater or less probability.

If we consider the larval forms of the Annelida, we see that their different shapes, however variously they may be expressed, are referable to the *Trochophore*. *The Trochophore is the typical larval form of the Annelid stem.* Even in the derived and much-modified groups, such as the *Oligochæta* and *Echiuridæ*, as well as in the aberrant genus *Myzostoma*, the larval *Trochophore* form can be recognized more or less distinctly. *Dinophilus* corresponds in its shape and organization to a so-called polytrochal larva, which it was possible to derive directly from the Trochophore (comp. p. 278). The embryos of the *Hirudinea* exhibit the greatest resemblance to those of the Oligochæta. However, they are much more modified than these, and consequently cannot be traced directly to the *Trochophore*, though this may be accomplished through the mediation of the Oligochæta.

Most likely the Trochophore of the Annelida embodies

the ontogenetic recapitulation of an ancestral form which
was common to the Annelida, Mollusca, and Molluscoidea,
and from which these animal stems branched off as inde-
pendent groups. The assumption that the Trochophore cor-
responds to an ancestral form is supported, not alone by
the circumstance that the larval forms in the groups men-
tioned can all of them be traced more or less directly to
the Trochophore : it acquires a further and important sup-
port from the fact that in the division *Rotifera* we see before
us forms which in their adult condition remain essentially
at the stage of organization of the unsegmented Trocho-
phore. We have already mentioned (p. 259) that not only
the Rotifer known by the generic name of Trochosphæra,
but also the rest of the Rotatoria, can readily be referred to
the plan of the Trochophore. The Rotatoria accordingly
are organisms which still exhibit the closest relationships to
the Trochophore-like ancestral form whose mode of locomo-
tion and plan of organization, with some secondary changes,
they have retained.

If we take into comparison the rest of the groups of the
so-called Vermes, there is apparent, in the first place, a
striking resemblance between the Trochophore of the An-
nelida and the larval form of the *Nemertini* known as
Pilidium (comp. p. 231), even though in their further de-
velopment the two groups pursue different paths. By means
of the Pilidium we are also led to bring certain larvæ of the
Turbellaria into remote comparison with the Trochophore
(comp. pp. 168 and 230).

In searching for the ancestral forms from which the
Trochophore-like archetype arose one meets with great diffi-
culties. In order to arrive at an idea of this ancestral form,
the Trochophore has been compared to a *Medusa.* Its
pelagic mode of life, its shape, and, above all, the nerve-
ring of the ciliated band discovered by KLEINENBERG, were
the things which led this author and BALFOUR to assume its
descent from a medusoid form. Derived in such a way, the
preoral band of cilia is, from its position, referred to the
margin of the umbrella, and the aboral dome of the Trocho-
phore to the ex-umbrella, whereas the part of the larva lying

behind the ciliated band must be considered as the sub-um-
brella, made to bulge downward.   A more careful considera-
tion, however, offers considerable difficulties to a derivation
of this kind.   Even if we disregard the fact that the Medusa
represents the most divergent and most highly developed
form of the Cnidaria type, and that forms which are highly
developed in one direction ordinarily do not become points
of departure for new developmental series, still the difficulty
of the derivation suggested is evident from a comparison
of the mode of locomotion of the two forms.   The Medusa
moves by means of oar-like strokes of a complicated loco-
motor apparatus, depending upon muscular action.   On the
other hand, the Trochophore, with its trochal organ operated
by ciliary motion, represents a much more primitive loco-
motor apparatus, directly comparable in its mode of action to
the ciliated planula (comp. p. 154, *et seq.*, the grounds
which have been advanced against the derivation of the
Ctenophora from Medusæ).   A chief difficulty in the
derivation under discussion is found in the presence of the
central nervous system at the apical region, where important
organs are never developed in the Medusæ.   We should then
have to look upon the nerve-ring of the Trochophore as the
chief part of the central nervous system, and the apical plate
as a subsequently acquired secondary part of it ; but in the
present state of our knowledge we are not justified in this.
We recognize that the two parts of the nervous system be-
long together, and have probably been developed in close
relation with the locomotor apparatus, as regulators of the
movements.   Thus perhaps the apical plate in its earliest
origin is to be traced back to a tuft of cilia functioning as
a rudder (such as is met with at the apical pole of many
Actinian larvæ), whereas the ring-nerve, it is to be assumed,
has been formed in connection with the development of the
trochal organ, both of them as localizations of a system of
nervous internuncial fibres, distributed under the entire
ectoderm.   It might be mentioned here that, in addition to
the apical plate, a nerve-ring is also met with in the *Pili-
dium*.

We have above adduced the difficulties which, according

to our point of view, are opposed to a derivation of the Tro-
chophore from the medusoid form, and have already made
some suggestions respecting a derivation of the Trochophore
which, although based upon hypothetical grounds, neverthe-
less appear to be better supported by the facts of compara-
tive anatomy and embryology than the former view.   This
view brings the Trochophore into relation with the ancestral
forms of the *Nemertini, Turbellaria,* and *Ctenophora,* and
regards it as having arisen tolerably directly from much
more primitive cœlenterate forms than is possible on the
assumption of derivation from Medusæ.   It should be ex-
pressly noted here that we necessarily abandon the realm of
positive demonstration in making these statements, which
scarcely have any higher value than that of mere conjec-
tures.

To us the facts appear to indicate that the ancestral form
arose rather directly from a uniformly ciliated gastrula-
like archetype by a change in the mode of locomotion.   Such
a primitive, completely and uniformly ciliated organism
exhibited an anterior apical and a posterior oral pole.
Secondary axes had not yet been developed; the form
presented at first the monaxial heteropolar type.   It is
possible, and in view of the ancestors of the Ctenophora
probable, that on this form certain differentiations made
their appearance without causing an abandonment of the
monaxial, heteropolar form, or the radial form that arose
from it.   Among these differentiations we reckon a tuft of
cilia at the animal pole functioning as a rudder (the earliest
fundament of the apical plate), an ectodermal pharyngeal
tube, and the formation of diverticula of the entodermal
portion of the intestine, by the regular distribution of which
around the chief axis the first impetus to the formation of
definite secondary axes was probably given.

It must be mentioned that many Actinian larvæ present exactly the
structure described (*Scyphu a*).   However, this resemblance is probably
founded merely on analogy, for in the Cnidaria we assume that the
formation of radial gastral pouches took place only after attachment
and the development of an Archhydra stage, whereas the Ctenophora and
Bilateria probably never had an attached ancestral form.

The original mode of locomotion of the uniformly ciliated, radial ancestor described, which had arisen from the gastrula stage by means of some further differentiations, was spiral, such as we may still see in the ciliated planulæ of many lower animals. It depended upon a combination of a progressive movement in the direction of the longitudinal axis with a rotation of the entire body about this axis. The ancestral forms of the Platyhelminthes have perhaps been directly developed from such a uniformly ciliated stock-form by the assumption of the creeping mode of life, and the ancestors of the Ctenophora may have been developed by a change in the method of pelagic swarming and by the formation of rows of ciliary plates. Whereas in the latter case the rotation around the longitudinal axis sank into insignificance, and the combined force of the ciliary plates was concentrated on propulsion in the direction of the longitudinal axis, in those forms which effected the transition to the Trochophore-like ancestor a change of movement took place. In these cases, though the body as a whole ceased to rotate, the rotatory movement was retained in the trochal organ in the form of a regular circular wave of contraction, whereby this organ was in position to undertake a function in relation to the body (now progressing in a constant position) similar to that of the ship's screw in relation to the hull of the ship. Hand in hand with this alteration in the mode of locomotion went a higher differentiation of the ciliary locomotor apparatus, by means of which the passage from the original uniform coat of cilia to distinct locomotor organs was brought about. As such are to be mentioned the tuft of cilia functioning as the rudder and the rows of cilia, but especially the preoral ciliated band.

It is possible that the bilaterally symmetrical distribution of the body-masses was directly developed in connection with the above-mentioned changes in the form of motion by means of which the body was balanced in its forward movement. At any rate, one of the most important factors for the development of bilateral symmetry is to be sought in the shifting of the mouth-opening, which now moved

forwards from the posterior pole of the body, thus deter-
mining as ventral the side of the body on which this
shifting took place. The first cause of this forward migra-
tion of the month, during which the opposite edges of the
posterior parts of the blastopore successively approached
each other until the slit thus produced was at last entirely
closed, is to be sought in the significance of the trochal
organ as a food-procuring apparatus and the importance
of the approach of the mouth toward it. By such a change
in the position of the mouth, the relations of the primary
axes were disturbed, so that henceforth the chief axis of
the body can no longer be referred directly to the primary
axis; for this reason the Bilateria are also designated as
Heteraxonia (HATSCHEK).

Owing to the resemblance which the Pilidium and many Turbellarian
larvæ present to the Trochophore, one might also be inclined to derive
the Platyhelminthes and Nemertini directly from a Trochophore-like
ancestor. The complete ciliation of these forms would then be not
primitive, but re-acquired after the transition to the creeping mode of
life (therefore as in Cœloplana, comp. p. 157). On the other hand, it
must be pointed out that ciliated bands are developed in great variety
in pelagic larvæ, and we are certainly not in position to prove the
homology of all these bands. Hence the resemblance of these larval
forms to the true Trochophore of the Annelida is perhaps to be referred
merely to analogy in development, which would have its cause in a
developmental tendency in this direction inherited from the common
ancestor.

As a result of the development of the most important
locomotor organs in the anterior half of the body, it came
about that the organs of the animal functions arose in this
region. It is this part of the body which, as *head*, we place
in contrast with the posterior, subsequently elongated por-
tion of the Trochophore, which is called the *trunk*, and gives
rise particularly to organs of vegetative functions. The
fruitfulness of the conception, in the interpretation of the
Annelid body, that head and trunk are distinct, has only
been equalled by the difficulty of determining the precise
boundaries between these two primary regions of the body.

In the first place, the question arises whether the mouth

is to be assigned to the head or to the trunk. In the solution of this problem the condition of the mesoderm plays a particularly important rôle. No real cœlom appears to be formed in the portion lying in front of the mouth; on the contrary, the first pair of primitive segments is said to surround the pharynx. If this were so, then a distinction would really be established between the preoral and the oral portions, and the latter would have the greater resemblance to the body segments. However, this distinction is later obliterated owing to the fact that portions of the mesoderm from the most anterior primitive segments migrate into the preoral region and form its musculature. Thus interpretations differ, inasmuch as the preoral part alone (KLEINENBERG) and also that together with the oral segment (HATSCHEK) have been taken to be the head portion. Moreover, induced by the peculiar phenomena in non-sexual reproduction, some authors have gone farther than this and considered a greater number of segments (as many as six) as the head portion of the worm (SEMPER, v. KENNEL). The first and last theories seem to us to go too far. Until the final settlement of the question how the mouth and the pharynx are related to the first primitive segment, we would reckon the mouth region as belonging to the head of the worm.

The transition from the Trochophore-like stock-form to the real Annelid ancestors (Archiannelida) took place by considerable growth in length, whereby the trunk portion of the worm became larger, and the primary head portion less and less conspicuous. At the same time a change in the mode of life took place, the pelagic being exchanged for the creeping habit.

The larval stages belonging to this transition are distinguished especially by the terminal growth of the body. Near the posterior end of the body, which we can henceforth distinguish as the anus-bearing terminal segment, is found a zone of proliferation, from which new cell material is continually being given off forward to the elongating trunk portion. Since, at the same time with this growth in length, the segmentation of the trunk is established, it

follows that the most anterior segments of the trunk are
formed first, and therefore are the most differentiated ones
in the developing larva, while behind follow younger and
younger ones. The growth of the Annelid body therefore
does not depend upon growth of the body in all directions,
but upon a partial (terminal) growth, since new segments
are always being supplied from a zone of proliferation lying
near the posterior end of the body (in front of the terminal
segment). This productiveness of a restricted portion of
the body strongly recalls certain kinds of non-sexual re-
production, and therefore the process has been called, even
in this case, a " budding of the segments." That, however,
is an inaccurate mode of expression. The most natural
comparisons are those with the tapeworm chain and with
the strobila of the Scyphomedusæ. The point of comparison
in all these cases lies in the production, from a certain zone
of proliferation, of homodynamic portions of the body, which
become to a certain extent independent. For this reason
the view has been expressed that in the segments of the
Annelid body we have before us single individuals (which
do not arrive at complete separation), and accordingly in
the entire body of the Annelid a stock or corm. It seems
scarcely favorable to this theory that the degree of in-
dependence which the individual segments present is com-
paratively slight. The most important organs (nervous
system, body musculature, blood-vascular system) show
themselves to be single fundaments of the entire body, and
are also developed as such even though they also exhibit
evidences of metamerism. Even the excretory canals may
give up their segmental isolation and become united to one
another by means of longitudinal canals. The comparison
with the single fundaments of the other systems of organs
inclines us to the opinion that the development of the
nephridia from separate fundaments (BERGH) represents a
coenogenetically altered condition, and that the nephridial
system was originally developed by separation from a com-
mon cord (HATSCHEK). By such an assumption the com-
parison of the nephridial system of the Annelida as a whole
with the excretory organs of the Platyhelminthes would

become possible, since the longitudinal stems in the two
cases could be looked upon as corresponding to each other
(whereby we even have in mind a former connection of the
permanent nephridia with the head kidney). At all events,
the anatomy and development of the Annelid body permit
the establishment of the interpretation of the entire body
as an individual. Just as in the consideration of the tape-
worm chain we were induced by the comparison with un-
segmented forms to refer the entire chain to an unsegmented
individual,[1] and, on the other hand, to see in the proglottis,
not a complete individual, but only the abstricted hinder
portion of the body of the Cestode, in the same manner,
and with much more reason, we adhere to the individuality
of the Annelid body. We can accordingly recognize in
metameric segmentation only the regular repetition of certain
groups of organs in the trunk at uniform intervals.

In the question of the origin of the metameric segmenta-
tion we shall have to ascertain whether the synchronism
of the terminal growth of the body and the appearance of
metameric segmentation correspond to a palingenetic con-
dition. In other words, in the hypothetical ancestral form
were new segments successively added behind during in-
crease in length, so that forms with many segments arose
from those with few by gradual increase in the number of
segments? The fact that the growth of the body in length
by the formation of new segments at the posterior end is
typical in all Annelids and the forms derived from them
(Arthropoda) is an argument in support of this theory. In
that case we might perhaps be inclined to the opinion, as
stated by HATSCHEK, that in ancestral forms enlarging by
terminal growth the differentiation, originally progressing
continuously, became intermittent, and thus reached the type
of the metameric animal. But another view may also be
maintained, and, as it seems to us, with quite as much
justice—a view which is based upon the assumption that
at first an unsegmented, elongated ancestral form was pro-
duced by terminal growth, whereupon the entire body be-

[1] There is a considerable difference between this and the process of
strobilization.

came separated at once into a large number of segments by a rearrangement of the individual organs. This assumption is supported by the consideration that with the lateral sinuous movement of the body, and with the rigidity of the tissues caused by increasing differentiation, the formation of alternating regions of greater and less motility was of considerable advantage to the individual, and rendered possible a further elongation of the body. The first cause for the appearance of metameric segmentation would then be sought in the manner of locomotion and in mechanical conditions. However, this latter view is not supported in any way by embryology.

Even though we have not been able to give a positive decision on these difficult questions, yet it seems to us appropriate, in the present state of knowledge, to indicate the direction of future inquiry by which a possible solution of the questions is to be sought.

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CHAPTER XI.

SIPUNCULIDÆ.

OUR knowledge of the development of the *Sipunculidæ* is still
very meagre. Concerning *Sipunculus* and *Phascolosoma*,
the embryology of which has been studied, we know that
they possess larvæ which may be compared to the *Trocho-
phore*. The development of *Sipunculus*, which has been
thoroughly dealt with by HATSCHEK, presents many peculiari-
ties, above all the formation of an embryonal membrane.
The *Trochophore*-like larva does not arise directly from the
embryo, but the latter is surrounded by a cellular mem-
brane, as if by an amnion.

I.—The Development of Sipunculus.

The first stages in the development of *Sipunculus* are not
known. By pelagic fishing, HATSCHEK captured the embryos
in the blastula stage. In these embryos the fundaments of
the three germ-layers can already be recognized (Fig. 158 *A*).
The thickened part of the spherical blastula consists of tall
cells, the entoderm; there is prominent among these a
particularly large cell, which, in contrast to the other
(prismatic) cells, retains a more spherical shape. This is
the first mesoderm cell. It lies in the median plane between
the ectoderm and entoderm, and marks the posterior part of
the embryo (Fig. 158 *A*). The free space which existed
between the embryo and the egg-membrane—the latter being
traversed by radial pores—disappears during the blastula
stage, owing to the fact that the cells apply themselves to
the egg-membrane. They send out cilia through the pores
of the membrane, so that the embryo, together with the egg-

membrane, now begins to rotate. The vegetative pole, which begins to flatten, and then to invaginate, remains free from cilia.

In the formation of the archenteron a small part of that portion of the blastula which is still to be assigned to the ectoderm (Fig. 158 *B*) is also invaginated. The boundary between it and the entoderm is marked by the mesoderm, which has increased to two cells (the primitive mesoderm cells) and now moves inward. The two cells are symmetrical in relation to the median plane. The depression of the ectoderm already mentioned, which follows that of the entoderm, gives the first impulse to the development of the permanent larval skin. It sinks in deeper and deeper and bends over forwards, forming in this way a lamella of thick cells (Fig. 158 *C* and *D*, *rp*). The plate remains temporarily united, by means of an amnion-like fold that is not extensive, it is true, with the primitive ectoderm, which soon appears only as the serosa (Fig. 158 *D*). HATSCHEK calls the plate the trunk-plate in contrast to the head-plate, which is also differentiated from the primitive ectoderm. This differentiation takes place as follows:—In the region of the animal pole (corresponding to the apical plate), which has now also become thickened, the cell plasma retracts from the egg-membrane in an annular furrow, and thus gives rise to a circular space (Fig. 158 *B* to *D*, *ka*) between the permanent ectoderm and an outer layer (serosa). The head-plate, therefore, corresponds to the apical plate. The space between it and the serosa (the amnion is only slightly developed here) HATSCHEK calls the head amniotic cavity (*ka*), and that between the trunk-plate and serosa the trunk amniotic cavity (*ra*). The fold which would correspond to the amnion on the trunk-plate is retained for a short time and is then included in the formation of the trunk-plate. The trunk- and head-plates alone supply the ectoderm of the larva. All the rest of the ectoderm of the embryo is employed in the formation of the embryonal membrane (serosa). The serosa grows over the trunk-plate and completely encloses it (Fig. 158 *D* and *E*, *se*); however, this is not the case at the opposite (animal) pole. The

head-plate is not overgrown by the serosa, and consequently a circular opening is always retained here.

In consequence of a complicated process of growth, regarding the details of which the reader must be referred to HATSCHEK's descriptions, the at first median band-like trunk-plate spreads considerably and grows out towards the sides and then dorsally, finally to unite, at the termination of the embryonic period, with the head-plate, which has likewise enlarged somewhat. During this circumcrescence of the internal parts by the trunk-plate, a change in the position of the embryo takes place. The posterior part of the trunk-plate had even before this turned toward the animal pole, and thereby was in a position to supply the dorsal part of the ectoderm (comp. Fig. 158 D and E). In the region of the *blastopore*, which closes, the œsophagus had been formed from the ectoderm at an early period (Fig. 158 D, bl). This part also changes its position, for it moves more toward the apical plate, whereas the entodermal sac is crowded further backwards (Fig. 158 E). As a result of this, the position of the mesoderm is necessarily altered (Fig. 158 C, D, and E). It is moved from the posterior part of the larva further forwards. Its cells have meanwhile greatly multiplied, and two mesodermal bands have arisen from it (Fig. 158 E, *mes*). The latter do not undergo a segmentation; on the contrary, a fissure makes its appearance in them, which separates them into a splanchnic and somatic layer. This differentiation is first noticeable in the anterior part of the mesodermal bands, and proceeds from in front backwards.

The complete development of the embryo is reached by the gradual closing of the permanent ectoderm. We saw that the primitively band-like trunk-plate curved over toward the dorsal side, and that its end moved toward the apical plate. Since the band-shaped trunk-plate lies in the median line, the embryo of such a stage appears in a median section, almost enclosed by the permanent ectoderm (Fig. 158 E); however, this is not actually the case, for, although the ventral and dorsal parts of the trunk-plate also spread out laterally, yet they remain separated on either

side by a broad space. The ventral and dorsal parts of the
trunk-plate now grow out more and more on the sides, and
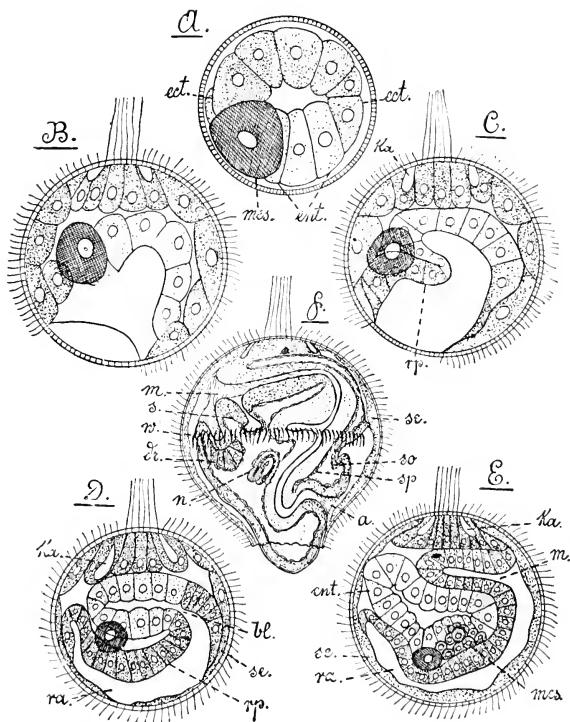
Fig. 158.—*A* to *F*, stages of development of *Sipunculus nudus* (after HATSCHEK).
A, blastula ; *B*, gastrula ; *C* to *E*, other stages, in which the development of the head-
and trunk-plates takes place ; *F*, embryo during hatching ; *a*, anus ; *bl*, blasto-
pore ; *dr*, glandular appendage of the fore-gut ; *ect*, ectoderm ; *ent*, entoderm ; *ka*,
head amniotic cavity ; *m*, mouth ; *mes*, mesoderm ; *n*, nephridium ; *ra*, trunk
amniotic cavity ; *rp*, trunk-plate ; *s*, pharynx ; *se*, serosa ; *so*, somatic ; *sp*, splanch-
nic, layer of the mesoderm ; *w*, ciliated band. The ectoderm is finely and the ento-
derm coarsely punctate ; the mesoderm is cross-hatched.

finally fuse in the lateral lines; furthermore, a complete fusion takes place with the head-plate (Fig. 158 *E* and *F*). An ectodermal invagination at the posterior dorsal part of the larva produces the hind-gut, and fuses with the entoderm. The deep and voluminous fundament of the fore-gut now does the same. Two invaginations make their appearance on the œsophagus: an anterior, which is developed into a gland with a ciliated efferent duct, and a posterior, the fundament of the pharynx (Fig. 158 *F*, *dr*, and *s*). Stout cilia make their appearance in the circumference of the body behind the mouth-opening, and form the post-oral ciliated band (Fig. 158 *F*). The embryo is now ready to hatch. It has up to the present retained its spherical shape; but at the time of hatching it passes into the permanent shape of the larva, owing to the appearance of a constriction behind the ridge that bears the circle of cilia (Fig. 159); this marks off the broad anterior part of the body from the conical posterior portion. At the same time the entire body enlarges, and its cellular walls consequently become thinner. Hatching takes place by the pointed end of the larva breaking through the serosa and egg-membrane at the pole opposite the apical plate and the emergence of the embryo at this point (Fig. 158 *F*). The connection with the serosa, as far as it still exists, breaks, and the tuft of cilia of the apical plate is withdrawn through the pores of the egg-membrane, to be retained by the larva. The egg-membrane itself remains for a while on the larva like a helmet.

The larva of *Sipunculus* strongly resembles the *Trochophore*, but differs from it in the absence of the preoral ciliated band and the great reduction of the preoral part of the prostomium (Fig. 159). As a result of this, the apical plate comes to lie in the vicinity of the mouth, which is shifted well toward the anterior end of the larva. The usual three regions of the intestine can be recognized, though the hind-gut opens to the exterior on the dorsal side (Fig. 159); this, however, is frequently observed in Annelid larvæ. A head kidney has not as yet been observed. The internal organization is of a higher grade than is general in the *Trochophore*, and in part already corresponds to that of

the adult worm. This applies, for example, to the arrangement of the mesoderm, which is seen clothing the walls of the body and intestine as the somatic and splanchnic layers, though, according to HATSCHEK, the somatic layer also supplies the covering of the fore- and hind-guts, so that only the covering of the entodermal part of the intestine (the mid-gut) arises from the splanchnic layer. From the somatic layer arise also the four retractors of the anterior part of the body, which are developed even in the larva, and extend from the head region to the anus (Fig. 159 r). In conse-

quence of this arrangement, the anterior part of the larva can be invaginated into the posterior part. A circular muscle lying behind the ciliated band (Fig. 159 rm) serves to close the opening of the invagination in the larva, which in this retracted condition is almost spherical.

The paired nephridia, which in their structure correspond to those of the Annelida, are also produced from the somatic layer of the mesoderm. At quite an early stage of the embryo a mesoderm cell was distinguishable from the rest by its strikingly yellow colour. Some other cells were then added to it. The entire
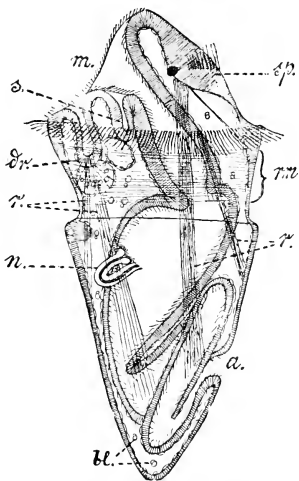
FIG. 159.—Larva of *Sipunculus nudus* (after HATSCHEK). *a*, anus ; *bl*, cells resembling blood corpuscles; *dr*, glandular appendage of the fore-gut ; *m*, mouth ; *n*, nephridium ; *r*, retractors ; *rm*, circular muscle; *s*, pharynx ; *sp*, apical plate.

structure assumed a looped form, and a lumen was excavated inside it (Figs. 158 *F*, 159 *n*). There are cells, likewise of mesodermic origin, resembling blood corpuscles, which were

detached from the peritoneal epithelium, and are found floating free in the body cavity.

The metamorphosis of the *Sipunculus* larva into the adult animal is first indicated in the considerable growth of the body and the reduction of the head portion. Connected with this is the complete displacement of the mouth to the anterior end and the further shoving forward of the anus, the latter being brought about by the more rapid growth of the extreme posterior portion of the body. The ciliated band gradually atrophies. It has nothing to do with the development of the tentacles, which take their origin as evaginations of the margins of the mouth. The brain arises from the lower layers of the apical plate, which has become several layers thick. The ventral nerve cord arises in the ventral middle line from an ectodermal thickening, which progresses from in front backwards. The œsophageal connectives grow from its anterior end towards the brain, therefore in a direction opposite to the growth of the ventral cord, and contrary to the method of outgrowth in the Annelida, where the apical plate grows out into the connectives.

Two additional pigment spots are added to the two which had already arisen in the larva in connection with the apical plate (Fig. 158 *F*). The provisional organs of the intestine— the glands and the so-called pharynx—atrophy; the intestine itself increases in length and is thrown into several loops (Fig. 159). On the dorsal side of the intestine there arises from its mesodermal covering a blood-vessel; but this does not take place until quite late. The longitudinal and circular muscle-layers of the dermo-muscular sac are differentiated much earlier. The nephridia are said to undergo a peculiar change, terminating internally in vesicular enlargements, while their external openings are retained.

The condition of the nephridia recalls the statements made by Schau-insland that in the Priapulidæ the nephridia are closed and, on the one hand, function with their blind ends as excretory organs, while, on the other hand, they are directly united with the germaria, and, in fact, according to Schauinsland's description, even arise from the latter. Thus even in closed nephridia their function as an efferent apparatus of the genital products would be explicable. It should be mentioned, however, that

the nephridia of the adult *Sipunculus* are described as opening towards
the body cavity, and that the sexual glands are explained as growths of
the peritoneal epithelium, the products of which are set free in the body
cavity, and from there pass into the funnels of the nephridia.

II.—The Development of Phascolosoma.

According to SELENKA's description, the development of
Phascolosoma elongatum is much simpler than that of *Sipun-
culus*. Following an unequal cleavage, there arises an
epibolic gastrula, which is said, however, to be converted into
a kind of *invagination gastrula* which soon ensue. Cilia, which,
gination of the macromeres, which soon ensue. Cilia, which,
as in *Sipunculus*, perforate the egg-membrane, make their
appearance early. They form a tuft at the apical pole and
a post-oral ciliated band; however, a preoral band is also
present, so that in *Phascolosoma* the resemblance to the
Trochophore is greater. The *blastopore* is said to be directly
converted into the mouth; the anus in this case, too, lies
on the dorsal side. The formation of an embryonal mem-
brane is not described by SELENKA; on the contrary, this in-
vestigator states that the egg-membrane
becomes the cuticula of the larva, as has
already been described for some Annelids.
The embryo (the larva) then simply elon-
gates, so that here a stage quite similar
to that in *Sipunculus* is reached, but in a
simpler manner.
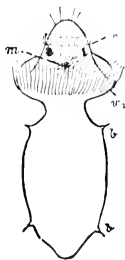
FIG. 160.—Larva of
*Phascolosoma elonga-
tum* (after SELENKA).
b, setæ; *m*, mouth;
v₁, preoral, *v₁*, post-
oral, ciliated bands.

The larva, which, as one of the last
stages, was observed by SELENKA, is elon-
gated (Fig. 160). The trunk, which is
much the more voluminous, is separated
from the small head portion by means of
a thick, collar-like ridge, which bears the
post-oral ciliated band. A large portion
of the head is occupied by the broad
preoral band of cilia, and at the anterior
end the ciliated tuft of the apical plate
projects. The head bears two eye-spots. The hooks which
constitute the armature of the adult animal make their ap-

pearance in front of the collar. Two pairs of rigid bristles (Fig. 160) arise on the trunk, each of which belongs to an ectodermal cell. A third pair is subsequently added to these. SELENKA is inclined to compare them to the setæ of the Annelida. The latter arise, it is true, as ectodermal structures, though not in so simple a way as here.

General Considerations.—With the limited knowledge that we possess of the development of the different genera of Sipunculidæ, it is difficult to pass judgment on the systematic position of this group. Until quite recently the *Sipunculidæ*, with the *Echiuridæ*, were usually united into the group of *Gephyrea*. The grounds which led to this association were rather of an external nature. A comparison of the anatomical and embryological data proves that the two groups exhibit no special resemblances. The so-called proboscis of the *Echiuridæ* corresponds to the elongated cephalic lobe of the larva; the mouth lies at its base, but in the Sipunculidæ at the tip of the *proboscis*. The cephalic lobe entirely degenerates even in the larva. (Comp. Fig. 159, p. 362, and Fig. 145, p. 309.) The differences in the structure of the nervous system, and especially the musculature, which separate the *Sipunculidæ* from the *Echiuridæ* and also from the *Annelida*, are striking. It seems very doubtful whether these differences can be maintained after a comprehensive knowledge of the development of the *Sipunculidæ*, and if so, to what extent. The chief point is whether or not the *Sipunculidæ* are to be derived from segmented forms, *i.e.*, whether they are related to the Annelida. In the Echiuridæ we saw that a segmentation was indicated in the larva, and through this and the remaining structural conditions of the larva we acquired an insight into their relationships to the Annelid stem. In *Sipunculus* such indications are lacking. To be sure, the mesoderm here also splits into two layers, progressing from in front backwards, and the differentiation of the nervous system, which, however, is aberrant in being produced from an unpaired fundament, takes place in the same direction; but no transitory segmentation is indicated, a head kidney is not present, the preoral ciliated band is lacking, and the

head portion sinks into complete insignificance (Fig. 159, p. 362). As regards the formation of the embryonal membrane, this might be a later acquisition, especially since it is said to be wanting in *Phascolosoma*. Moreover, SELENKA argues that the pairs of so-called setæ in the latter form might indicate a segmentation; but this evidence cannot be considered as conclusive.

Finally, it should be stated that the structure and development of the *Sipunculidæ* do not disprove relationships to the Annelida, but that as yet no justification exists for uniting them with these. We place them here next to the Annelida, because definite relationships to any other branch of the animal kingdom are not demonstrable and because in the shape of their larva they are most nearly related to the Annelida. A closer relationship to *Phoronis* and the *Molluscoidea* appears to us not yet sufficiently established.

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CHAPTER XII.

CHÆTOGNATHA.

THE Chætognatha occupy an altogether isolated position as regards their structure and mode of development. Though they most nearly resemble the Annelida in peculiarities of structure, they differ from this group in important embryological features. Among the most characteristic peculiarities of the development of the Chætognatha are to be mentioned the origin of the mesoderm by the formation of two archenteric diverticula and the early differentiation of the fundament of the sexual organs. Owing to the absence of peculiar larval forms, it is evident that the development of the Chætognatha is abbreviated. The developmental history of the Chætognatha has been made known chiefly by GEGENBAUR, KOWALEVSKY, BÜTSCHLI, and O. HERTWIG.

The eggs of the Chætognatha (Sagitta) after fertilization has taken place are discharged into the surrounding water.[1] They are spherical, transparent, and contain numerous clear yolk spherules. They are surrounded by a vitelline membrane and an outer gelatinous mantle. Cleavage must be considered as total and equal, and leads to the formation of a regular blastula, which is characterized by the tall prismatic form of its cells, which are grouped about a comparatively small cleavage cavity. One half of the embryo soon flattens and invaginates, whereby the cleavage cavity is reduced to a fissure. In this way a very regular invagination gastrula is formed (Fig. 161 *A*), the blastopore of

[1] [BOVERI states that the eggs at the time of ovipositing in passing through the narrow orifices assume an elongated form, but that they recover the rounded shape in the water. When the eggs are laid the first polar spindle is already formed, and every egg also contains a spermatozoön.—K.]

which soon narrows. At an early period two large cells, the *genital cells*, become noticeable at the bottom of the archenteric invagination, directly opposite to the blastopore. A plane passing between these two cells would correspond to the future plane of symmetry. In the course of further development the genital cells withdraw from epithelial continuity in the wall of the archenteron, passing into the archenteric cavity. Here they divide so that four genital cells lying in the transverse axis can be distinguished (Fig. 161 *B*). Of these the two middle ones represent the fundaments of the two testes, the two outer, on the other hand, those of the ovaries of the two sides. In the anterior widened portion of the archenteron the formation of two folds now takes place from in front backwards; these push the genital fundaments before them (Fig. 161 *B*), and by their development the archenteron is divided into three spaces lying side by side, the middle one of which represents the cavity of the mid-gut, the two lateral ones, on the other hand, those of the paired cœlomic sacs. [1]

While the embryo now increases in length, the blastopore closes and the permanent mouth-opening breaks through, the latter being accompanied by the development of the fore-gut, which probably arises as an ectodermal invagination (Fig. 161 *C*, *st*). The middle one of these three previously formed diverticula acquires in this way an opening anteriorly. In the view from the dorsal side (Fig. 162 *A*) the blastopore and permanent mouth appear to lie directly opposite each other, but side views show that the blastopore is moved a little, as it seems, towards the ventral side of the embryo, so that accordingly the permanent longitudinal axis occupies a position oblique to the chief axis of the gastrula.

With their further growth in length the two folds are pushed farther and farther backwards (Fig. 161 *C*). In this

[1] [According to JOURDAIN, the two evaginations of the archenteron do not produce the cœlom, but their cavities disappear, and at the same time between ectoderm and entoderm there is formed in the mesoderm a fissure, which becomes the permanent body cavity. This statement contradicts those of the authors mentioned above.—K.]

way the two primitive cells of the testes are also pushed backwards (Fig. 161 C), whereas the primitive cells of the
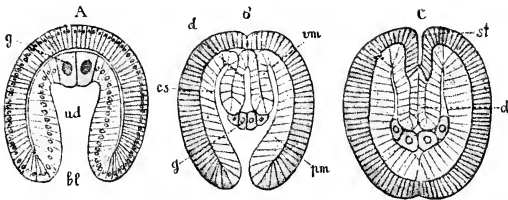
FIG. 161.—Three embryos of *Sagitta* at the stage of the formation of the germ-layers, in frontal section (after O. HERTWIG, from LANG'S *Lehrbuch*). *bl*, blasto-pore; *ud*, archenteron; *g*, primitive cells of the sexual organs; *vm*, visceral (-splanchnic), *pm*, parietal (somatic), layer of the mesoderm; *d*, fundament of the mid-gut; *cs*, cœlomic sacs; *st*, stomodæum (fore-gut).

ovaries lie at the sides of the folds and in this way are moved rather into the pair of cœlomic sacs, in accordance with their subsequent permanent position (Fig. 162). The embryo bends more and more towards the ventral side, during which a ventral ectodermal thickening becomes
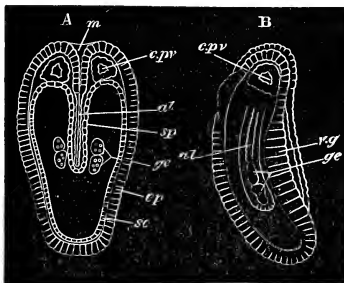
FIG. 162.—Dorsal and lateral views of an advanced embryo of *Sagitta* (after BÜTSCHLI, from BALFOUR'S *Comparative Embryology*). *m*, mouth; *al*, intestinal canal; *vg*, fundament of the ventral ganglion; *ep*, ectoderm; *c pv*, c· pl alic part of the body cavity; *so*, somatic, *sp*, splanchnic, layer of the mesoderm; *ge*, sexual organs.

noticeable as the fundament of the ventral ganglion (Fig. 162 B, *vg*).

Many obscure points still exist regarding the further development. In a species studied by Bütschli two portions of the cœlomic diverticula lying in the head cavities are constricted off at an early period (Fig. 162 c, *pv*); the walls of these are said to be employed chiefly in the formation of the musculature of the head. In the species studied by O. Hertwig, on the other hand, the formation of such paired head cavities could not be recognized, for here in the course of the further development the walls of the mid-gut and the cœlomic sacs are so closely applied to each other that these organs soon present only a slit-like lumen, which finally disappears entirely. A solid, laterally compressed ectodermal cord and two, likewise solid, lateral mesodermal masses, which contain within them the genital products, can now be distinguished. All three of the cords grow out backwards, not only in the region of the future trunk, but also in the tail region, so that the latter also has an entodermal fundament; it is, however, smaller than that of the trunk region. The rudimentary tail portion of the intestinal canal is subsequently employed in the formation of the sagittal septum separating the two caudal cavities from each other; here it atrophies without acquiring a lumen. It has not as yet been observed either in what manner the transverse septum between the trunk- and tail-cavities is formed, how the canal opening is developed, or even how the efferent sexual ducts are produced. Of interest is the great extension of the ventral ganglionic mass, which remains united with the skin throughout life (Fig. 162 B, *vg*, and Fig.

163 *bg*), extends in the young animal along the ventral side and the lateral parts of the entire trunk region, and does not become relatively more restricted until later. The *transversely striated* fibres of the four longitudinal muscle-bands are differentiated from the cells of the somatic layer of the lining of the cœlom after the type of epithelial musculature (Fig. 162 A, *so*). The fins arise as simple evaginations of the lateral parts of the ectoderm, whereas the cuticular skeleton found in them probably arises as a secretion of this ectodermal cell-layer at its base. In later stages of development the two cœlomic sacs move in the trunk region into close contact above and below the intestinal canal, so that a

Fig. 163. — Transverse section through the trunk of *Sagitta* (after O. Hertwig, from Lang's *Lehrbuch*). *lh*, body cavity; *mes*, mesentery of the intestine; *md*, mid-gut; *lm*, longitudinal musculature; *bg*, ventral ganglion.

dorsal and a ventral mesentery are formed by their contiguous walls (Fig. 163 *mes*). The young Sagitta upon hatching from the egg exhibits essentially the form of the adult animal.

General Considerations.—The problem as to the position of the Chætognatha in the zoölogical system is not brought any nearer to solution even by embryology, and for the time being can be treated only with the utmost reserve. The agreement which exists between the transverse section through *Sagitta* and that through *Polygordius* has already been pointed out by O. HERTWIG. As a matter of fact, a significant resemblance in the tectonic of the two groups is shown in the presence of paired entodermal sacs lined with epithelium, a dorsal and ventral intestinal mesentery, and the four longitudinal muscle-bands arranged in pinnate lamellæ, to which in some cases the indication of a transverse musculature is added. The chief difficulty in arriving at a safe conclusion regarding the position of the *Chætognatha* is our ignorance in regard to the excretory system. The sexual organs, particularly those of the male portion of the body, exhibit an important resemblance to the conditions in the *Annelida*, and if it is permissible to refer the efferent sexual ducts to metamorphosed nephridia, we should have to ascribe to *Sagitta* at least two trunk somites, and accordingly explain the Chætognatha as forms in which, perhaps in connection with the manner of locomotion, a primitive segmentation of the body has been retained in a degenerated form only.

Embryologically considered, the Chætognatha are distinguished from the Annelida by the absence of a Trochophore-like embryonal or larval stage, and, above all, by the characteristic folding off of the mesoderm. In order to harmonize this kind of mesoderm formation with the development of mesodermal bands in the Annelida, one would have to assume that [in the Chætognatha] the mesodermal elements increased considerably by proliferation as early as in the blastula and gastrula stages, so that in this way paired mesodermal bands arose, which at first remained lying at the surface of the walls of the archenteron, retaining an epithelial connection with the entoderm, and only later, by the formation of diverticula, became detached. By this assumption it is comprehensible how, even in closely related animals, two so apparently different kinds of mesoderm formation might be realized.

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CHAPTER XIII.

ENTEROPNEUSTA.

Under the name of *Enteropneusta* it is customary to place the isolated form *Balanoglossus* next to the *Echinodermata*, since it scarcely presents closer relationship to any other division. At the close of this chapter something further will be said on its probable position in the system. In order to make ourselves more easily understood concerning the developmental processes, it seems necessary to discuss first some morphological conditions.[1]

Anatomical.—*Balanoglossus* possesses an elongated vermiform body, on which different regions can be recognized externally. Anteriorly the so-called acorn [balanus], less appropriately called proboscis, is marked off from the rest of the body; upon this follows the muscular collar, and then the branchial region, which gradually merges into the posterior part of the body (Fig. 164). Acorn and collar are essentially a locomotor apparatus, and therefore are largely composed of muscle fibres, which can be distinguished as external circular and internal longitudinal muscles. The cavities inside both organs which are left between the longitudinal muscles and connective-tissue cells can be filled with water from the outside by means of one or two dorsal pores lying at the base of the acorn (Fig. 165 *p*). Similar pores also conduct water into the cavities in the collar (Spengel). These conditions have been compared to those of the water-vascular system of

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[1] [It should be mentioned here that since the publication of our description of the development of Balanoglossus the important works of Spengel (No. VI.) and Morgan (Nos. II., IV.) have appeared, necessitating some modifications in the account which we have given. The most important of these will be pointed out in what follows.—K.]

the Echinodermata, and it was indeed supposed that the
acorn represented a rudiment of this system, especially since
the cavity of the acorn in its earliest condition presents a
certain resemblance to the water-vascular system as it origi-
nates in the Echinodermata. It appears certain that the
acorn serves as an organ of locomotion. It was believed that
it took in water from the outside by means of the proboscis
pore, and that there-
fore it operated in the
same way as the am-
bulacral feet of the
Echinoderms (SPEN-
GEL). However, it has
been maintained, on
the other hand, that
particles of pigment
distributed in the water
are never found inside
the acorn, and that the
proboscis pore therefore
does not serve for the
reception, but only for
the elimination, of sub-
stances from the inside
(BATESON). This ob-
servation is of parti-
cular interest, inasmuch
as the acorn contains
a glandular structure,
which has been inter-
preted as an excretory
organ. The locomotion
of Balanoglossus is
effected by peristaltic
movements on the part
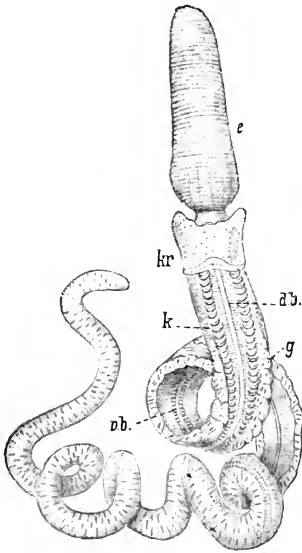
FIG. 164. — *Balanoglossus Kowalevskii* (after
A. AGASSIZ). *e*, acorn ; *kr*, collar; *k*, branchial
region ; *g*, genital region of the body ; *db*,
dorsal, *vb*, ventral, blood-vessel.

of the acorn, which thus pushes its way into the sand. The
collar follows it, also taking part in the same way in the pro-
gression of the animal. At the same time the sand enters
the mouth-opening, which lies at the base of the acorn,

gradually fills the entire intestine, and finally passes out
through the anus at the posterior end of the body as a
sausage-like cord.   Thus the animal eats its way, as it were,
through the sand.

The intestinal canal commences immediately under the
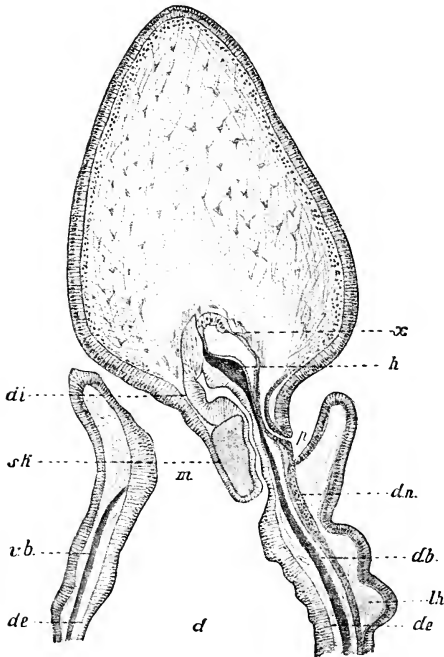
Fig. 165.—Sagittal section through the acorn and collar of *Balanoglossus
sarniensis* (made somewhat diagrammatic, after KÖHLER).   *d*, intestine ; *de*, intes-
tinal epithelium ; *db*, dorsal blood-vessel ; *di*, diverticulum of the intestine ; *dn*,
dorsal nerve ; *h*, the so-called heart ; *lh*, the body cavity ; *m*, mouth ; *p*, proboscis
pore ; *sk*, skeletal body ; *vb*, ventral blood-vessel ; *x*, the so-called proboscis gland.

acorn with the broad mouth-opening, which cannot be
closed (Fig. 165).   It extends backwards tolerably straight.

The appendicular structures which arise from the intestine,
and in part remain intimately united with it, are important
for the organization of the animal. The intestine produces
in its anterior part a dorsal evagination, which extends into
the base of the acorn (Fig. 165 *di*). Between the ventral
wall of this evagination and the epidermis of the acorn is
inserted the anterior part of the so-called proboscis- or acorn-
framework (Fig. 165 *sk*), a skeletal body, the unpaired part
of which has the position described, whereas two arms,
which project from it backwards and downwards, embrace
the fore-gut like a hoop. They lie in folds of the intestinal
wall; they could not be introduced into the figure. The
entire skeletal body, according to KÖHLER, BATESON, and
MORGAN, is a product of the intestinal epithelium, *i.e.*, the
above-mentioned evagination of it, [whereas SPENGEL (No.
VI.) interprets the acorn-skeleton as only a modification of
the bounding membrane (*Grenzmembran*), and also makes
the cœlomic sacs share in its formation. According to
SPENGEL, the histological structure of the acorn-skeleton in no
way agrees with that of the chorda dorsalis of vertebrates;
notwithstanding, this has been repeatedly emphasized by
different observers, and has been regarded as one of the
points for comparison between Enteropneusta and Vertebrata
(comp. *infra*).—K.]

The gills, which are most important for the whole inter-
pretation of the animal, occur somewhat further back on the
intestine, behind the collar region of the body. They
are paired, pouch-like outfoldings of the dorsal wall of
the intestine lying on both sides of the middle line (Fig. 166
k). Each of these pockets, which are lined with cilia, sends
upwards a short duct, which opens on the dorsal surface by
means of a pore (Fig. 166 *p*). Externally the rows of
branchial pockets can be recognized by the transverse arched
bands (Fig. 164 *k*). Behind, these transverse arches become
less extensive, which indicates that the formation of new
gills takes place even in the later stages of the animal's life.
A skeleton, formed of delicate chitinous hoops, which is
embedded in the walls of the branchial pouches, serves as a
protection for the gills. The water is taken in by the mouth,

passes from the fore-gut to the gill-pockets, and from there to the outside world by means of the dorsal pores.[1]

The intestine also presents paired dorsal evaginations in the parts which lie behind the gill region. These are the hepatic appendages. They also influence the shape of the body, inasmuch as they cause the skin to protrude (Fig. 164), and the musculature is only slightly developed at these places. The hindermost portion of the intestine lacks the appendicular structures, and extends straight to the anus.

One mesentery extending in the dorsal and another in the ventral line serve for the attachment of the intestine. By means of the mesenteries the body cavity is divided into a right and a left portion, but the two parts are confluent in many species, owing to the perforation of the dorsal mesentery. The body cavity of the collar is distinct from that of the trunk, and also differs from it in its mode of origin; moreover, it is for the most part reduced by being filled with connective tissue and musculature (Fig. 165). In the trunk, on the contrary, the greater part of the body cavity is said to persist, and its wall is composed of the longitudinal and circular musculature of the somatic

Fig. 166. — Transverse section through the branchial region of *Balanoglossus minutus* (after Spengel). *d*, intestine; *db*, dorsal blood-vessel; *dn*, dorsal nerve; *g*, genital organ; *k*, gill-pockets; *lh*, body cavity; *p*, pore of the gill-pockets; *so*, somatic, *sp*, splanchnic, layer of the mesoderm; *vb*, ventral blood-vessel; *vn*, ventral nerve.

and splanchnic layers (Spengel). However, according to other statements, even the trunk cavity is said to lose the

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[1] [A full account of the very complicated structure of the gills is given in Spengel's monograph (No. VI.), to which we particularly call attention in the matter of this and other anatomical conditions, and especially in view of the correction which it has since undergone.—K.]

nature of a true cœlom and to be filled with connective
tissue and muscles (KÖHLER).

The two chief vascular trunks of *Balanoglossus* (Figs. 165
and 166 *vb* and *db*) extend in the ventral and dorsal middle
lines between the wall of the intestine and that of the body.
The blood flows forward in the dorsal vessel, backward in
the ventral. They give off branches at regular intervals,
which extend to the body-wall, to the intestine, and to other
organs. According to KOWALEVSKY, there are also two
lateral trunks which receive vessels from the intestine and
from the gills. Their presence was confirmed by KÖHLER.
It still appears doubtful whether the saccular structure lying
at the base of the acorn and at least connected with the
vessels of the body, which was maintained by KÖHLER and
BATESON to be the central organ of the blood-vascular system,
is to be looked upon as a heart. In Fig. 165 it (*h*) is seen
lying on the dorsal side of the intestinal diverticulum. An
organ (*x*) lies above it the significance of which is still less
certain. It is a closed saccular body, the epithelial lining of
which is greatly thickened anteriorly (Fig. 165 *x*). Owing
to its intimate relation to the blood-vascular system, due to
its position, SPENGEL looked upon the anterior part of this
organ as an internal gill (acorn gill), whereas BATESON and
KÖHLER explain it as a gland (proboscis gland), which has
an excretory function. To be sure, a difficulty occurs with
this explanation, namely, the absence of the efferent duct ;
for it is not evident how the proboscis pore conveys away the
products of this "gland," which is a closed sac. Apart from
this, and in the absence of any other excretory organ, this
interpretation is nevertheless natural.

A thick cord, which lies in the dorsal mid-line of the collar,
is to be looked upon as the central organ of the nervous
system (Fig. 165 *dn*). It is said to possess a cavity which
would be comparable to the central canal of the spinal cord
of the Vertebrata (BATESON), but this is denied by SPENGEL.
According to both SPENGEL and KÖHLER, the cavity is
traversed by cords of cells, so that only irregular spaces
appear in it. KÖHLER further states that the following pecu-
liar condition exists : the internal space of the nerve cord

opens to the outside at its posterior end, the cells of its walls merging into the epithelial cells of the body-wall. Similar communications of the inner space are also said to exist at the anterior end (neuropore according to BATESON). A stout nerve, which extends along the entire dorsal mid-line of the body, is given off from the central organ. This in turn gives off two nerves just behind the collar, which extend downwards (ventrad), unite in the region of the first pair of gill-pockets, and extend backwards in the body as the ventral median nerve (Fig. 166 *vn*).

The genital organs of *Balanoglossus* either belong to the branchial region of the body or lie behind this. *Balanoglossus* is diœcious. Male and female organs are entirely alike as regards form and position. The genital glands lie in the form of simple or branched tubes on both sides of the body, and their external openings are found one behind the other, forming two rows on the dorsal surface (Fig. 166 *g*). In addition to these lateral rows of sexual organs (Fig. 164 *g*), two others (median) lying between the gill-pockets and the dorsal blood-vessel may make their appearance. In many species the part of the body succeeding the gill-pouches can also be called the genital region, for the sexual organs are especially well developed there. Owing to the fact that the parts which contain the sexual glands undergo a great flattening and lateral extension, wing-like extensions of the body are produced in certain species, *e.g. B. claviger* and *B. minutus*, studied by KOWALEVSKY.

Development without the Tornaria Larva.—The fertilization of the eggs takes place outside the body in the sea-water, into which in the American species studied by BATESON (*Balanoglossus Kowalevskii*) both kinds of sexual products are said to pass by the rupturing of the body-wall. Artificial fertilization could not be undertaken, though BATESON found the eggs in large quantities in the slimy sand inhabited by the adult animals. The eggs are closely enveloped by a delicate membrane, which separates from the egg when fertilization has taken place. Cleavage is total and tolerably equal. A blastula arises as

the result of it, which is at first spherical, but subsequently becomes flattened on one side. On this side an invagination then takes place, and the result is a typical invagination gastrula. Soon, however, the originally wide blastopore contracts to a short, narrow fissure. At the same time the external surface of the embryo becomes covered with short cilia, and a circle of stouter cilia makes its appearance in the vicinity of the blastopore. Subsequently the blastopore entirely closes. The two primary germ-layers remain united at this point, but only by a plug of cells; finally, they

separate entirely from each other, so that the embryo then consists of two separate cell-vesicles lying one within the other. At the same time the embryo elongates somewhat and then assumes a shape such as is represented in Fig. 168 A. At about this stage or even somewhat earlier, the embryo breaks through the egg-membrane and becomes a free larva, which does not, however, lead a pelagic existence, but lives on the bottom and is found in places where the water is not very deep.

Fig. 167.—Diagram of a longitudinal section through a larva of *Balanoglossus Kowalevskii* (after BATESON). c_I, anterior, c_{II}, middle, c_{III}, posterior, cœlomic sacs; d, intestine.

The internal structure of the larva is soon changed in such a way that an internal segmentation can be recognized. The elongated, completely closed archenteron bulges out at its anterior end, and forms a pair of diverticula, which are directed backwards (Fig. 167 c_I). These are constricted off from the archenteron in connection with each other, and lie in front of it as closed vesicles. In the same way two pairs of cœlomic sacs are formed further back as evaginations of

the archenteron (Fig. 167 c_{II} and c_{III}); these also become
detached, and are subsequently found next to the intestine
as flattened sacs. The mouth is formed at a somewhat later
stage on the ventral surface at the point where a transverse
furrow has made its appearance on the outside of the larva
(Fig. 168 A). The anus arises at the posterior end of the
larva near the place where the blastopore closed. Both
mouth and anus are formed by the fusion of the inner with
the outer germ-layer. During these processes the external
shape of the larva undergoes important changes. At first a
transverse furrow, which gradually deepens, and behind
which a second one
soon makes its appear-
ance, arises at about
the middle of the body
(Fig. 168 A and B).
While the first furrow,
even as early as this,
marks off the anterior
portion — namely, the
acorn—from the rest of
the body, the second
furrow, together with
the first, bounds the
future collar. Behind
this the gill region is
now also indicated by
the appearance of two
pores as evidence of
the first pair of gill-
pouches (Fig. 168 B

FIG. 168.—A to C, free-swimming larvæ of
Balanoglossus Kowalevskii in different stages of
development (after BATESON). e, acorn ["pro-
boscis"]; k, branchial openings; kr, collar.

and C, k). The part of the larva lying behind the ciliated
band gradually elongates (Fig. 168 C). Thus the principal
parts of the body of the adult animal are established in the
larva even at this stage.

Development by means of the Tornaria Larva.—

Not all species of *Balanoglossus*, however, develop from
the egg into the form of the adult animal in so simple a

manner as that described above, for some species pass
through a larval stage, the shape of which recalls the larvæ
of the Echinodermata. The larva called *Tornaria* was de-
scribed by JOH. MÜLLER as an Echinoderm larva. Its
shape, which, moreover, exhibits modifications in the different
species, is illustrated by Fig. 169. On the ventral side of
the bell-shaped larva lies the mouth-opening, from which
the œsophagus ascends, and then bends backwards, to be-
come continuous with the capacious stomach. Upon this
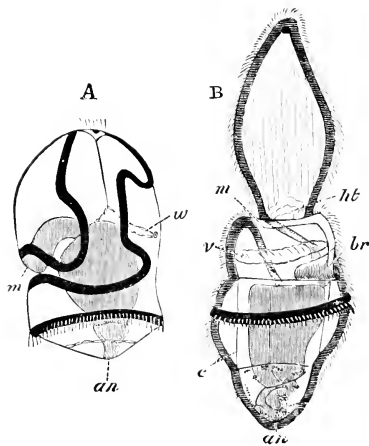
FIG. 169.—*A* an l *B*, *Tornaria* and later stage of development of *Balanoglossus*
(after KOWALEVSKY, from BALFOUR's *Comparative Embryology*). The broad black
lines indicate the ciliated band and the ring of cilia behind it. *an*, anus; *br*,
gill-pocket; *c*, body cavity; *ht*, "heart"; *m*, mouth; *w*, the so-called water-vas-
cular vesicle.

follows the hind-gut, which opens to the exterior through
the anus at the posterior end of the larva. The surface of
the larva becomes engirdled by ciliated bands, which, how-
ever, are distinguished from those of the Echinoderm larvæ
by their different parts acquiring a greater independence.
In the first place, we distinguish a preoral from a post-oral

ciliated band, both of which are provided with several
flexures (Fig. 169 A). They almost come in contact with
each other at the anterior end of the larva. At this point
is found an ectodermal thickening, comparable to the apical
plate of the Annelid larvæ, with two eye-spots lying over it.
From this region a contractile band extends backwards.
Mesenchymatous cells seem to arise between the intestine
and the body-wall. The posterior part of the larva is en-
circled by a ring of cilia which is independent of the other
ciliated band (Fig. 169 A), and in later stages of the larva
another one may also make its appearance behind this.

[The ciliated band of the anterior part of the body may undergo more
or less extensive outfoldings, by which the external form of the larva is
considerably modified. These outgrowths are sometimes large, such as
we shall find in the larvæ of Echinoderms, and these influence, as has
been said, the entire form of the body. Continual outgrowths of the
ciliated band of limited extent result in the formation of tentacle-like
structures.—K.]

  The condition of the larva described is only gradually
reached during its free pelagic life. At first the transverse
(posterior) rings of cilia are lacking, and the preoral and
post-oral ciliated bands have a more simple course. In the
further development of the *Tornaria* its anterior end elon-
gates and becomes the acorn of the *Balanoglossus.* Preoral
and post-oral ciliated bands then disappear, and instead of
these the entire body becomes covered with cilia (Fig.
169 B). The eye-spots are still retained for a while at the
tip of the anterior end. The middle region of the body is
encircled by the transverse ciliated band, and it can thus be
seen that the parts lying behind it have also elongated.
Two openings make their appearance externally on the
dorsal side of the anterior part of the body, the external
openings of the gill-pockets. With this nearly the same
stage is reached which we saw arising by direct means from
the larva described by BATESON. The simpler mode of de-
velopment is doubtless to be considered as the derived, and
that of the Tornaria as the more primitive, since the absence
of mouth and anus in a free-swimming larva does not
represent a primitive condition.

Further Developmental Processes of Both Types.

—Thus far we have chiefly considered the external shape of
the *Tornaria*. As regards the internal development, we find
confirmed the processes which, following BATESON, we have
already described. In the youngest stages of *Tornaria* yet
observed (Fig. 170), the archenteron, which in this case
never loses its connection with the ectoderm, develops an
unpaired evagination. This is said to be the fundament of
the so-called water-vascular vesicle, which, like the corre-
sponding organ of the Echinoderm larva, opens out by means
of a pore on the dorsal surface (Fig. 169 *A*). This in
particular has given rise to a comparison with the Echino-
derm larvæ. In addition to this diverticulum, two pairs of
evaginations arise farther back on the intestine (AGASSIZ).

They are the cœlomic sacs, which soon
become detached from the intestine,
and lie close to it on either side as
two pairs of flattened vesicles. They
soon become considerably enlarged,
and then their walls are applied to the
wall of the body and that of the in-
testine as the somatic and splanchnic
layers.[1] A mesentery is developed
dorsally and ventrally, separating the
sacs of the body cavity of the two
sides; but, according to SPENGEL, the
dorsal mesentery may afterwards de-
generate. The hindermost pair of
cœlomic sacs supplies the greater
part of the body cavity,—namely, that of the entire trunk,
—whereas the body cavity of the collar arises from the
anterior pair, and the cavity of the acorn is developed from
the so-called water-vascular vesicle (SPENGEL). The re-
semblance of the latter to the paired structures points to
the fact that they originally had the same significance, and
the appearance of two acorn pores in *Balanoglossus Kupfferi*

FIG. 170.—Early stage of
a *Tornaria* (after GOETTE,
from BALFOUR'S *Compara-
tive Embryology*). *m*, mouth;
an, anus; *W*, so-called
water-vascular vesicle.

[1] As is to be seen in Fig. 172 (p. 387), entirely similar conditions
appear also in *Balanoglossus Kowalevskii*, which does not develop by
means of a Tornaria.

seems to indicate the paired origin of even this anterior
cœlomic sac. The acorn pore arises from the dorsal pore
of the *Tornaria*. In the *Balanoglossus* which does not pass
through the *Tornaria* stage, the anterior cœlomic sac, as
BATESON unreservedly calls it, forms a pointed process, the
end of which fuses with the ectoderm and breaks through
to the exterior.

After the cœlomic sacs have separated from the archen-
teron, the remaining entoderm produces, in the form of a
forward evagination, the intestinal diverticulum, which lies
at the base of the acorn (comp. Fig. 165 *di*), and from
this the formation of the acorn stalk probably takes place.
Even earlier than this, the gill-pockets develop as paired
evaginations from a portion of the intestine behind the
diverticulum. They are directed toward the dorsal surface
(Fig. 169 *B*), with which they soon unite, since they open to
the exterior by means of pores which are at first rather large
(Fig. 168 *C*). In several forms at first only one pair of gill-
pockets is to be observed (Figs. 168 *C* and 169 *B*); in the
Tornaria studied by AGASSIZ, on the contrary, four pairs of
them make their appearance simultaneously (Fig. 171).
The form of the gill-pockets, which is at first so simple,
is later much more complicated, for their walls become
folded, and the skeletal hoops are developed between them.
The formation of new gill-pockets continues to take place
even when the *Balanoglossus* has long since assumed its
permanent shape. After the posterior part of the body has
considerably increased in length, the paired evaginations of
the intestine which have been interpreted as hepatic append-
ages arise behind the gill region.

In the *Tornaria* there is found next to the so-called water-vascular
vesicle, or even sunk into a depression in it, a spherical vesicle, which
ordinarily is called the heart of the *Tornaria* (Figs. 169 *B* and 171
ht [not *h*, Fig. 165]). It does not merit this name, for, according to
SPENGEL, it is developed into the organ which BATESON and KÖHLER have
called the saccular posterior portion of the "proboscis gland" (comp.
Fig. 165). In *Balanoglossus Kowalevskii* the proboscis gland arises by
delamination from the tissues of the anterior cœlomic sac after this has
already spread out inside the acorn. This mode of origin seems to us

to indicate that even the so-called heart of the *Tornaria* might arise from the water-vascular vesicle or, what is the same thing, from the anterior cœlomic sac.[1] The early appearance of the organ in the *Tornaria* is favorable to the explanation (excretory) which has been given to the fully developed organ. In other divisions of the animal kingdom also we see the excretory system established at a very early period.

Likewise the organ which is interpreted as the real heart first appears, according to BATESON, as a fissure in the mesodermal tissue. This fissure makes its appearance between the fundament of the "proboscis gland" and the intestinal diverticulum, and is only gradually surrounded by a firm wall. It has not been determined whether or not it is from the beginning connected with the blood-vessels of the body. The blood-vessels probably arise from the mesoderm in the same way as the supposed central organ.

FIG. 171.—Stage of development of *Balanoglossus* (after AGASSIZ, from BALFOUR's *Comparative Embryology*). *an*, anus; *br*, gillpockets; *ht*, "heart"; *m*, mouth; *W*, the so-called water-vascular vesicle.

[The observations of authors are not in agreement respecting the origin of the cœlomic sacs, for SPENGEL (No. VI., Appendix to *Literature* on Enteropneusta) and BOURNE (No. I., Appendix) maintain that they arise from the hind-gut, whereas MORGAN (Nos. III., IV.) refers them to the entoderm, as was formerly done. MORGAN, moreover, assumes a different method of origin in the different species of Balanoglossus, for in one case (Tornaria from the Bahamas) he even refers them to scattered mesenchyma cells of the primary body cavity.

Also the origin of the so-called heart-sac is not yet sufficiently clear. MORGAN would refer it likewise to an accumulation of mesenchyma cells, whereas SPENGEL adheres to his former account of the ectodermal origin of this organ. Moreover, it seems to be impossible to reconcile the new results with the earlier account, and for this reason we must refer to the original articles.—K.]

The earliest fundaments of the genital organs occur as pyriform sacs, and are found in close connection with the ectoderm, a fact

[1] SPENGEL, however, affirms that the "heart" is formed as a thickening of the epidermis next the acorn pore; but perhaps this statement can be harmonized with the opinion expressed above by assuming that in this case the development of the so-called heart took place later, that is to say, when the lining of the internal cavity of the acorn by means of the water-vascular vesicle had already been accomplished. This, however, is only conjecture.

which caused BATESON to believe them derived from it, and not from the mesoderm, as would seem more natural, especially since at this time the mesodermal tissue is already found closely applied to the ectoderm. However, BATESON states that the origin of the genital organs is as yet not certainly determined.

[SPENGEL found the union of the nascent gonads with the ectoderm less intimate, and was inclined to refer their production to the mesenchyma of the body cavity. The connection with the ectoderm is only secondary. According to MORGAN, they arise as proliferations of the wall of the cœlomic sacs of the trunk, which at first have no connection with the ectoderm.—K.]

The central part of the nervous system arises, according to BATESON, as follows :—A part of the cells of the deepest layer of the ectoderm in the median line of the collar is
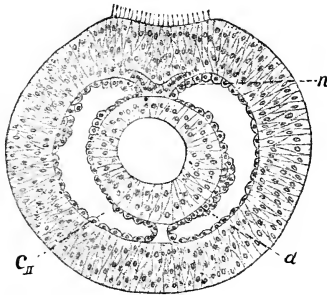
FIG. 172.—Transverse section through the anterior part of the collar of a larva of *Balanoglossus Kowalevskii* which is at about the stage of Fig. 168 *B* (p. 381) (after BATESON). Above is seen the dorsal ciliated groove. *d*, intestine; *n*, fundament of the nerve cord ; c_{II}, cavity of the middle cœlomic sac, which is already applied to the wall of the body and that of the intestine as somatic and splanchnic layers.

differentiated in a peculiar way, and is finally detached from the ectoderm along the entire length of the collar (Fig. 172 *n*). This process, moreover, is said to be accompanied by a superficial depression of the ectoderm, which is noticeable as a dorsal, longitudinal ciliated groove on the recently developed collar of the young larva (Fig. 172, after BATESON). SPENGEL also speaks of the development of the nervous system as the result of a dorsal invagination in the middle

line of the collar. The cavities, however, which occur in
the central nervous system of the adult animal, are not to
be referred to a formation comparable with the neural tube
of the Vertebrata, but arise in the cell-layer which was split
off from the ectoderm, in all probability by the appearance
of fissures. However, at the end of the central cord, where
it merges into the indifferent cells of the ectoderm and
where the latter is considerably thinner, a kind of folding
process seems to take place; at this point also the lumen of
the central cord is said to communicate with the outside
world (*neuropore*?). There seems to be no relation between
the dorsal groove and the blastopore; for the groove does
not extend so far back. A direct connection with the
conditions occurring in the Chordonia is therefore not in-
dicated by this (comp. *infra*).[1] Like the chief, central parts
of the nervous system, its peripheral portions are also
differentiated from the lower cell-layers of the ectoderm,
which, according to BATESON, everywhere exhibits large
accumulations of sensory cells.

General Considerations. — The external resemblance
of the *Tornaria* to the Echinoderm larvæ and the oc-
currence of the water-vascular vesicle, opening out by
means of a dorsal pore, have caused Balanoglossus to be
brought into relation with the Echinodermata. Corre-
spondingly, the acorn, the lining of which is supplied by
the so-called water-vascular vesicle, has been explained as
the last remnant of the water-vascular system, as the single
remaining ambulacral tentacle. The nature of the skin,
provided with calcareous structures, is, in addition to the
water-vascular system, characteristic of the Echinodermata.
The entire absence of calcareous bodies in Balanoglossus
and the different condition of the skin, together with
the other peculiarities in the entire structure of the body,

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[1] [According to SPENGEL's description, it must be assumed that the
account given by the previous observers does not at all relate to the first
fundament of the nervous system, and that in its formation, which takes
place at an early period, there is no invagination. Differentiations of
the ectoderm without any invagination give rise to the nervous system,
which only subsequently sinks in deeper.— K.]

do not allow us to put any great weight on such an in-
terpretation of the acorn. A comparison of the Tornaria
with the Echinoderm larva is difficult to carry out, for the
ciliated bands so characteristic of the latter present here
quite a different distribution. Moreover, the *Tornaria* ap-
pears to possess a kind of apical plate, which is absent in
the Echinoderm larvæ. The latter likewise exhibit no
eye-spots. The resemblance between the *Tornaria* and the
Echinoderm larvæ is therefore of a rather superficial nature.
The possession of an apical plate and the cords radiating
from it point rather to relationships of the *Tornaria* with
the *Trochophore*.

The occurrence in Balanoglossus of paired cœlomic sacs,
lying one behind the other, indicates a segmentation. In
this, it is true, a resemblance to the *Echinodermata* would
exist, if the statement should be confirmed that in the
latter also several pairs of cœlomic sacs are developed
(comp. p. 414). This internal segmentation of the larva
subsequently disappears, and the segmentation which can
be recognized on the adult *Balanoglossus* has nothing to
do with it.

In searching through the animal kingdom after relationships for
Balanoglossus, characterized as it pre-eminently is by the possession
of gills, a comparison with the Chordata has been reached ; but there is
as yet no adequate basis for this comparison. It is *Amphioxus* which
has been especially in mind, and the comparison has been based chiefly
on the gills, on the intestinal diverticulum, called by authors the
chorda, and its skeletal body, and on the formation of the nervous
system. A striking resemblance is noticeable between the anterior
cœlomic sacs of *Balanoglossus* and the most anterior archenteric diver-
ticula of *Amphioxus*, which also make their appearance very early, and
one of which greatly enlarges and opens to the exterior by means of
a ciliated canal, like the so-called water-vascular vesicle or the anterior
cœlomic sac in *Balanoglossus*.

[To what precedes we append the following : The supposed relations
between *Enteropneusta* and *Chordata* have become, according to recent
observations at least, very doubtful. The diverticulum of the intestine
in the acorn, or rather the acorn skeleton, is, as it appears, comparable
with the chorda neither in regard to its origin nor structure. The needed
agreement in the formation of the nervous system seems, in fact, to be
wanting. The gills of Balanoglossus, it is true, are strikingly similar

in structure to those of Amphioxus; but a detailed comparison reveals in them organs of different phylogenetic origin (SPENGEL). The cœlom of the Enteropneusta exhibits other conditions than in the Chordata. The probability of the relationship of *Balanoglossus* to the *Echinoderms*, on the contrary, has, it may be said, been increased by recent investigations. A comparison of Tornaria with the larvæ of Echinoderms, so far as regards the external form, and particularly the structure, is perhaps still possible. The apical plate present in Tornaria is, according to recent observations, also found in the larvæ of Echinoderms—*e.g.*, in Antedon—although in a greatly reduced condition. The cœlom seems to be segmented in the Echinoderms as well as in the Enteropneusta—a fact which is certainly of importance. However, it is precisely the interpretation of the cœlom in Balanoglossus which is not yet adequate, since the different portions of the intestine, from which it takes its origin, are not fully understood. Unfortunately it must be admitted that even yet the relationships of Balanoglossus are shrouded in darkness.—K.]

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CHAPTER XIV.

ECHINODERMATA.[1]

DEVELOPMENT in the five divisions of the Echinodermata offers so much in common that we shall treat of these together as far as possible. In the development of the Echinodermata we distinguish the following four periods:—

1. *The formation of the primary germ-layers and the mesenchyma, together with the establishment of mouth and anus.*

2. *The origin of the enterocœle and hydrocœle.*

3. *The formation of the typical larval form.*

4. *The metamorphosis of the larva into the Echinoderm.*

I. THE FORMATION OF THE PRIMARY GERM-LAYERS AND THE MESENCHYMA, TOGETHER WITH THE ESTABLISHMENT OF MOUTH AND ANUS.

As far as is known, the cleavage of the Echinoderm egg is always total. In the Holothurioidea (Synapta), moreover, it is strictly equal; whereas in the star-fishes and sea-urchins it takes place less regularly. Within the mass of cells which has arisen by cleavage there is found even during this period a cavity which, in ,the further course of cleavage, continues to enlarge, and becomes an extensive blastocœle. The result of cleavage is always a *cœlo-blastula*. The next stage of development, too, exhibits an essential agreement in the different groups of Echinoderms, for in all of them it consists of an *invagination gastrula*. In the details, however, certain deviations from the common plan of development occur in the different forms.

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[1] The maturation and fertilization of the Echinoderm egg will be discussed in the general part.

Holothurioidea.—The earliest stages of development are the simplest in the Holothurioidea. We follow SELENKA's account (No. 54) of the development of *Synapta digitata*.

Cleavage is entirely regular. By means of the first division the egg is halved. Since the newly formed blastomeres always divide into equal parts, this process being repeated nine times consecutively, there finally arises a stage the prismatic cells of which are approximately equal in size, and arranged in the form of a hollow sphere. They have already acquired cilia, although the *blastula* is still enclosed by the vitelline membrane. (A similar stage in *Holothuria* is shown in Fig. 180 *A*.) At this stage the
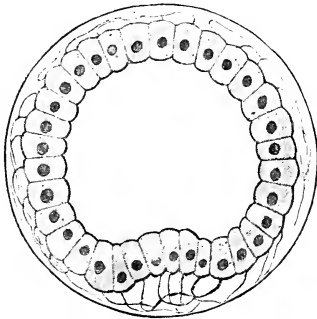
FIG. 173.—Blastosphere of *Synapta digitata* at the beginning of gastrulation, still lying within the egg-membrane (after SELENKA).

further division of the blastomeres is suspended for a considerable time, only subsequently to proceed slowly at the vegetative pole, and at first at this pole alone. Gastrulation is initiated by means of this cell-proliferation realized at the vegetative pole (Fig. 173). The result is a regular gastrula with a small archenteron (Fig. 174). In this stage the embryo becomes a free-swarming larva, which moves about by the aid of its long cilia. The gastrula very soon undergoes a change, for the archenteron bends towards the wall of the gastrula, and unites with the ectoderm

(Fig. 175). This region corresponds to the dorsal surface
of the larva. After the fusion of ectoderm and entoderm,
the lumen of the archenteron communicates with the
outer world, thus establishing the so-called dorsal pore
(Fig. 176). JOHANNES MÜLLER, who, even in his time, was
acquainted with this process, considered the dorsal pore to
be the mouth of the larva; but that is not its fate, for the
archenteron soon separates into two portions, of which the
one connected with the dorsal pore constitutes the funda-
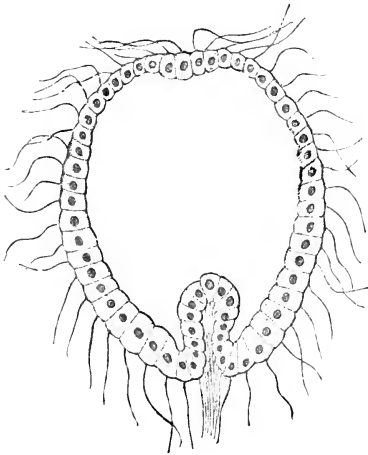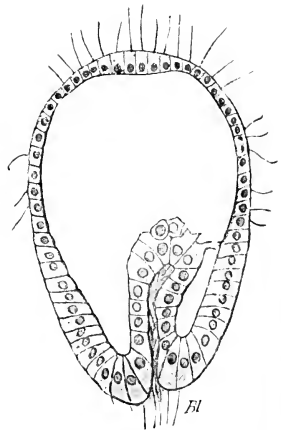
FIG. 174.   FIG. 175.

FIGS. 174 and 175.—Gastrula stages of *Synapta digitata* (after SELENKA). In Fig. 175
the mesenchyma begins to develop. *Bl*, blastopore.

ment of the water-vascular system and body cavity, while
the other becomes the intestine. With the multiplication
of its cells the latter acquires a knee-like bend (Fig. 177),
and, while increasing in length, turns toward the ventral
side. Even before it reaches this, the communication be-
tween the upper and lower portions of the archenteron is
interrupted (Figs. 177 and 178). Of these two portions

only the lower interests us for the present. Its blind end
enlarges a little, and comes into contact with the ventral
wall of the larva (Fig. 178). The corresponding part
of the wall sinks in, forming a cup-like depression (Fig.
179), the intestine fuses with it, and an opening leading
into the intestine now breaks through at this point: the
mouth-opening of the larva. The mouth-opening is there-
fore a new formation. The intestine opens to the outside
at the posterior end by means of the blastopore; the
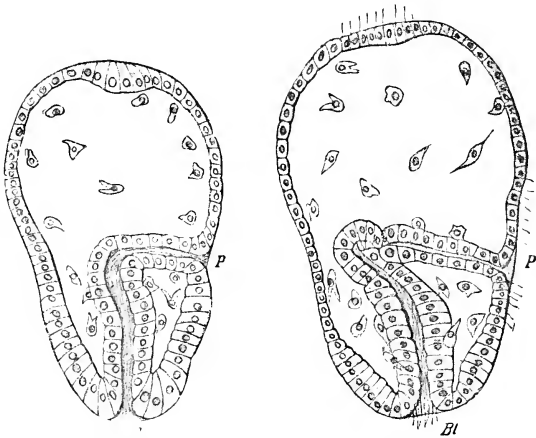
FIG. 176.   FIG. 177.

FIGS. 176 and 177.—Larvæ of *Synapta digitata*, showing the formation of the dor-
sal pore (*P*) and the vaso-peritoneal vesicle (after SELENKA). *Bl*, blastopore.

gastrula mouth consequently has become the anus of the
larva.

With these changes the larva has also undergone a certain
differentiation in external shape. Its bilateral symmetry is
already expressed. The mouth and anus mark definite
regions of the body. The former lies on the ventral surface,
the latter at the posterior end of the larva. Moreover, as we
will mention in anticipation of the sequel, the ventral surface

is ordinarily flattened somewhat, whereas the dorsal side is
more convex.

Before concluding the consideration of the first develop-
mental processes of *Synapta*, we must refer to a process
which takes place before the change in position of the arch-
enteron already described; this is the formation of the *mesen-
chyma*. At the time when the blind end of the archenteron
begins to bend toward the dorsal surface, there appear at its
apex two cells which project out beyond the other cells (Fig.
175), and are called by SELENKA the two primitive cells of the
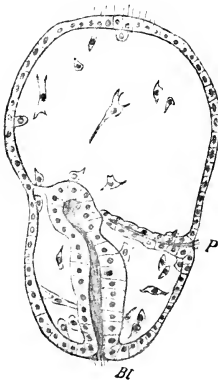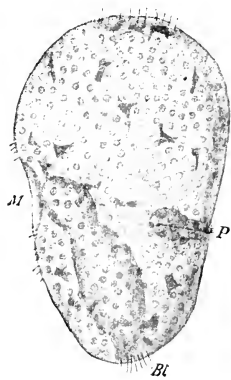
<div align="center">FIG. 178.   FIG. 179.</div>

FIGS. 178 and 179.—Larvæ of *Synapta digitata*, showing the formation of the
intestine and vaso-peritoneal vesicle (after SELENKA). *Bl*, blastopore; *M*, mouth;
P, dorsal pore.

mesenchyma. These cells then separate from their connec-
tion with the archenteron, migrate into the blastocœle, and
apply themselves to the ectoderm, but not at predetermined
points. Subsequently a large number of such mesenchyma-
tous or migratory cells are found in the blastocœle (Figs.
176 to 179). According to SELENKA's description, they arise by
the division of the two primitive mesenchyma cells; but
the process of mesenchyma formation in other Holothurioidea

shows that it is not two primitive mesenchyma cells that give rise to the entire mesenchyma, but that a large number of cells separate from their connection with the others and migrate into the blastocœle, where they subsequently increase in numbers (Fig. 180 *B*). In *Cucumaria doliolum* and *Holothuria tubulosa* the formation of the mesenchyma precedes gastrulation, or takes place at the same time with it (Fig. 180 *B*). The previously somewhat thickened place of the blastula indicates the region from which the migratory cells detach themselves. From four to ten cells enter the blastocœle, where they remain until they are forced farther
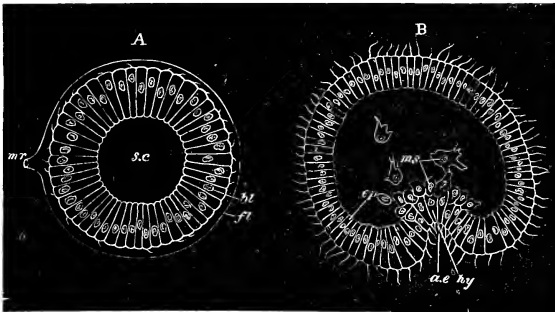
Fig. 180.—*A*, blastula stage still within the egg-membrane, and *B*, larva of *Holothuria tubulosa* at the stage when gastrulation and the formation of the mesenchyma begin (after SELENKA, from BALFOUR's *Comparative Embryology*). *ae*, archenteric cavity; *bl*, blastula; *ep*, ectoderm; *fl*, egg-membrane; *hy*, entoderm; *mr*, micropyle; *ms*, mesenchymatous cells; *sc*, cleavage cavity.

inwards by the first steps of invagination. The process is, on the whole, the same as in *Synapta*. The formation of the mesenchyma takes place on the same part of the larva, only it occurs a little earlier. We shall see that in the sea-urchins the mesenchyma takes its origin still earlier, even in the blastula stage.

The migratory cells, according to the observations of some authors, move about in the blastocœle with great facility, so that it appears as if the space between ectoderm and entoderm were filled with fluid. This

view is advocated, for example, by LUDWIG (No. 35), whereas other inves-
tigators (HENSEN, SELENKA) ascribe a gelatinous consistency to the con-
tents of the cleavage cavity.

Echinoidea.—According to the recent investigations of
SELENKA on *Strongylocentrotus lividus, Sphærechinus granu-
laris,* and *Echinus microtuberculatus,* and of FLEISCHMANN on
Echinocardium cordatum, cleavage does not take place so
regularly in the sea-urchins as in the Holothurians. During
the first four cleavage phases only do the furrows extend to
all the blastomeres ; then for a time some of the elements of
the circles of cells now present take no part in the further
cleavage, so that they soon greatly surpass in size the blasto-
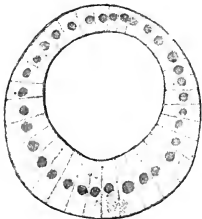
FIG. 181.

FIG. 182.

FIG. 181.—Blastula stage of
Strongylocentrotus lividus (after
SELENKA). The ciliation of the
larva is omitted in this and most
of the following figures.
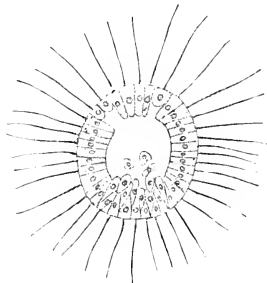
FIG. 182.—Blastula stage of *Strongylo-
centrotus lividus* showing the migration
of mesenchyma cells (after KORSCHELT).
The flagella are represented too stout.

meres at the opposite pole of the egg. Since, however, the
difference in the size of the blastomeres disappears as cleav-
age progresses, a regular *blastula,* consisting of a layer of
rather tall cells of nearly equal size, results from cleavage
even in the Echinoidea (Fig. 181).

In the Echinoidea the formation of the mesenchyma regu-
larly precedes gastrulation. At the end of cleavage there
occur in the *blastula* a flattening of the cells at the animal
pole and, on the other hand, a thickening of those at the

vegetative pole (Fig. 181). The cleavage cavity is diminished in size as a result of the considerable elongation of the cells at the vegetative pole, and the embryo becomes slightly oval in shape. A long flagellum makes its appearance on each of the cells of the blastoderm; the embryo begins to rotate within the vitelline membrane, and finally breaks through the latter to swarm out as a larva. At the same time a more active multiplication of the cells begins at the thickened part of the blastula, as the result of which some of them soon become forced into the cleavage cavity (Fig. 182), where, like Amœbæ, they creep about as migratory cells. These are followed by others; after multiplying rapidly in the blasto-cœle, they almost fill it.
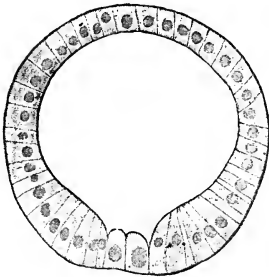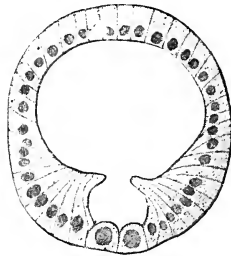
FIG. 183.   FIG. 184.

FIGS. 183 and 184.—Blastula stages showing the commencement of formation of mesenchyma (primitive mesenchyma cells) (after SELENKA and HATSCHEK). The flagella are omitted here, as also in Fig. 185.

We have described the formation of the mesenchyma as it appeared to us from personal observations (No. 26). However, other statements have been made on this point. According to the observations of SELENKA and HATSCHEK (No. 54), there arises some time after the swarming out of the larva a funnel-like depression (Figs. 183 and 184) at the vegetative pole, which owes its production to the shortening and thickening of two cells lying at that pole of the blastula. These two cells were looked upon by the observers last named as the *primitive cells of the mesenchyma*; to this interpretation FLEISCHMANN also adheres. According to him, there are present at the vegetative pole four such primitive mesenchyma cells, which have been differentiated there during cleavage. The primitive mesenchyma cells are said to correspond to the primitive cells of the

mesoderm, which constitute in the Annelida, as well as in some other forms, the starting-point for the formation of the mesoderm (comp. pp. 264 and 282).

Two groups of cells arise by the multiplication of the primitive mesenchyma cells, either by their being forced into the blastula by the pressure of the surrounding cells (Fig. 185, after SELENKA), or by new cells being constricted off from them (FLEISCHMANN). Out of these groups there are said finally to arise two bilaterally symmetrical cell-bands, which correspond to the mesodermal bands of the Annelida. As a result of these processes, the larva would show at a very early stage bilateral symmetry, which becomes intensified by the flattening which takes place from the dorsal to the ventral side.

This conception of the origin of the mesenchyma from the two primitive mesenchyma cells was generalized by SELENKA, for he also found the two primitive cells in other Echinoderms (Holothurioidea and Ophiuroidea). Thus in Synapta there are the two cells lying at the summit of the archenteron (Fig. 175), and also in Ophioglypha two cells which detach themselves from the cells of the blastula. This kind of mesenchyma development is not by any means so typical as it is said by SELENKA and HATSCHEK to be in the Echinoidea, and recalls much more the formation at pleasure of mesenchyma cells which, like the succeeding ones, separate from the cell-wall of the blastula or gastrula, as is known to take place in the

FIG. 185.— Blastula stage of *Strongylocentrotus lividus*, with mesenchyma cells which have migrated into the blastocœle (after SELENKA)

Asteroidea and *Crinoidea* (comp. pp. 402 and 403). METSCHNIKOFF has accordingly opposed the theory of mesenchyma formation espoused by SELENKA and HATSCHEK, and, on the whole, we agree with his conclusions.

The appearances which led HATSCHEK and SELENKA to believe in the existence of primitive mesenchyma cells are to be explained by the fact that the cells of the blastula at the time of dividing are shortened, and become stouter. Thus it happens that directly after the division of such a shortened cell two small cells, surrounded by tall, prismatic cells, come to lie side by side, and thus such stages arise as those of HATSCHEK and SELENKA (Figs. 183 and 184). Such shortened cells occur in various parts of the circumference of the blastula, when the development of the

mesenchyma at the thickened pole is already under way (Fig. 182). It can be observed in the living blastula that the shortened cells elongate, and soon attain the length of the surrounding cells. The mesenchyma, then, does not take its origin from primitive mesenchyma cells, but by the proliferation of a large number of cells. Moreover, the migratory cells which have entered the blastocœle do not form mesenchyma bands, but are irregularly scattered.

Gastrulation in the Echinoidea takes place after the detachment of the mesenchyma cells, in the ordinary manner (Selenka, No. 53). The archenteron grows out in half a day to a comparatively long sac-like tube. Between it and the ectoderm there are frequently stretched some of the mesen-
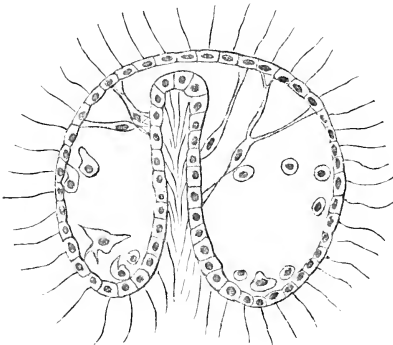
Fig. 186.—Gastrula stage of *Toxopneustes brevispinosus* (after Selenka). The mesenchyma cells stretch across suspensor-like between the ectoderm and archenteron.

chyma cells, which probably serve as suspensors for the archenteron (Fig. 186). The larval mouth in the Echinoidea is formed in a direct manner, for the end of the archenteron (after the abstriction of the entero-hydrocœle) bends toward the ventral surface and fuses with the ectoderm, whereupon the mouth-opening breaks through. The gastrula mouth here too becomes the anus.

Asteroidea.—Cleavage, although unequal, differs only a little from the equal type. The difference in the size of the

blastomeres becomes imperceptible even in the sixteen-cell
stage, and from that onwards. LUDWIG, in his description of
the development of *Asterina gibbosa*, lays particular stress on
the fact that from the very beginning a cavity exists between
the cleavage spheres, and consequently the blastosphere is
formed at a very early period. The result of cleavage in
the star-fishes is also a *blastula*, which is formed of a layer
of equal-sized cells. The *gastrula* arises from this by invagi-
nation.

The formation of the mesenchyma takes place, according
to the observations of METSCHNIKOFF on *Astropecten*, after
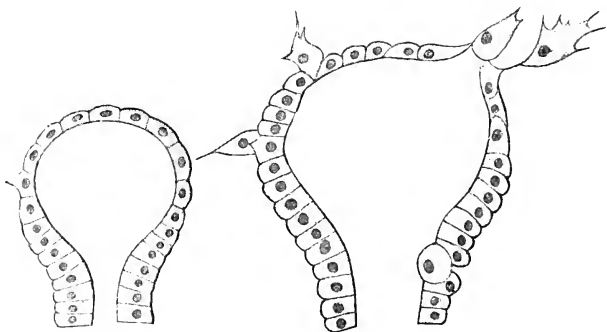
FIG. 187.   FIG. 188.

FIGS. 187 and 188.—Blind end of the archenteron of gastrula stages of *Astropecten
pentacanthus* during the formation of the mesenchyma (after METSCHNIKOFF).

gastrulation is completed. The originally cylindrical cells of
the archenteron at its blind end become flattened out (Fig.
187); then they begin to put forth short pseudopodial pro-
cesses, and finally some of them detach themselves from the
rest. Others, usually four or five at a time, soon follow
these (Fig. 188). It is said that the migration of entoderm
cells may be so active that a more or less considerable open-
ing arises at the upper end of the archenteron.

It is seen that the conditions described by METSCHNIKOFF resemble
those of which we have learned through SELENKA as existing in the

Holothurians. There also the mesenchyma cells separate from the apex of the archenteron. To be sure, according to SELENKA, only two cells—namely, the primitive mesenchyma cells—arise in this way. METSCHNIKOFF declares that his search for such a stage with two cells has always been in vain. His observations allow him to reject even in the case of the Holothurians the idea of the origin of the mesenchyma from two primitive cells, and to assume instead a continuous emigration of cells from the entoderm, especially since certain observations of SELENKA seem to him to corroborate his own view. For SELENKA found larvæ in which the free end of the archenteron was irregularly outlined or covered with stellate cells. SELENKA explains this phenomenon as being pathological, whereas METSCHNIKOFF considers it warrantable to look upon such larvæ as individuals in which an emigration of numerous entoderm cells is now taking place.

The mouth-opening and the stomodæum in *Asterina* arise in the form of a hollow plug, which is invaginated at the front end of the ventral side of the embryo, and fuses with the entoderm at that point (LUDWIG). At this stage of development the embryo abandons the egg-membrane, and, as an approximately pyriform larva, swims about free in the water by means of cilia, which cover its entire external surface.

Ophiuroidea.

—Cleavage appears to take place in the same way as in the *Asteroidea* (LUDWIG, SELENKA). The blastula, which also exists here, exhibits a thickening at its vegetative pole. The mesenchyma is formed within it in the same way as in the *Echinoidea*; according to SELENKA, it originates from the two primitive cells, but according to METSCHNIKOFF from a continuous emigration of cells from the thickened wall.

Not much weight should be given to the view, advocated by FEWKES, that there is a bilaterally symmetrical arrangement of the mesenchyma in *Ophiopholis*, especially since the author himself did not find the mesenchyma bands in the sea-urchin (*Echinarachinus parma*) studied by him (No. 13).

Crinoidea.

—Nothing is known of the earliest developmental processes of the Crinoidea, except the statements concerning *Antedon*. In this form, too, a blastula is developed after equal cleavage, and the gastrula is formed by invagination. The formation of the mesenchyma takes

place from the archenteron, but only after gastrulation
(BARROIS, No. 6; BURY, No. 7), as in Synapta and the Aste-
roidea. The cells of the archenteron, especially those lying
at its apex, lose their regular arrangement, apparently as the
result of a rapid cell-proliferation occurring at this point, so
that the archenteron no longer presents strictly a single
layer of cells, but is composed of cells irregularly grouped.
A large number of these cells migrate into the cleavage
cavity, and form the mesenchyma (Fig. 189).

The various kinds of mesenchyma formation are not so different from
one another as they at first sight appear to be. It is always substantially
the same region of the blastula from which the mesenchyma takes its
origin, the only difference being that in the one case this has already
undergone invagination, while in the other the invagination does not
take place until later. It seems as if those methods of mesenchyma
formation were the more primitive in
which the cells take their origin from the
archenteron. Later the cœlomic sacs are
also developed from the archenteron, and
thus the development of the mesenchyma
and the mesoderm could be correlated.
There are found various transitional stages
of this anticipatory misplacement, i.e.,
between the origin of the mesenchyma
from the *archenteron* and its development
from the thickened pole of the *blastula*,
as, for example, in the *Holothurians*. In
Synapta the mesenchyma arises from the
archenteron, whereas in *Holothuria* it
begins at the same time as gastrulation.

FIG. 189.—Development of the
mesenchyma in the gastrula of
Antedon rosacea (after BURY).
bl, blastopore.

The metamorphoses which the archenteron of Antedon
undergoes are different from those in other Echinodermata
in so far as the blastopore does not become the anus, but
closes, after which the archenteron is constricted off from
the ectoderm and lies as a spacious sac in the interior of the
embryo. Mouth and anus arise as new formations, but not
until much later. There is certainly a connection between
these complicated formative processes and the fact that the
larva of Antedon abandons the egg-membrane much later
(the seventh day of development) than other Echinoderm
larvæ.

The statements of authors differ regarding the position of the blasto-
pore; according to BARROIS, it is found at one pole of the larva, whereas
BURY and GOETTE locate it more toward the future ventral side (Fig. 189).

II. THE ORIGIN OF THE ENTEROCŒLE AND HYDROCŒLE.

In the first part of this chapter we traced the develop-
ment of the Echinoderm larva to the point at which the
mesenchyma was formed and the larval mouth had broken
through on the ventral side. Even before this occurs, im-
portant developmental processes, which result in the abstric-
tion of the fundaments of the body cavity and water-vascular
system, take place in the archenteron. Both of these arise
in all Echinoderms as diverticula of the archenteron. We
apply to them the names employed by LUDWIG, *enterocœle*
and *hydrocœle*, without, however, abandoning for the common
fundament of both the older, but very significant, name of
vaso-peritoneal vesicle (SELENKA).

The formation of the body cavity and the water-vascular
system, although taking place in various ways in the differ-
ent divisions of the Echinodermata, nevertheless exhibits
close relationships between the different groups. We shall
accordingly treat them here in the order in which they
follow each other most naturally.

Asteroidea [AGASSIZ (No. 1), METSCHNIKOFF (No. 37),
GREEFF (Nos. 18 and 19)].—Before the mouth-opening of
the larva is formed, two bilaterally symmetrical outfoldings
arise at the blind end of the archenteron. These soon
become considerably enlarged by growing out toward the
posterior end of the larva (Fig. 190 *A* and *B*). Then
each of the two vesicles separates from the intestine, and
the left-hand one unites by means of a tube with the dorsal
surface of the larva. This pair of vesicles constitutes the
fundaments of the body cavity and water-vascular system.
Their further development takes place in such a way that the
left vesicle is constricted in its posterior portion, whereby
a part finally becomes separated off. The abstricted
anterior part constitutes the earliest fundament of the
water-vascular system [hydrocœle]. It is soon transformed

into a five-lobed, rosette-like structure, in which the subsequent shape of the water-vascular system, with its five chief stems, is already expressed. The two chief vesicles, which remain after the abstriction of the hydrocœle, undergo a metamorphosis similar to that which we shall describe farther on for Asterina gibbosa. We only add at present that they represent the fundament of the body cavity, the enterocœle.

It can be seen from the above description that in the establishment of the vaso-peritoneal vesicles a bilateral symmetry is expressed, which, however, is again deranged
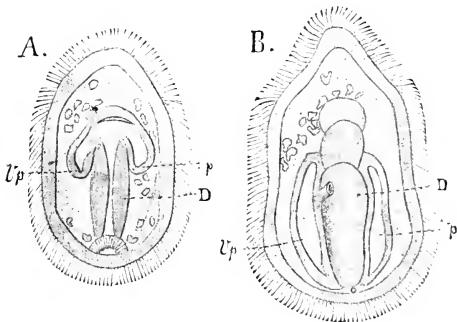
Fig. 190.—*A* and *B*, two starfish larvæ at the time of the development of the entero-hydrocœle (after Metschnikoff). *D*, intestine ; *Vp*, vaso-peritoneal vesicle, the dorsal pore of which can be recognized in *B* ; *p*, peritoneal vesicle (right-hand enterocœle).

by the development of only *one* hydrocœle. A more exact bilateral symmetry, extending to the formation of the hydrocœle, appears, on the other hand, to exist during these stages in the

Ophiuroidea.—In this group also, according to the statements of Metschnikoff (No. 37), two vaso-peritoneal vesicles are constricted off from the intestine, but each of them is said to divide into an enterocœlic and a hydrocœlic vesicle. Ordinarily, however, only the anterior left one of the two hydrocœles develops further, whereas the right

one in most cases degenerates, only occasionally giving
rise to a right-hand water-vascular rosette with a dorsal
pore (MÜLLER, METSCHNIKOFF). In exceptional cases in
the Asteroidea also, there is said to be formed, in addition
to the left-hand one, a right-hand hydrocœlic vesicle, which,
quite like the other, develops into a five-rayed water-vascular
rosette, provided with a dorsal pore. In that case, a hydro-
cœle and an enterocœle would therefore be present on both
sides, and the symmetry would be complete.

The development of enterocœle and hydrocœle does not
take place in all **Asteroidea** in the way described, for
the double character in the fundament of the entero-
hydrocœle may not be so prominent, owing to the fact
that the vesicles of the two sides are no longer constricted
off from the archenteron separately, a condition which is
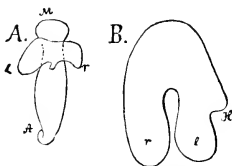
FIG. 191.—*A*, intestine of *Asteracanthion glacialis* and the vaso-peritoneal vesicle
constricted off from it (after GOETTE). The dorsal pore is already formed ; *r* and *l*,
right and left sacs of the vaso-peritoneal vesicle ; *A*, anus ; *M*, region of the
mouth, which does not develop until later. *B*, vaso-peritoneal vesicle of *Asterina
gibbosa*, with its right and left sacs (*r* and *l*), on the latter the fundament of the
hydrocœle (*H*) (after LUDWIG).

important for the reason that it is a transition to the corre-
sponding process in the Echinoidea. GOETTE observed in
larvæ of *Asteracanthion glacialis* that the process usually
takes place in the manner described, but that during the
abstriction from the archenteron the vesicles may in this
same form remain united with each other (Fig. 191 *A*).
Now, according to LUDWIG, this latter condition is the
common one in *Asterina*. The vaso-peritoneal vesicle
appears in the form of two lateral outfoldings at the blind
end of the archenteron (Fig. 192 *A*). The two outfoldings
grow toward the posterior pole of the larva (Fig. 192 *B*),

and the bipartite vesicle separates off from the archenteron
(Fig. 192 C). Meanwhile the blastopore has closed. In
their further development the two arms of the vesicle grow
around the intestine. They come in contact with each other
behind [and dorsad of] the intestine, and there form the
mesentery, which extends from the intestine to the body-
wall [in a direction oblique to the sagittal plane]. The
fundament of the water-vascular system now first makes its
appearance in the vaso-peritoneal vesicle as an outfolding
of the left half of the vesicle (Fig. 191 B, II). Projecting
at first only a little beyond the wall of the vaso-peritoneal
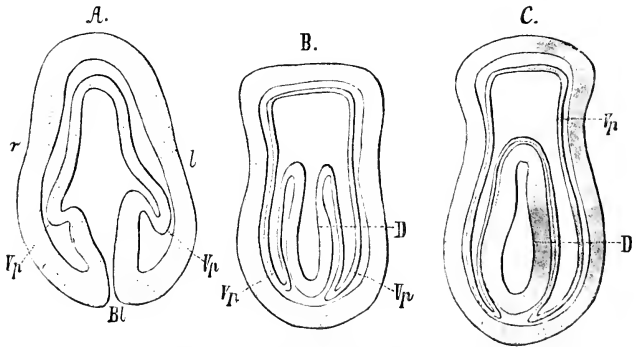
Fig. 192.—A to C, sections through larvæ of *Asterina gibbosa* (after Ludwig). *Bl*,
blastopore; *D*, intestine; *Vp*, vaso-peritoneal vesicle; *r* and *l*, right and left
sides.

vesicle, it soon gives rise to five lobes, thus producing the
earliest fundament of the five radial stems of the water-
vascular system. At about the same time, an invagination
of the ectoderm takes place on the dorsal side of the larva
opposite the larval mouth; it grows inwards, and opens into
the left half of the vesicle. This is the dorsal pore of the
larva, which therefore effects a communication of the out-
side world with enterocœle and hydrocœle, for the separa-
tion of the latter from the enterocœle does not take place
until later.

The processes which we have followed in the development of the enterocœle and hydrocœle of *Asterina* bear a close resemblance to those which give rise to the formation of the vaso-peritoneal system of the

Echinoidea.—As in *Asterina*, the blind end of the arch-enteron is transformed into the fundament of the vaso-peritoneal vesicle (SELENKA, No. 53). Two outpocketings are developed from it, the two being constricted off in common from the intestine (Fig. 193 *A* to *C*). It is not until later that they separate into a right and left vesicle; the former constitutes a part of the enterocœle, but the latter represents not only the other part of the enterocœle, but also the hydrocœle. Accordingly by another constriction the left vesicle is divided into two, and in this manner gives rise
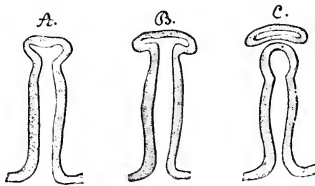
FIG. 193.—*A* to *C*, longitudinal sections of the archenteron of *Echinus miliaris*, showing the development of the vaso-peritoneal vesicle (after SELENKA).

to the left enterocœlic sac and the hydrocœle. The same process is said by METSCHNIKOFF to take place in the right vesicle, so that a hydrocœle is formed on the right side also, in a manner similar to that described for the Asteroidea and Ophiuroidea. The right hydrocœle is said subsequently to degenerate. These statements are noteworthy only for the reason that they may indicate that the water-vascular system is traceable to an organ of paired origin.

A mode of origin of the hydro-enterocœle still more modified than that in the forms hitherto considered is exhibited in the

Holothurioidea, although it can be referred to the same plan. We have already seen in *Synapta* (comp. Figs. 176 to 179, pp. 395, 396) that a part of the archenteron detaches

itself from the rest, and unites with the dorsal wall of the larva. As its further development shows, this abstricted portion of the archenteron corresponds to the vaso-peritoneal vesicle of the other Echinodermata (Fig. 179). It communicates directly with the outside world by means of the dorsal pore, just as in certain Asteroidea. It is not until this stage that a constriction makes its appearance in the posterior
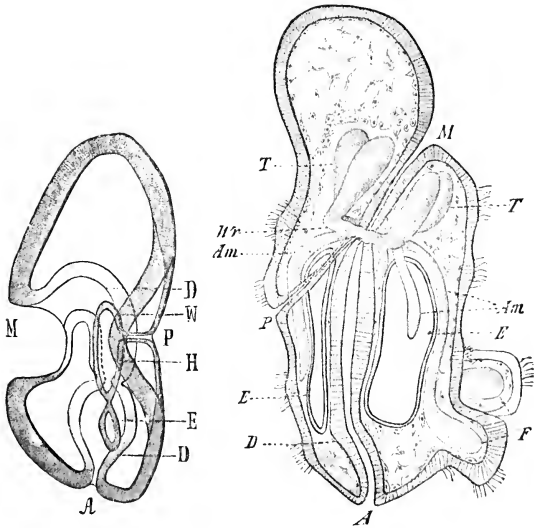
FIG. 194.

FIG. 195.

Fig. 194. — Optical longitudinal section of an Auricularia larva of *Holothuria tubulosa* (after SELENKA). *A*, anus; *D*, intestine; *E*, enterocœle; *H*, hydrocœle; *M*, mouth; *P*, dorsal pore; *W*, ciliated band.

Fig. 195.—Longitudinal section of a larva of *Cucumaria doliolum*, somewhat diagrammatic (after SELENKA). *A*, anus; *Am*, ambulacral (radial) vessels; *D*, intestine; *E*, enterocœles; *F*, feet; *M*, mouth; *P*, dorsal pore, leading through the stone canal to the watervascular ring, *Wr*; *T*, tentacular vesicles; *Wr*, water-vascular ring.

third of the vaso-peritoneal vesicle (in *Holothuria tubulosa*), which divides the vesicle into the hydrocœle, connected with the dorsal pore, and the less extensive enterocœle (Fig. 194

II and *E*). The former is soon transformed into a five-lobed structure, which grows around the stomodæum of the larva, and thus proves to be the water-vascular ring of the animal (Fig. 195). Five outgrowths from it indicate the primary tentacles.

The enterocœle has in the meantime grown out into a sac, which has bent around under the intestine and then divided into a right and a left peritoneal vesicle. These are symmetrically placed on the intestine (Fig. 195). They enlarge and finally obliterate the cleavage cavity. Their cavity becomes the permanent body cavity, and their walls the peritoneum. Where their walls come together the mesentery of the intestine arises.

In the development of the entero-hydrocœle the *Holothurioidea* differ from the forms previously considered, owing to the fact that the vaso-peritoneal vesicle does not present a bilaterally symmetrical shape from the beginning, this being expressed very late, not until the abstriction of the enterocœle from the hydrocœle has taken place. The hydrocœle in the Holothurioidea, in contrast to the other forms, separates very early from the enterocœle.

In the **Crinoidea** the conditions are quite peculiar, probably owing to the fact that the archenteron surrenders its connection with the ectoderm at a very early period, and lies as an isolated sac in the interior of the blastula. On the third day this sac acquires an annular constriction (Fig. 196 *A*), which later becomes considerably deeper, so that there arise two vesicles, which are connected by only a narrow neck. The two vesicles may be distinguished as anterior and posterior, for, corresponding to the subsequent development of the embryo, an anterior and a posterior part of the body can be distinguished even now. The anterior pole is marked by the accumulation of numerous mesenchyma cells, and the posterior by the position of the vesicular archenteron. The posterior of the two vesicles now changes its shape by elongating in the transverse direction and then acquiring a slight constriction at the middle (Fig. 196 *B*). Two hollow processes grow out backward from the point of junction of the two vesicles, and bend around the constricted

part of the posterior vesicle. Moreover, the anterior vesicle
has also altered in shape, for it divides into an extensive
saccular and a more narrow, canal-shaped portion (Fig. 196
B). The fundaments of the most important parts are thus
produced. The posterior bipartite vesicle constitutes the
fundament of the enterocœles. It first separates from the
other parts, and then divides into a right and left cœlomic
sac. Of the two processes from the neck between the anterior
and posterior vesicles, only the larger, dorsal one is said
to be retained, to constitute the fundament of the intestine,
whereas the smaller, ventral one disappears (Barrois). The
anterior vesicle, the hydrocœle, which already exhibits the
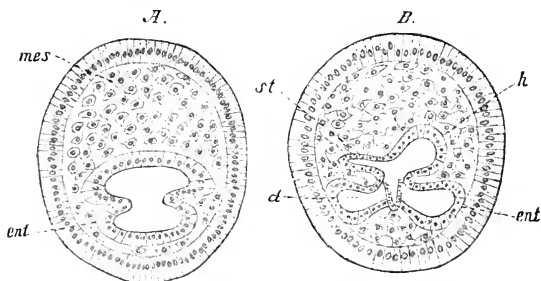
FIG. 196.—A and B, embryos of *Antedon rosacea* in optical section ; development
of the enterocœle (*ent*) and hydrocœle (*h*) (after J. Barrois). *d*, intestine ; *mes*,
cells of the mesenchyma; *st*, stone canal.

separation into water-vascular vesicle and stone canal,
remains united with the intestine for some time (Fig. 196
B). Later the hydrocœle also separates from the intestine,
and then, as in other Echinoderm larvæ, the two enterocœles
and the hydrocœle are found lying next to the intestine,
which has now considerably enlarged. However, the oral
and anal openings, as well as the water-vascular pore, are
still lacking.

A vaso-peritoneal vesicle can scarcely be spoken of in
Antedon, unless the condition in which the already paired
enterocœles are still connected with the hydrocœle by means

of the narrow neck is to be considered as such. The entero-
cœles in *Antedon* separate from the common fundament of
the intestine and hydrocœle at a very early period.

In the development of Antedon the statements of GOETTE, BARROIS, and
BURY are opposed to one another. In what precedes we have followed
those of BARROIS, for they agree fairly well with those of BURY. Differ-
ences between these two authors exist in so far as, according to BURY, the
two processes from the neck, connecting anterior and posterior vesicles,
unite and together constitute the intestine, which at first is circular in
form, and through which there extends for a while a solid cord, uniting
the two enterocœles. Furthermore, according to BURY, only the larger
portion of the anterior vesicle represents the fundament of the hydro-
cœle; the smaller portion, after separating from the hydrocœle, still
supplies a part of the body cavity (anterior body cavity), and later is
connected with the outer world by means of a canal, whereas a union
of this part of the body cavity with the hydrocœle and the formation of
the stone canal take place only secondarily. According to this, a part
at least of the enterocœle would arise at the same time as the hydro-
cœle. According to the statements of BARROIS, on the other hand, the
hydrocœle in this case, contrary to all other Echinoderms, takes its origin
independently of the enterocœle. The same is to be gathered from
GOETTE's description, which, however, it is difficult to harmonize with
those of BARROIS and BURY.

Features appear in the development of *Antedon* which,
besides influencing the shape of the archenteron, also modify
its derivatives, the enterocœle and hydrocœle. In accord-
ance with the attached mode of life of the later larval
stages, the further development also exhibits important
deviations from the development of the other Echinoderms.

**Statements on the Development of the Entero-hydrocœle not
in accord with the Preceding.**—The studies of N. C. APOSTOLIDES on
the development of two Ophiurans (*Ophiotrix versicolor* [Lusitanica Lin.,
cf. FEWKES, No. 13] and *Amphiura squamata*) also contain statements
on the mode of formation of the water-vascular system, but the results
are so different from anything hitherto known of Echinoderm develop-
ment that we mention them only on account of their remarkableness.
In both forms the *gastrula* is said to arise not by invagination, as is
known to be the case in other Echinoderms, but rather by *delamination*.
Likewise the fundament of the *water-vascular system* is said to be de-
veloped in a different way, namely, by an *accumulation of two masses of
cells*, one on either side of the archenteron. These, according to the

description of the author, evidently must come from the mesenchyma. Examples of both genera were previously studied by BALFOUR (*Comparative Embryology*) and METSCHNIKOFF, and were found to be like other Echinoderms in regard to the structures in question.

The studies of BURY (No 8) on the early development of the enterohydrocœle are, on the contrary, important. If, in spite of this, we have not given them a correspondingly prominent place in our account of these conditions, it is owing chiefly to the fact that BURY's statements on this subject are almost directly opposed to those of other authors, and that, furthermore, they neither trace the fundaments of those organs back to the earliest stages, nor devote sufficient attention to the later history of them. For these reasons, BURY's investigations, which, after all, include only a few stages from the middle, do not seem to us to be sufficiently conclusive upon the development of this important system of organs, deviating so fundamentally as they do from all other descriptions.

BURY assumes that all Echinoderm larvæ have not two enterocœlic sacs, as had previously been believed, but two *pairs* of them, either actually present or to be recognized from their fundaments. Thus the larval body would exhibit an internal segmentation. These conditions can be clearly seen in the larvæ of *Ophiurans* and *Echinoids*, in which the larger, anterior enterocœles lie at the side of the œsophagus, and the smaller, posterior ones next to the stomach. The anterior and posterior pairs have arisen by division of the primary enterocœles. The left anterior enterocœlic sac opens to the exterior by means of the water pore. The union of the latter with the enterocœlic sac does not correspond to the subsequent stone canal, for the hydrocœle does not arise until later, and then either from the anterior or posterior enterocœle, from which it is constricted off; it is only secondarily that it unites with the anterior enterocœle. Originally, then, only the body cavity communicates (by means of the dorsal pore) with the outer world. The hydrocœle does not unite with the body cavity, and thus with the outer world, until later. Such conditions were also found by LUDWIG in later stages of *Asterina* (comp. pp. 408 and 436), and are retained throughout life in the Crinoidea (comp. p. 447 and Fig. 224, p. 453).

BURY's observations seem to coincide with those of METSCHNIKOFF, who also observed a division of the right enterocœlic vesicle in *Ophiurans* and *Echinoids*, but referred it to the formation of a right hydrocœle, which subsequently degenerates. Thus METSCHNIKOFF argues for a primitively paired fundament of the hydrocœle, whereas BURY, like other authors, derives it as an unpaired structure from one of the two enterocœles of the left side.

In other Echinoderm larvæ BURY finds the internal segmentation less sharply expressed. In the *Asteroidea* an anterior and posterior enterocœle can still be distinguished; they are, however, no longer separate, but coalesce with each other. The *Holothurioidea* are said to have, in addition to the two posterior enterocœles, a left anterior one, which,

however, from the beginning exists only as an indistinct appendage of the hydrocœle; likewise in the Crinoidea (*Antedon*) only an anterior enterocœle is present, which, united with the hydrocœle, is constricted off from the archenteron. What BURY here considers as anterior enterocœle and hydrocœle together, other authors look upon as hydrocœle only. Where the conditions are of such a character as they are in the *Holothurioidea* and *Crinoidea*, and to some extent in the Asteroidea, BURY conceives a partial degeneration of the originally paired and segmentally arranged enterocœles.

It is not to be denied that in most forms the common entero-hydrocœle, the so-called vaso-peritoneal vesicle, communicates (by means of the dorsal pore) with the outside world; but whether it was the enterocœle alone which originally possessed this union, and whether the hydrocœle was united with it only secondarily, does not yet seem to be proved by BURY's investigations as long as the origin and subsequent fate of his anterior and posterior enterocœles remain unknown.

III. THE DEVELOPMENT OF THE TYPICAL LARVAL FORMS.

Having become acquainted with the most important processes which take place within the body of the larva, we turn to the consideration of its external shape. This is very different in the separate groups of Echinoderms. Like MÜLLER, we start with a simple fundamental form, from which to derive the different larval forms. This fundamental type is an elongate, oval to pyriform larva, which is somewhat flattened on the ventral side. This larval form arose from the gastrula, the blastopore of which is metamorphosed into the anus, while the archenteron bends around toward the ventral side and here connects with the outside world by means of the larval mouth. The larva possesses still another opening in addition to these two, namely, the dorsal pore of the water-vascular system. The flagella with which the larva was at first uniformly covered disappear in part, and are retained only on limited areas, which are called ciliated bands.

Crinoidea.—The larva of *Antedon* is one of the most simply constructed of Echinoderm larvæ. At first of fairly uniform, oval shape, it is subsequently slightly curved toward the somewhat flattened ventral surface. In place of the com-

plete covering of cilia of the first few days, it subsequently
acquires five ciliated rings, which encircle the body trans-
versely, and a tuft of long cilia at the anterior end. The
most anterior of the ciliated rings is less sharply marked
than the others (BURY), owing to which earlier authors
spoke of only four rings of cilia. The larva swims with the
tuft of cilia directed forwards. [Under the tuft lies a
thickening of the ectoderm which was recognized already by
NACHTRIEB (No. XXa, Appendix to *Literature*) as an apical

plate. It has been confirmed
as such by the recent thorough
investigations of SEELIGER (No.
XXVI.). Indications of an
apical plate also appear in the
younger stages of other Echi-
noderm larvæ (Asteroidea and
Echinoidea).—K.] If we com-
pare the larva of Antedon with
that of the other Echinoderms,
in which the blastopore be-
comes the anus, we must look
upon the end opposite the anus
—namely, the one provided
with the tuft of cilia—as the
anterior end of the larva, and
more especially because the so-
called larval mouth lies nearer
to this end. Recent authors
designate as the mouth a cili-
ated depression which lies on
the ventral side between the
second and third rings of cilia
(Fig. 197). This pit does not

FIG. 197.— Larva of *Antedon rosacea*,
with ciliated rings and tuft of cilia
(after GOETTE and W. THOMSON) The
earliest skeletal pieces are already
formed as fenestrated plates. *Gr*, pit
which serves the larva in attaching
itself; *Lm*, the so-called larval mouth.

represent an actual mouth-opening, for it is not connected
with the intestine, but the so-called vestibule is subsequently
formed at this point, and the mouth-opening arises at its
bottom.

A small pit is found on the ventral surface near the
anterior end of the larva, which later serves the larva in

attaching itself. Furthermore, on the left side, between the third and fourth ciliated bands, the water pore makes its appearance as a clear spot on the yellowish-brown larva. In addition to the systems of organs already considered, the earliest fundaments of the skeleton can be recognized (Fig. 197).

Holothurioidea.—The larvæ of the Holothurioidea usually exhibit a typical form, which was designated by Joh. Müller as the *Auricularia*. Its derivation from the fundamental form of the Echinoderm larva is illustrated by the following diagram[1] (Fig. 198), in which the shaded part represents the deep depression of the body, within which the mouth-opening (*m*) lies. This part is surrounded by a band of cilia, the transverse tracts of which, those lying in front of the mouth and in front of the anus, have been distinguished
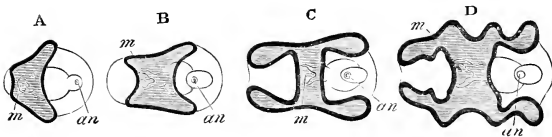
Fig. 198.—*A* to *D*, development of the *Auricularia* from the fundamental form of the Echinoderm larva[1] (diagram after Joh. Müller, from Balfour's *Comparative Embryology*). The broad black line indicates the ciliated band, the shaded area the depressed part of the surface. *an*, anus; *m*, mouth.

from the tracts extending lengthwise on both sides, the so-called longitudinal parts of the ciliated band (Figs. 198 *A* and *B*). The anus lies near the posterior pole of the larva.

In its further development the body of the larva, in front as well as behind, becomes more hollowed out on both sides, while the elevated parts of the ventral surface persist and grow toward each other (Fig. 198 *B* and *C*). In this way there results a larval form, on the ventral side of which an

[1] The manner of orientation chosen by Joh. Müller has been retained in this and in the following diagrammatic figures (200, 202, and 203) for practical reasons only. It would be better if they were placed with the mouth upwards and the anus down, as has been done, for example, in Figs. 199, 204, 209, and 211.

anterior, so-called preoral, and a posterior, anal area can be distinguished as elevated parts from the depressed portions (Fig. 198 C and D). At the anterior and posterior ends the two areas bend around toward the dorsal surface. Fig. 199 A shows a larva at about this stage as seen from the side. The further development of the shape of the larva

is finally attained by the extension of the depressed, or hollowed-out, region more to the periphery, and by the production of lobular processes at the margins of the body, owing to the outgrowth of certain parts (Fig. 198 D). Calcareous deposits, having the shape of delicate miniature wheels, may make their appearance in these ear-like appendages
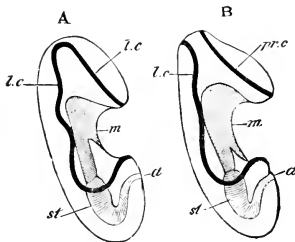
FIG. 199.—A and B, larva of a Holothurioid and an Asteroid respectively seen from the side (from BALFOUR'S Comparative Embryology). a, anus; l.c, ciliated band; m, mouth; pr.c, adoral band of cilia of the Bipinnaria; st, stomach.

(Fig. 205, p. 426). Along the periphery of the lobes runs an uninterrupted ciliated band, which borders the two ventral areas as well as the dorsal surface.

In each of the two depressed lateral surfaces of the Auricularia larva lies a structure resembling a ciliated band; but these structures bear no relation to the ciliated band itself. Each of these two bands exhibits the form of a blunt angle opening toward the ventral surface. The cords consist of ciliated cells and fine longitudinal fibres lying under them. Strands of fibres pass from them to the ciliated band. Accordingly METSCHNIKOFF (No. 37) and SEMON (No. 55) interpret the two cords as the central nervous system of the larva. They also occur under similar circumstances—to anticipate—in the Pluteus larvæ of the Ophiuroidea. On the other hand, corresponding structures do not occur in the larvæ of the Echinoidea and Asteroidea. According to SEMON, however, fine fibres, similar to those in the nerve cords of the Auricularia larvæ, occur in the ciliated band of these larvæ, so that the nerve apparatus would be connected with the ciliated bands in the same way as in the larvæ of the Annelida (comp. p. 266).

[A very large Holothurian larva (Auricularia nudibranchiata), which

attains a length of 6 mm. and is characterized by the complicated form of its ciliated band, has been recently described by CHUN (No. VII., *Appendix to Literature*). The ciliated band of this larva is extraordinarily tortuous, and exhibits arabesque-like foldings. Somewhat similar conditions were previously mentioned in the case of a very large Tornaria. CHUN's paper, which is important in many respects, contains an account—to which attention may be called here—of a sac-like invagination of the hind-gut of the larva, from which, according to CHUN's conjecture, the respiratory trees of the Holothurian may arise.—K.]

The Auricularia larva does not occur in all the Holothurioidea. Thus, for instance, the larva of *Cucumaria doliolum* at the time of the formation of the mouth assumes a cylindrical form (SELENKA). The flagella disappear zone by zone, until the larva retains only four to five bands of cilia, a ciliated anal area, and a ciliated cephalic zone. With this the so-called pupal stage is reached, which does not make its appearance in the development of other Holothurians until later (comp. p. 427). Another Holothurian, *Psolinus brevis*, develops, according to KOWALEVSKY (No. 28), altogether without a metamorphosis. The young Holothurians arise directly from the eggs, which are laid in the sea-water. In *Phyllophorus urna* the larvæ, which are probably completely and uniformly ciliated, are said to swim about in the body cavity of the parent. When they abandon the parent, they already possess five tentacles and two feet. A similar condition is found, according to LUDWIG (No. 33), in the likewise viviparous *Chirodota rotifera*.

Asteroidea.—The larval form of the Asteroidea, like that of the Holothurioidea, can be derived from the fundamental form. If Figs. 200 *B* and 198 *C*, from JOH. MÜLLER's diagrams, are compared, one sees that in the Asteroid larva the preoral area of the ventral surfaces, together with the part of the ciliated band surrounding it, is isolated. The depression on the ventral surface is continued farther forward here than in the Holothurian larva. In this way the connection of the preoral area with the dorsal surface is interrupted, and the ciliated band is separated into two parts. Thus two ciliated bands arise, which, from their positions, may be designated as the adoral and adanal (Figs. 200 *A*

and 199 *B*). Of these the latter is much the longer (Fig. 200 *A* to *D*).

By the bulging and growing outward of the peripheral parts of the larva, there arise longer and shorter processes, which are bordered by the ciliated bands (Fig. 200 *C*). This larval form received from its discoverer, Sars, the name of "*Bipinnaria*" (*asterigera*), which it continued to bear even after its relation to the starfishes was recognized.
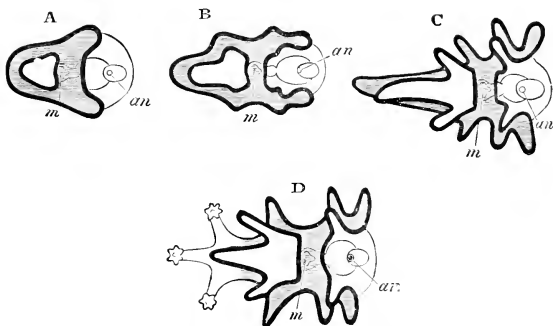
Fig. 200.—Development of the *Bipinnaria* and *Brachiolaria* from the fundamental form of the Echinoderm larva (diagram after Joh. Müller, from Balfour's *Comparative Embryology*). The broad black line indicates the ciliated band, the shaded part the depressed portion of the surface. (Comp. footnote on p. 417 in regard to the orientation of the figures.) *an*, anus; *m*, mouth.

The opinion which Semon advances concerning the origin of the *Bipinnaria* larva does not agree with the description of it which we have just given. Semon finds in the Echinoderm larva a ciliated band surrounding the mouth, a loop of which occasionally extends into the œsophagus (as in the *Auricularia*). This "adoral" ciliated band has nothing to do with the continuous ciliated band, but exists independently of it. In the *Bipinnaria* the "adoral" ciliated band of Semon is said also to supply that part of the ciliated band which we called the adoral part, so that the latter is not, as we described it, to be looked upon as a detached part of the continuous ciliated band. As long as strict proof of such a mode of origin is not forthcoming, we are unable to accept this opinion. The agreement of the preoral area in *Auricularia* and *Bipinnaria* is too striking for one not to assume that its isolation took place by means of

a deeper and deeper incision on the part of the lateral depressions.[1] (Comp. also in this connection Figs. 200 and 198, as well as Fig. 199 *A* and *B*.) Joh. Müller figures Auricularians in which the two depressions almost meet at the anterior end of the larva. Furthermore, the breaking up of the ciliated band discovered by Semon and the metamorphosis of the component parts into the epithelium of the fore-gut mentioned by him make the band appear to be more probably an oral ciliary apparatus, serving for the capture of food (comp. p. 427).

The *Brachiolaria* arises from the *Bipinnaria* of the starfish as a subsequent stage by the formation of two additional processes at the base of the longer (dorsal) appendage (Fig. 200 *D*). In this way are formed the so-called Brachiolarian arms, which are different from the others. They are not bordered by a ciliated band, but possess wartlike elevations at the ends, which probably serve the larva for attachment in later stages.

In the starfishes, too, many exceptions to the typical form of the larva are found. This is the case in *Asterina gibbosa*, the development of which has been made known through the thorough researches of H. Ludwig. The larva, which at first is pyriform, acquires a ridge-like thickening, en-
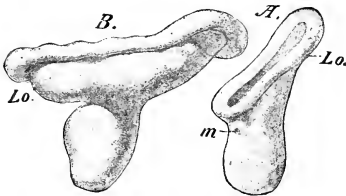
Fig. 201.—*A* and *B*, larvæ of *Asterina gibbosa* (after Ludwig). *A*, a younger stage seen from in front; *B*, older stage seen from the side; *Lo*, larval organ; *m*, mouth.

closing a depressed area, at the anterior end (Fig. 201 *Lo*). This thickening finally acquires a volume surpassing that of the rest of the larval body (Fig. 201 *B*). The peculiar organ consists of two lobes, and since the anterior

[1] [This interpretation is confirmed by the investigations carried on since the above statement was written.—K.]

one of these occasionally divides, a certain resemblance
to the Brachiolarian arm is produced. For in this way
there arise two lobes, which lie symmetrically in front
of the mouth, and a third unpaired lobe, which is farther
removed from the mouth-opening. But the arms of the
Brachiolaria which lie in front of the mouth have a similar
position, and therefore LUDWIG homologizes the larval
organs of Asterina with the latter. The organ is muscular,
and serves the larva for attachment. Similar, but multifid,
larval appendages have also been described by SARS, JOH.
MÜLLER, AGASSIZ, THOMPSON, and others, for *Echinaster* and
Asteracanthion (*Mülleri*).

Nothing more detailed has been learned of a vermiform
Echinoderm larva described by JOH. MÜLLER, which was
divided into five segments by transverse constrictions, and
to the under-surface of which a five-lobed star was attached.
According to JOH. MÜLLER's account, it develops into a star-
fish.

Ophiuroidea.—The *Pluteus* larvæ of the Ophiuroidea ex-
hibit an essentially different shape from that of the larvæ
thus far considered. But they also arise from the same
fundamental form. As in the cases previously considered,
there is a continuous ciliated band, which borders the deep
depressions of the body (Fig. 202 *A*). The subsequent
characteristic shape of the larva depends, in the first place,
upon the fact that the anal area increases considerably in
extent, while the preoral area, on the contrary, almost
entirely disappears (Fig. 202 *B*). Apart from this, the
shape of the larva is determined by the long processes into
which its peripheral portions grow out (Fig. 202 *C* and *D*).
These are bordered by the ciliated band, which is still, and
always remains, continuous. As the form of the *Pluteus* is
reached, the anal area becomes pointed (Fig. 202 *D*). The
two ventral, posterior arms are especially well developed.
They are also significant for the reason that they are always
present, whereas the other arms may be more or less sup-
pressed.

The *Pluteus* larvæ, unlike the *Auricularia* and *Bipinnaria*,
possess a calcareous skeleton. As early as the gastrula

stage of the larva two triradiate calcareous bodies are
secreted by the mesenchyma cells in the vicinity of the
blastopore. These soon elongate owing to the activity of
the mesenchyma cells. They increase considerably in
volume, branch, and send out rod-like processes into the
arms as soon as the latter are developed. The calcareous
rods fuse at the posterior end of the larva, and appear to be
united here by a kind of ring having a transverse position
(Fig. 211, p. 438). In this way there arises an excellent
supporting apparatus for the larva and its appendages.
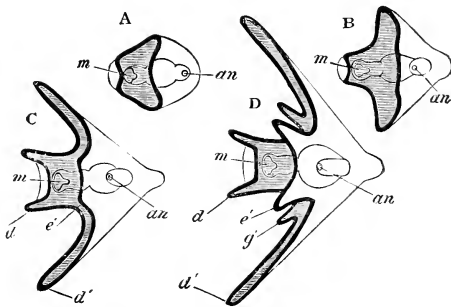
Fig. 202.—*A* to *D*, evolution of the *Ophiuran Pluteus* from the fundamental form
of the Echinoderm larva (diagram after JOH. MÜLLER, from BALFOUR's *Comparative
Embryology*). The broad black line indicates the ciliated band, the shaded area
the depressed part of the external surface. In regard to the orientation, what is
said on p. 417 (footnote) applies here also. *an*, anus; *m*, mouth. The other letters
refer to the nomenclature of the appendages, which is not further considered here.

Amphiura squamata develops without any real meta-
morphosis. *Amphiura* is viviparous. The earliest develop-
mental processes are nearly the same as those that we have
already learned about. There arises an oval embryo, which
assumes a bilaterally symmetrical shape, but which does
not develop into a ciliated larva, passing, on the contrary,
directly into the five-rayed star. The young, even at the
time when they come into the world, exhibit the organization
of the parent. It is interesting, however, that, despite this,
the larval skeleton of the *Pluteus* is begun in the embryos.

This points to the fact that even in *Amphiura* or its ancestors a metamorphosis took place, which, however, was abandoned owing to a change in the mode of life.

Echinoidea.—The larva resembles that of the Ophiuroidea, and, like it, is called a *Pluteus*. In it also the anal area preponderates on the ventral surface. The ciliated band is simple. A calcareous skeleton is found inside the body and its appendages (Figs. 204 and 212, p. 440).

The derivation of the Echinoid Pluteus from the fundamental form is nearly the same as in the Ophiurans, and is explained by the diagrams of Fig. 203. The shape of the different sea-urchin larvæ is quite varied, according to the greater or less development of the arms. The larvæ of
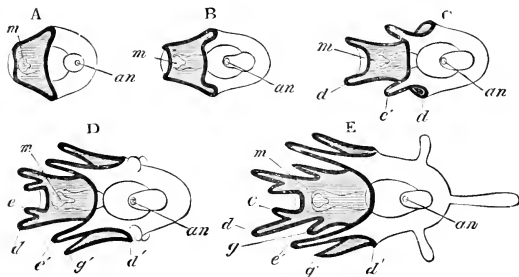
Fig. 203.—Evolution of the *Echinoid Pluteus* from the fundamental form of the Echinoderm larva (diagram after JOH. MÜLLER, from BALFOUR's *Comparative Embryology*). For further particulars consult the explanation of Fig. 202.

Echinus and *Spatangus* may be distinguished as particularly characteristic forms. On the anal area of the former, after the development of all eight processes, the so-called ciliated epaulettes make their appearance (Fig. 202 *D*). These are two pairs of ciliated projections of the body, which lie on either side immediately behind the ciliated band, but isolated from it. According to A. AGASSIZ, they should be interpreted as detached parts of the ciliated band.

The larvæ of *Spatangus* do not possess the ciliated epaulettes, but have three processes on the anal area (Fig. 203

E), which are supported by calcareous rods, like the other processes of the body. In the *Pluteus* of *Arbacia* there are only two processes on the anal area (Fig. 204), but they are particularly long. Furthermore, in addition to the ordinary Pluteus-arms, it possesses two pairs of auricular processes (Fig. 204) which, like the arms, are surrounded by the ciliated band (JOH. MÜLLER, FEWKES). A pedicellaria of the future sea-urchin can already be recognized on the anal area of this larva.
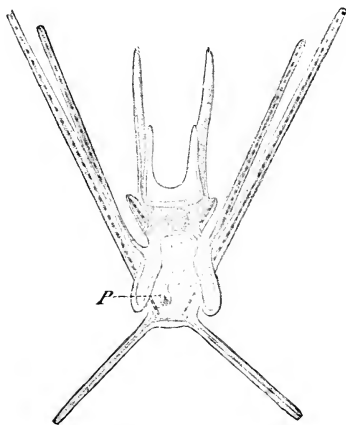
FIG. 204.—Pluteus larva of *Arbacia pustulosa* (after JOH. MÜLLER). *P*, pedicellaria. The skeletal rods are dark.

The skeletal parts are developed very early as products of the mesenchyma (SELENKA, No. 53; LUDWIG, No. 34). There is first secreted between two cells a calcareous concretion, which soon enlarges and becomes triradiate. The skeletogenous cells then migrate along their respective rays, gradually moving farther away, while they continue to secrete calcareous salts. In this way finally arise the long skeletal rods, which may be many times branched and perforated like a network (Figs. 204 and 212, p. 440).

The typical larval form may also be omitted in the sea-urchins. Thus A. AGASSIZ (No. 4) describes a viviparous

Spatangoid, Hemiaster australis, the eggs of which develop
within the ovary, and then pass into a kind of brood-cavity,
which lies over the ambulacral furrow and is formed of
close-set and connivent spines. Here the young sea-urchins
undergo direct development.

IV. THE METAMORPHOSIS OF THE LARVA INTO THE ECHINODERM.

The metamorphosis of the larva into the Echinoderm takes
place most simply in the *Holothurioidea*, and therefore we
consider this group first.
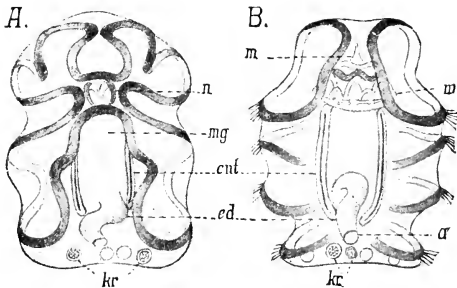
Fig. 205.—*A* and *B*, metamorphosis of the Auricularia larva of *Synapta digitata*
into the pupal form (after Semon). *a*, anus; *ed*, proctodæum; *cnt*, enterocœle;
kr, calcareous wheels; *m*, oral funnel; *mg*, stomach; *n*, nerve bands; *w*, water-
vascular ring with the evaginations (tentacular and radial vessels).

Holothurioidea.—The metamorphosis of the *Auricularia*
into the *Holothurian* is manifested in the external shape of
the larva by the gradual disappearance of its lobular pro-
cesses and the alteration of the ciliated band, which breaks
up into several pieces (Fig. 205 *A* and *B*). The larger
number of these pieces alter their positions by acquiring
a transverse position in place of a longitudinal one (Fig.
205 *B*). At the same time the protuberances of the larval
body disappear, and it assumes more of a cylindrical form,
whereby, according to Semon, its circumference is strikingly
diminished. Finally the different pieces of the ciliated

band grow together into five rings, which surround the
larva like the hoops of a barrel (Fig. 206). This is the
so-called pupal stage, which is also assumed by some Holo-
thurians (e.g. Cucumaria) without passing through the
Auricularia form. This stage is remarkable owing to its
resemblance to the larva of Antedon, with which it has in
common even the number of the ciliated rings.

According to SEMON, we may imagine that the rearrangement and loss
of continuity in the ciliated band are the result of the migration of the
band together with the adjacent body epithelium, probably in con-
sequence of internal processes of growth.

In the metamorphosis of the ciliated band we have not
yet considered the parts lying near the mouth, which do
not share in the formation of the external ciliation of the
pupal stage. Parts of the longitudinal and transverse
portions of the ciliated band approach very close to the
region of the mouth-opening (Fig. 205 A). After the
breaking up of the ciliated band, four parts can be dis-
tinguished, which closely surround the mouth, and finally
form a continuous ring about it. They gradually move
more into the infundibular depression which leads to the
mouth-opening. By a marked narrowing of the funnel
they come to lie inside the larva, and are employed to
clothe the tips of the five anteriorly directed evaginations
of the hydrocœle (therefore for the formation of tentacles)
(Fig. 205 B). The nerve bands have moved down into the
funnel even before the parts of the ciliated band have, and
are to a certain extent forced down by them (Fig. 205 A,
n), for the nerve bands occupied a position nearer to the
mouth-opening than the ciliated bands. Their free ends
then unite at the bottom of the funnel and there form the
nerve-ring of the Synapta (SEMON). It was precisely those
four parts of the ciliated band that moved into the funnel
which were united to the nerve bands by means of nerve
fibres. Probably this connection is retained during the
metamorphosis, and as soon as the ciliated band has covered
the five tentacles the five large tentacular nerves are es-
tablished on the nerve-ring, whereas the five radial nerves

do not bud forth from it until later (SEMON). The parts of the nervous system, which at first lie superficially, are finally overgrown by the rest of the ectoderm, and since mesenchyma cells crowd in over them, they come to lie at a still greater depth.

The ciliated band, which, according to SEMON, encircles the mouth, changes its position during the metamorphosis of the larva by coming to lie wholly in the stomodæum. Here its cells are said to spread themselves out on the wall and constitute the epithelium.

Our previous account of the internal organization of the Holothurian larva was confined to the formation of the intestine, the two enterocœlic sacs, which extended between
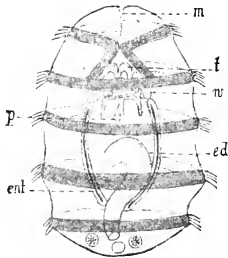
FIG. 206. — Pupal stage of the larva of *Synapta digitata* (after SEMON). *ed*, proctodæum; *ent*, enterocœle; *m*, oral funnel; *w*, water-vascular ring with evaginations forwards (tentacles [*t*]) and backwards (radial vessels and Polian vesicles [*p*]).

the intestine and the body-wall, and the hydrocœle. We saw the latter growing around the stomodæum of the larva as a five-lobed structure. It already represented the fundament of the water-vascular ring and the five tentacles of the Holothurian. Five secondary evaginations of the water-vascular ring arise between the five primary tentacles, and at first are also directed upwards (Fig. 205 *B*). Later, however, five of the ten evaginations of the water-vascular ring now present bend over the calcareous arches and grow out backwards (Figs. 206 and 207), so that there are now five tentacles and five radial vessels (SEMON). The question now arises whether it is the five vessels first developed (the so-called primary tentacles) which bend over backwards, and thus correspond to the radial vessels of other Echinoderms—as seems most natural, though this has been denied—or whether it is the five vessels of the second group, which correspond to radial vessels. As to the homologies of the ambulacral vessels in the different

divisions of Echinoderms, which apparently seem to be so clear, the opinions of authors are nevertheless at variance (comp. SEMON, No. 55).

[Through LUDWIG's (No. XV.) recent investigations of Cucumaria planci, these conditions have been satisfactorily elucidated. The five invaginations of the water-vascular ring first formed really produce the radial vessels. They are, it is true, at first directed forward, but soon bend backward, thus marking the radii. The tentacular vessels do not arise directly from the ring-canal, but branch off from the radial canals; however, every radial canal does not give rise to a tentacular vessel, the latter being distributed unsymmetrically to three radial canals only.—K.]

The internal conditions are more evident in Fig. 207, a longitudinal section of the pupal stage of *Cucumaria* (after SELENKA). The tentacular evaginations are seen coming off from the water-vascular ring forwards, and posteriorly those of the radial vessels. The Polian vesicles also take their origin as evaginations of the water-vascular ring. In the stage under consideration the ring is still in connection with the outside world by means of the stone canal and the dorsal pore. This connection is afterwards broken, since a cluster of mesenchyma cells subsequently applies itself to the stone canal
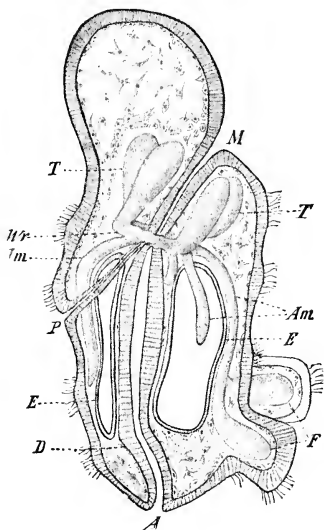
FIG. 207.—Longitudinal section of a larva of *Cucumaria doliolum*, somewhat diagrammatic (after SELENKA). *A*, anus; *Am*, ambulacral (radial) vessels; *D*, intestine; *E*, enterocœles; *F*, feet; *M*, mouth; *P*, dorsal pore, leading through the stone canal to the water-vascular ring; *T*, tentacular vessels; *Wr*, water-vascular ring.

at about the middle of its course, and here deposits a semi-
lunar calcareous ridge, which must be looked upon as cor-
responding to the madreporic plate. Where it rests upon
the stone canal, the latter is cut through by a constriction,
and one half henceforth hangs down from the ring-canal
free in the body cavity, whereas the other half is gradually
obliterated.

Externally the pupal stage now approaches more the
adult Holothurian, owing to the fact that the first two feet,
the development of which is to be traced to evaginations of
the corresponding radial vessel, make their appearance on
the posterior part of the ventral surface (Figs. 207 F and
208 f). At the same time the tentacles also advance in their
development. We saw in *Synapta* that a part of the ciliated
band moved down into the oral funnel to supply the ecto-
dermal covering of the tentacular vessels, which consists
partly of sensory cells. The oral funnel then closed to an
extremely narrow fissure, and there was thus formed a
kind of vestibule (comp. the corresponding processes in the
development of the vestibule of *Antedon*, p. 446). The
tentacles, to which the nerve-ring is still joined, lie in the
vestibule. The nerve-ring lies at the point where the calca-
reous ring,—the supporting apparatus of the tentacles, con-
sisting at first of five and later of ten rods,—is attached to
the tentacles. When the tentacles have reached the neces-
sary development, they are extended out through the fissure,
which widens again (Fig. 208), and the young Holothurian
now moves both by means of those ciliated bands which still
remain, and by means of adhesion with the tentacles and
feet when the latter are present.
In *Synapta*, as is known, the
feet are not developed, even the
radial vessels degenerating.

The shape of the Holothurian
would thus be attained if the
young animal did not lack the
larger number of tentacles and
feet, and if its body-covering
already possessed its permanent

Fig. 208. — Holothurian larva with
ciliated bands, extended tentacles
(*T*), and developing feet (*f*) (after
Joh. Müller).

structure. Additional tentacles and feet are developed in the same way as those which we have already learned about, namely, by evaginations of the parts of the water-vascular system already formed. The ciliated bands are said by SEMON to disappear owing to their cells spreading themselves out over the entire surface of the larva, and substituting themselves for the originally flat body epithelium, which now makes way for a thick epithelial layer. With progressing growth the mouth and anus of the larva are shifted from the more ventral position toward the anterior and posterior ends of the animal respectively.

Now that we have followed the Holothurian larva in its development as far as the young animal, there remain for consideration only a few important internal developmental processes, which relate to the derivation of the middle germ-layer. As we were obliged in the previous description to take into consideration various forms, so are we under the same necessity in the following statements, which for the greater part we take from the works of SELENKA and SEMON.

Having treated of the origin of the mesenchyma cells in the first division of the chapter, we intentionally left the subject for the time being. By far the greater part of these cells become connective tissue. Whereas they are usually applied to the inner surface of the ectoderm as isolated cells, they are accumulated on both sides of the proctodæum in larger groups, which give rise to the calcareous spherules and calcareous wheels. They also occur in large numbers in the region of the stone canal and of the water-vascular ring, forming in one place the well-known calcareous deposits and in the other the calcareous ring surrounding the œsophagus. The mesenchyma cells give rise by multiplication to a kind of cutis under the entire ectoderm (METSCHNIKOFF, No. 37). Underneath the ciliated band they form, according to SEMON, groove-like sheaths, which probably serve as supports for the ciliary apparatus. Fissures in the mesenchyma are said to give rise to the blood-vessels of the Holothurian. Thus the vessels accompanying the intestine first make their appearance as lacunar spaces in the mesenchyma lying dorsad and ventrad of the intestine. The blood cells, on the contrary, are said to have been detached from the walls of the hydro-enterocœle and to have taken part in the formation of these vessels. These free cells, which are found in the body cavity as well as in the ambulacral vessels and blood-vessels, would therefore, according to this view, not arise from the primitive mesenchyma (SEMON).

Of all the musculature only that of the stomodæum originates from the mesenchyma. It persists, being carried over from the larva to the young animal (SELENKA). The rest of the musculature arises partly

from the water-vascular system, the epithelium of which produces an external layer of contractile cells. According to SELENKA, the five powerful longitudinal muscles of the Holothurian arise in this way from the radial ambulacral vessels. This, however, is denied by SEMON. According to him, the circular and longitudinal muscle layers of the body-wall and the intestine take their origin from the enterocœle. Its two sacs have expanded considerably and applied themselves to the wall of the body and that of the intestine as the somatic and splanchnic layers, thus giving rise to the musculature and epithelial lining of the body cavity. A mesentery is developed on the dorsal and another on the ventral side of the intestine. While, however, the ventral one is broken through, and the two enterocœles become confluent here, the dorsal one persists, and thus throughout life indicates the origin of the body cavity from two separate sacs, as well as the bilateral plan of the body in general.

The fundament of the nervous system has already been discussed. As regards the development of the genital system, authors are not able to make any very trustworthy statements.

[The organogeny of the Holothurians has received a new and thorough treatment in LUDWIG's memoir on Cucumaria planci.—K.]

Asteroidea.—Whereas earlier investigators were inclined to believe that the starfish arose as a bud, so to speak, on the larva, we know to-day that even here there is a metamorphosis of the larval body into that of the adult animal. It is true that certain modifications make their appearance in this connection, for the body of the Echinoderm is at first established in only a comparatively small portion of the larval body. It is but gradually that the larger part of the larval body is employed in the formation of the starfish. In certain cases, it is true, this latter process seems to be omitted, and the Echinoderm then takes its origin from only one part of the body of the larva. In the latter method of development the young starfish is detached from the body of the larva, and the latter is said to be able to live for a considerable time (JOH. MÜLLER, KOREN ET DANIELSSEN). Such a condition might cause the process to be looked upon as budding. This view, however, is disproved by the metamorphosis of the entire body of the larva in other starfishes, which will be described later.

The metamorphosis of *Bipinnaria* or *Brachiolaria* into the starfish has been studied most exhaustively by A. AGASSIZ (No. 1) and METSCHNIKOFF (No. 37).

The earliest trace of the starfish is formed in the posterior part of the larval body. The five-rayed fundament of the water-vascular system lies at the left of the stomach (Fig. 209 *H*), while on the right side of it an accumulation of mesenchyma cells takes place, in which the first skeletal parts are already secreted (Fig. 209 *K*). The ventral or ambulacral side of the starfish is indicated by the water-vascular rosette, and the dorsal or antambulacral side by
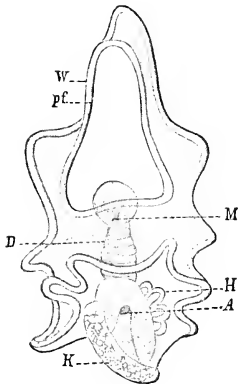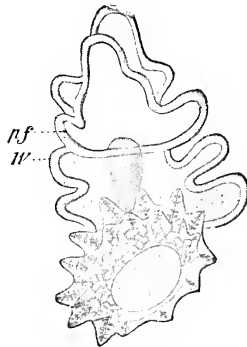
FIG. 209.   FIG. 210.

FIGS. 209 and 210.—*Bipinnaria* larvæ with the fundament of the starfish in different stages of development (after JOH. MÜLLER). *A*, anus ; *D*, intestine ; *H*, water-vascular rosette ; *K*, calcareous secretions lying in the fundament of the antambulacral surface of the starfish ; *M*, mouth ; *pf*, preoral area of the larva ; *W*, ciliated band.

the skeletal structures. The two sides are established independently. Even at a very early period the five-rayed structure of the starfish can be recognized in them. This is indicated on the ambulacral surface by the fact that five folds arise in the larval skin immediately over the radii of the water-vascular rosette, while on the antambulacral surface the calcareous rods are deposited in the form of a pentagon. On both sides a thickening of the epidermis is connected with the differentiation of the cutis-forming

K. H. E.   F F

mesenchyma cells at the sides of the stomach. The comprehension of this process is rendered more difficult by the fact that the ambulacral and antambulacral surfaces are not parallel, but nearly at right angles to each other. Between the two lies the capacious stomach. In Fig. 209, which, however, corresponds to a somewhat earlier stage, the water-vascular rosette (*II*) is seen to be partly covered by the stomach, whereas this in turn is partly covered by the fundament of the antambulacral surface. The latter develops further in such a way that from the calcareous concretions a number of plates are formed (comp. *infra*), which cover a pentagonal area. This grows out then into five processes, thus establishing the dorsal surface of the arms, upon which there appear wart-like elevations, from which the spines arise later.

At this stage the starfish already approaches the shape of the adult animal, at least as far as regards its dorsal external surface, and is seen attached to the larva, the posterior end of which it has quite absorbed (Fig. 210). Its anterior portion is still well preserved. Now, however, degeneration also begins here. It gradually shrinks, its substance being consumed by the phagocytic mesenchyma cells, undergoing intracellular digestion, and being doubtless employed in the formation of the new body (METSCHNIKOFF, No. 40). At the same time with these processes the size of the stomach decreases, as a result of which the two surfaces of the starfish, which were separately developed, are able to approach each other. They cover each other, and finally fuse. The hitherto unclosed water-vascular rosette grows around the œsophagus, and its radii elongate to form the ambulacral vessels, which in their turn give rise to the feet. In this process the distal end of the vascular fundament becomes the so-called tentacle, but the feet are established laterally in pairs. The youngest feet are always found next to the tentacle, therefore at the tip of the arm, whereas the oldest are crowded toward its base. The eye makes its appearance as an accumulation of red pigment at the base of the tentacle at a very early period.

Even before this, there have been produced on the antam-

bulacral surface secretions of calcareous salts, which at first formed delicate rods and subsequently united into reticular plates. Eleven such plates can soon be recognized, a central one and (arranged about it in a circle) two rows of alternating plates, the fundaments of the radial and interradial plates. One of the former, which at first lies at the left next to the dorsal pore, subsequently grows around it, and thus becomes the madreporic plate (LUDWIG). According to LUDWIG, the ambulacral or vertebral plates of the arms make their appearance very early as five pairs of calcareous bodies at the base of the five hydrocœle pockets. They therefore have even now the position which they retain afterwards, namely, on the outer side of the future ambulacral vessel. The other skeletal pieces of the arm are not developed until later.

The question now is, What relation does the larval intestine have to the newly formed starfish? The older statements are not precise on this point; for this reason we adhere to the recent investigations of LUDWIG on Asterina gibbosa, a form, however, which is developed neither from a Bipinnaria nor from a Brachiolaria (comp. *supra*, p. 421). Yet in this species the two surfaces of the starfish are established independently, and afterwards unite as described above. From this, one may perhaps conclude that the processes in question resemble those in the typical larva. In *Asterina* the stomodæum of the larva separates from the stomach and hangs down from the larval mouth as an internal blind rudiment. For a time the intestine is without any connection with the outside world. The permanent mouth of the starfish is then developed by an outfolding of the stomach, growing out toward the body-wall and finally breaking through to the outside world. The stomach itself is transmitted to the starfish. It subsequently acquires five outpocketings, which bifurcate at their tips, the fundaments of the five pairs of intestinal cæca. The larval anus is obliterated even before the union of the intestine with the mouth takes place, and the new anus does not arise until after the formation of the mouth-opening. It breaks through at the margin of the central plate, between it and

an interradial plate. According to the observation of
Agassiz, the mouth arises by a shortening of the long
œsophagus, and the anus persists.

The condition of the *dorsal pore* and the *stone canal*, as described by
Ludwig for *Asterina*, is interesting. In this form, after the separation
of the enterocœle and hydrocœle, a canal is developed on the latter,
which, attached to the water-vascular rosette, opens into the enterocœle
quite near the place where the dorsal pore is connected with the entero-
cœle. This is the stone canal, which does not unite with the dorsal
pore until later. Thus there is a stage in which the stone canal does
not open directly from the water-vascular ring to the outside world, but,
on the contrary, leads into the body cavity. This, however, is in turn
connected with the outside world by means of the dorsal pore. Ludwig
compares this condition to that which he described for the Crinoids (Nos.
30, 32). In them the water penetrates by means of the pores in the cup
(*Kelchporen*) into the body cavity, to be taken from there and con-
ducted into the water-vascular ring by the stone canals, of which there
are several hanging down from the water-vascular ring into the body
cavity.

The earliest fundament of the *blood-vascular system* arises, according
to Ludwig, at the place where the intestine grows out to form the œso-
phagus. In the mesenchymatous layer lying between the walls of the
hydrocœle, the enterocœle, and the intestine, there is formed a fissure,
which exhibits a lining of very flat cells. This is the fundament of the
first blood-vascular ring. The structure ordinarily described as the
central plexus of the blood-vascular system also arises as a fissure next
to the stone canal (comp. General Considerations, p. 456).

The nervous system of *Asterina* is first established in the form of a
circular epithelial thickening, which surrounds the region of the future
mouth-opening. Its development is certainly similar to that of the
central nervous system of the Holothurioidea, with which we are already
familiar.

The metamorphosis of those starfish larvæ which differ from the Bipin-
naria- and Brachiolaria-forms, as, for example, that of *Asterina gibbosa*
(Fig. 201, p. 421), is likewise accompanied by the transmission of the
greater part of the larval organs to the starfish (Ludwig). Only the mouth
and anus have to be formed anew, and the larval organ suffers degenera-
tion, being gradually absorbed. Here also the starfish arises from an
ambulacral and an antambulacral fundament, which at first are separate.
The development of *Pteraster militaris* seems to resemble that of
Asterina (Koren et Danielssen). In this starfish, however, a kind of
brooding occurs ; a membrane stretches out over the spines on the back
of the animal, forming a brood-chamber. Into this the eggs pass, and
there develop into the larvæ and young starfishes.

Ophiuroidea.—Although the larvæ of the Ophiuroidea and Asteroidea are so different in shape, their metamorphosis presents a certain resemblance. In the Pluteus larva too the ambulacral and antambulacral surfaces are begun separately, and only after their subsequent union give rise to the complete star (JOH. MÜLLER, METSCHNIKOFF). In the *Pluteus* the five-rayed water-vascular rosette, which opens to the outside world on the dorsal side of the larva, lies ventrad of the œsophagus. It is on this that the first steps in metamorphosis are manifested, for it is over its different radii that the mesenchyma and contiguous larval skin become thickened. In this way the fundament of the ambulacral surface of the star is produced. Each of the five radii of the rosette, which represent the future ambulacral vessels, produces two lateral evaginations; thus the larvæ acquire the fundaments of the first feet, which are soon followed by a second and a third pair, etc. While these processes are taking place on the ventral side of the *Pluteus*, the first indications of the antambulacral surface of the *Ophiuran* have made their appearance on its dorsal surface, in the form of five outgrowths of the larval skin. They are arranged in a line, so that three of them lie on the larger and two on the smaller part of the umbrella. The five skeletal pieces arise in them as products of the mesenchyma cells. Although the principal parts for the production of the star are now present, nevertheless a total rearrangement must take place to accomplish its formation. This begins by the growth of the heretofore semicircular water-vascular rosette, together with its appendages, around the œsophagus, to form the water-vascular ring. With the closure of the ring, the two vessels which at first were farthest apart naturally have come to lie close together, and at the same time the form of a star has now been reached, first on the ambulacral surface. This is, however, not the case on the antambulacral surface. Here also the dermal outgrowths (dorsal) undergo considerable changes in position; but it is not until the larval appendages begin to degenerate that the antambulacral parts cover the ambulacral, and thus complete the star. The internal parts of the larva—the

enterocœlic body cavity, the intestine, etc.—then form a part
of the permanent star; the mouth is said to persist, whereas
the anus disappears. Upon the completion of these processes,
which result in the establishment of the permanent shape
of the animal, the calcareous skeleton of the *Pluteus* disin-
tegrates. The rods break up into pieces; as a result of this,
the arms collapse, and the skeleton, together with the larval
body, appears finally to be resorbed by the young Ophiuran.
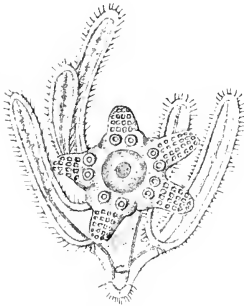
Like the arms of the starfish,
those of the Ophiuran grow at the
tips, with the exception of the
terminal pieces, which correspond
to the skeletal pieces first formed
on the dorsal surface. Therefore
the new pieces are interpolated
between the terminal pieces and
the adjacent ones. The skeletal
parts thus follow a law quite
similar to that of the feet, the de-
velopment of which always takes
place between the (terminal) ten-
tacle and the pair of feet next to
it. The origin of the arm-plates
is interesting; according to Ludwig
(No. 34), they result from the
fusion of two calcareous plates ly-
ing on either side of the median
line of the arm.

Echinoidea.—According to Metschnikoff's description
(No. 37), a difference exists between the metamorphosis of
the Echinoidea and that of other Echinoderms, inasmuch as
there is developed an invagination of the larval skin, at the
bottom of which the earliest fundament of the body of the
sea-urchin makes its appearance. Thus it happens that
the earliest fundament is not exposed, but is covered by a
fold of the larval skin as though by an amnion. Since, how-
ever, the larval skin here too becomes directly converted
into that of the sea-urchin, this difference does not appear
to us to be in any way important.

The processes of the metamorphosis of the *Pluteus* into

the sea-urchin are as follows: inside the *Pluteus* of *Strongylo-
centrotus lividus*, which is provided with four arms, we find
nearly the same conditions that have been described apropos
of the development of the enterocœle and hydrocœle. The
enterocœlic sacs lie to the right and left of the stomach; the
hydrocœle lies over the left one of these, and has the form
of a retort, the neck of which opens to the exterior on the
back of the larva, somewhat as in Figs. 212 and 213,
figures of a *Spatangoid*; the conditions in these forms are,
however, somewhat different, as will be mentioned farther
on. Later, when the *Pluteus* has become six-armed, an
invagination of the outer skin is formed over the hydrocœle
(Fig. 212). This arises from a thickening of the epidermis,
which gradually sinks in and finally rests with its bottom
upon the hydrocœle.[1] The thickened discoid bottom of the
dermal invagination is the earliest fundament of the lower
(oral) surface of the body of the sea-urchin (called "Echinoid
disc" by JOH. MÜLLER). The much thinner lateral parts of
the invagination overlie this as an amnion-like covering
(Fig. 213). The opening of the invagination has narrowed,
but persists, whereas in the Spatangoids other conditions
subsequently make their appearance (comp. *infra*). The
hydrocœle now grows out into five processes, and the
Echinoid disc does the same, by developing a dermal cover-
ing over each of the five hydrocœle processes. In this way
the first five feet of the sea-urchin arise. They extend into
the cavity of the invagination, almost filling it.

During the changes described in the region of the Echinoid
disc, the first indications of the dorsal surface of the sea-
urchin also become noticeable. Two roundish dermal eleva-

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[1] Figures which FEWKES (No. 13) gives of the developmental stages of
Echinarachnius parma may confirm METSCHNIKOFF's description, although
this cannot be gathered from the text of the work. Likewise it seems to
us from the figures of COLTON AND GARMAN (No. 11) that the metamor-
phosis of *Arbacia* is like that described by METSCHNIKOFF for *Echinoids*
and *Spatangoids*. A cavity appears on the *Pluteus*, in which the first
formed feet become visible. The work of COLTON AND GARMAN was un-
fortunately not accessible to us, and is known only through the descrip-
tion of BROOKS (*Handbook of Invertebrate Zoology*, Boston, 1882).

tions are developed on the umbrella of the Pluteus, one on
the dorsal surface and one on the anal area. Each of these
soon assumes a trilobed form, and they prove to be the two
first pedicellaria of the sea-urchin. Fig. 214 shows this
condition in another sea-urchin (*Arbacia pustulosa*).[1] With
the progress of development the disc continually increases
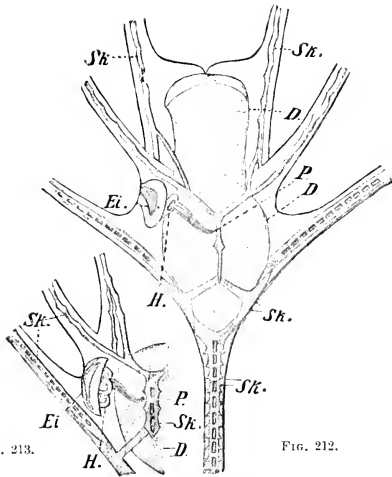
FIGS. 212 and 213.—Parts of a *Spatangoid Pluteus* (after METSCHNIKOFF). *D*,
intestine; *Ei*, invagination of the larval skin, which in Fig. 213 covers the
hydrocœle (*H*). The latter opens to the exterior by means of the dorsal pore. *H*,
hydrocœle; *P*, dorsal pore; *Sk*, larval skeleton.

in circumference, and at the same time the opening of the
invagination also widens again. The contractile feet are
finally extruded through the latter, and are now seen to

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[1] [Very thorough and accurate investigations of these features of de-
velopment have recently been carried on by THÉEL (No. XXIX.) on
Echinocyamus, a form in which the larval development and the meta-
morphosis could be established almost without a gap. Unfortunately
his fine results cannot be stated here in brief form, and we are compelled
to refer to the original paper.—K.]

execute tactile movements.   At this time the larval skeleton
begins to break up, and the arms of the *Pluteus* degenerate
as a result of this (Fig 215).   The body thereby assumes
nearly the form of a hemisphere with the disc as the base.
The circumference of the disc has increased more and more,
and correspondingly the opening of the invagination has
also become enlarged.   The amnion-like envelope meantime
gradually diminishes in prominence ; at length it forms only
a circular fold, surrounding the circumference of the disc,
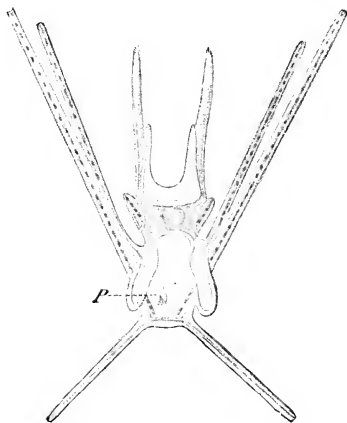
Fig. 214.—Pluteus larva of *Arbacia pustulosa* (after Joh. Müller).   The skeletal
rods are dark.   *P*, pedicellaria.

and finally disappears.   Thus the amnion seems to become
directly converted into the skin of the sea-urchin, and, in
fact, would seem to supply that part of the skin which unites
the sole-like ventral surface with the arched back.   Fig.
215 represents a young sea-urchin which still possesses, in
addition to the feet, some of the Pluteus arms.   Its feet are
already employed as locomotor organs.   In Fig. 216 the
young sea-urchin spines are already seen making their

appearance by the side of the pedicellariæ. They arise as
evaginations of the skin in which reticulated calcareous rods
are deposited. The first of the dorsal plates to make its
appearance is the central one, which is perforated by the
anus. Other plates are then secreted about it, in a spiral
line, *i.e.* in such a way that the newly arising plates crowd
away the older ones from the anal plate, since they are
interpolated between it and the older plates (Agassiz).
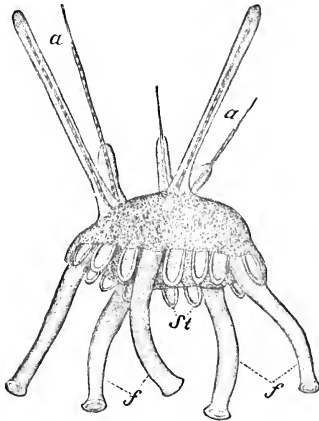
FIG. 215.—Young sea-urchin (*Arbacia punctulata*) with parts of the Pluteus larva
attached (after Colton and Garman, from Brooks's *Handbook*). *a*, partially de-
generated arms of the Pluteus; *f*, feet; *St*, spines.

The internal larval organs become a part of the sea-urchin, although
a new œsophagus is said to be developed, which is not grown around
by the water-vascular rosette, but grows through the previously formed
water-vascular ring (Bury),—a condition, therefore, somewhat different
from that which we observed in the development of the other groups of
Echinoderms. The dorsal pore persists, and also its connection with the
water-vascular ring by means of the stone canal. The outgrowth of the
water-vascular rosette into the ambulacral trunks appears to take place,
according to Agassiz, in the same way as in the starfishes, for new feet
are continually interpolated between the terminal foot and the adjoining
pair.

In the metamorphosis of the **Spatangoid Pluteus** into the sea-urchin the invagination is said by METSCHNIKOFF to close. At the bottom of it the earliest fundament of the sea-urchin then makes its appearance. Furthermore the "amnion" is said to become detached from the larval skin. In the protrusion of the feet the amnion, as well as part of the larval skin, would therefore have to be broken through.

Crinoidea.—We left the larva of Antedon rosacea at a stage in which the nearly ovate form exhibited slight curving toward the ventral side. The further development is characterized by the fact that the larva abandons its free life and grows into an attached stalked form. It therefore passes through a stage in which it resembles a stalked Crinoid. This is known as the pentacrinoid stage. Traces
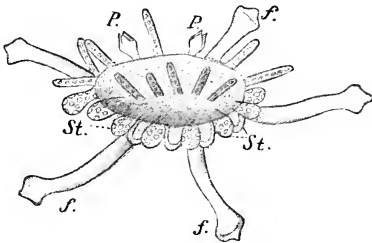
Fig. 216.—Young sea-urchin (*Arbacia pustulosa*) with degenerated Pluteus arms attached (after JOH. MÜLLER). *f*, feet; *P*, pedicellariæ; *St*, spines.

of this stage are already shown in the free-swimming larva through the fundaments of the skeleton, which make their appearance in the mesenchymatous tissue of the larva. They are first seen as small granules, which, however, soon enlarge into triradial and quadriradial forms, and finally become fenestrated plates (Fig. 217). Two rows of five plates each can be distinguished,—the *oralia* and *basalia* constituting the calyx,—and a piece lying below these, the future terminal plate of the stem (Figs. 217, 221, and 222, p. 450). According to BURY, it is this plate of the skeleton which first makes its appearance deep in the body of the larva. Inas-

much as new segments (the stem-joints) are interpolated between it and the basalia, it moves farther downward. The stem-joints take their origin at the base of the calyx. The youngest, therefore, lie next to this, the oldest, on the other hand, next to the terminal plate. At first they form annular plates, but soon alter their shape and become thick segments by the secretion of rod-like calcareous concretions on both their surfaces.

Between the uppermost stem-joints and the basalia lies a larger skeletal piece, which has been called the centrodorsal plate (Fig. 223 *cd*, p. 451). It forms the important foundation of the basal plate of the calyx. According to BURY, it arises by the union of several skeletal pieces. For three sub-basal plates make their appearance below the *basalia*; these at length fuse with one another into a five-pointed star and finally unite with the uppermost joint of the stem to form the centrodorsal plate. This condition is important, because certain fossil Crinoids (*Ichthyocrinoidæ*) also possess three sub-basal plates with the same arrangement.

FIG. 217.—Larva of *Antedon rosacea*, with ciliated bands and tuft of cilia, as well as fundaments of the skeletal plates inside. *Gr*, pit, by means of which the larva attaches itself; *Lm*, the so-called larval mouth.

The series of plates of the calyx are at first not arranged in a closed ring, but in the form of a horseshoe, the open side of which corresponds to the position of the "larval mouth."

Before the skeleton attains the development described, the larva has already given up its free life. After about twelve hours of swarming it attaches itself by means of the

preoral pit (Fig. 217), which then quickly broadens into an adhesive disc. At this stage of attachment the larva lies with its entire ventral surface on the object to which it attaches itself. At first it still possesses its typical ciliation, but that is soon lost. At the same time its shape changes, the anterior end, with which the larva attaches itself and which subsequently grows out into the stem, diminishing in size and the opposite end becoming broader. The club-shaped larva now rises from its support, to which only the small end remains united. Accordingly we now designate the club-shaped portion, which becomes the calyx, as the upper part, the narrowed portion as the lower part, of the larva (Fig. 218).
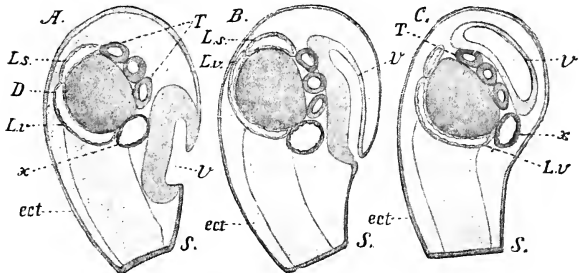
Fig. 218.—*A* to *C*, early stages of development of the attached larva of *Antedon rosacea* (after J. Barrois). Development of the vestibule (*V*) by invagination of the ectoderm (*ect*). *D*, intestine; *Ls*, subambulacral; *Lv*, visceral, body cavity; *S*, stalk of the larva; *T*, tentacular vessel; *x*, stone canal (?).

The most important change which takes place in the larva after this metamorphosis of its external shape affects its ventral surface. The wide pit which is found there, and which is called the larval mouth, becomes obliterated during the attachment of the larva, but a new invagination of the ectoderm takes place at the same spot, which is deeper than the pre-existing one. Here also, as in the region of the "larval mouth," the ectoderm is greatly thickened (Fig. 218 *A*). The invagination soon enters into relationships with the internal organs, for its upper margin extends out

toward the upper pole of the larva, and thus the floor of the
pit comes to lie over against the internal organs (Fig. 218 *B*).
At the same time the opening of the invagination narrows,
and is finally entirely closed and [the invaginated layer]
detached. In this way the invaginated part of the ectoderm
comes to lie inside as a closed sac, and since it follows still
more the tendency existing from the beginning, it moves
quite to the upper end of the larva (Fig. 218 *C*). This sac
subsequently changes in such a way that its floor overlies
the evaginations of the water-vascular system (tentacular
vessels), and its roof unites with the mesenchyma and the
outer ectodermal lamella to form the roof of the vestibule
(Figs. 219 and 220)—the chamber on the floor of which the
mouth subsequently arises, and the roof of which disappears
to set free the tentacles. However, before the beginning of
these processes, which bring the larva nearer to its per-
manent shape, important changes take place in the internal
organs.

Just as the Antedon larva, with its five ciliated rings, recalls the cask-
like shape of the Holothurian larva, so, too, the development of the
vestibule and the investment of the tentacles by its floor show a certain
resemblance to the formation in the Holothurian larva of the vestibule
in which the tentacles lie (comp. p. 427). Here, as there, it is a de-
pression of the ectoderm which forms the vestibule and supplies the
external covering of the tentacular vessels. In both cases the process
takes place in the region of the mouth, which, however, exhibits a
different position in regard to the ciliated rings.

We left the internal organs at a stage of development at
which the two enterocœles and the hydrocœle lay at the
side of the saccular intestine. The latter, which at first lies
ventrad of the intestine, moves, with the metamorphosis of
the larva into the pentacrinoid form, to a position over the
intestinal sac (Figs. 218 and 219), and grows out into the
shape of a horseshoe, its two arms finally uniting into a ring.
At the same time there are formed five upward evaginations,
which are covered over by the ectodermal cell-layer which
forms the floor of the vestibule (Figs. 218 *C* and 219). The
prolongation of the hydrocœle, which was recognizable even

at the time of its establishment, has in the meantime elongated as far as the outer body-wall and fused with it (Fig. 219), forming in this way the stone canal (BARROIS). As in the other Echinoderms, so also in the Crinoids, at least while they are young, a communication exists between the water-vascular system and the outside world; this fact was established by PERRIER and confirmed by BARROIS.

As is well known, a large number of stone canals hanging down into the body cavity occur in the adult Crinoids. LUDWIG (No. 32) had already shown that in the penta-crinoid stage of the Antedon larva at first only *one* stone canal is present; but he believed that this also, arising from the water-vascular ring, ended free in the body cavity, whence it took up into it the water which entered through a pore in the body-wall. This view corresponds nearly to that which was defended upon embryological grounds by BURY. According to him, the free process of the fundament of the hydrocœle, which was considered by BARROIS as a stone canal, is rather a third cœlomic sac. This enlarges, comes into connection with the body-wall by means of a process (parietal canal), and thus opens to the outside world by means of the water-vascular pore. It is only secondarily then that the hydrocœle, by means of a stone canal, is united to this part of the body cavity. The description of these conditions coincides with that given by LUDWIG for *Asterina*, where the stone canal

FIG. 219.—Longitudinal section of an *Antedon* larva (after figures by PERRIER). *D*, intestine; *Ls*, subambulacral, *Lv*, visceral, part of the body cavity; *S*, stalk of the larva; *St*, stone canal; *T*, tentacle; *V*, vestibule; *Wr*, water-vascular ring, from which spring the tentacular vessels and the stone canal.

also opens into the enterocœle, and is connected with the dorsal pore only by means of this (comp. *supra*, p. 436). According to PERRIER, the pore described by LUDWIG, which lies in one of the oral plates, corresponds to the external opening of the stone canal. The stone canal is said to be easily separated from the pore in dissecting, and then hangs from the water-vascular ring free in the body cavity.

In later stages of the larva still other canals are developed as evagina-
tions of the water-vascular ring and the peritoneum which covers it.
They grow out toward the body-wall and unite with it. At the time
when the larva detaches itself, five such canals are present, all of which
communicate with the outside world. Afterwards, however, the forma-
tion of the evaginations and the pores of the cup is said no longer to
take place simultaneously, so that the former may multiply independently
of the latter, and *vice versâ*. Thus a condition would arise such as was
described by LUDWIG,—cup-pores leading to the interior, and free appen-
dages of the water-vascular ring opening into the body cavity. The canal
which was first formed attains an extraordinary development, and
PERRIER regards it alone as homologous to the stone canal of other
Echinoderms, those formed later being of a secondary nature.

The conditions of the body cavity of the Antedon larva are
complicated. The two cœlomic sacs, which at first lie at
the right and left of the intestine, subsequently, when the
larva passes into the pentacrinoid stage, arrange themselves
above and below the intestine (Figs. 218 and 219). PERRIER
designates the parts of the body cavity as the subambulacral
and visceral portions. Where the two come together there
is produced a mesentery, extending transversely across the
body (Figs. 219 and 220). Furthermore, according to BURY,
two longitudinal mesenteries are formed, owing to the facts
that the two cœlomic sacs are (in cross-section) nearly
horseshoe-shaped, and that the two arms of each sac grow
out toward each other. In each case they meet in a longi-
tudinal mesentery, the one belonging to the upper entero-
cœle lying in the anal radius and that of the lower (visceral)
enterocœle in the preceding radius (reckoned according to
the course of the intestine). As the cœlomic sacs enlarge
they apply themselves to the intestine and water-vascular
ring as the splanchnic layer, and to the mesenchymatous
tissue of the body-wall as the somatic layer. The aboral
body cavity, as was pointed out by GOETTE, sends a process
into the narrow posterior part of the larval body (Fig. 220).
According to PERRIER, this process consists of both layers of
the mesoderm (Fig. 219), and GOETTE's conjecture is con-
firmed, viz. that the chambered organ, which in the adult
animal lies within the centrodorsal plate as an important
part of the blood-vascular system, arises from this posterior

process of the body cavity. We shall revert to this part of
the body cavity and its derivatives later.

An entirely clear insight into the structural conditions of the body
cavity, which are obviously difficult to follow, cannot be gained from the
authors' statements (GOETTE, PERRIER, BARROIS, BURY), since they do not
agree. The older statement of GOETTE, according to which the body
cavity also takes part in the formation of the vestibule, appears in
another light since the descriptions which BARROIS and BURY give of
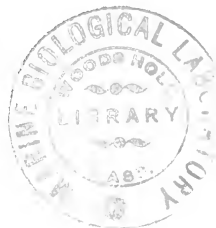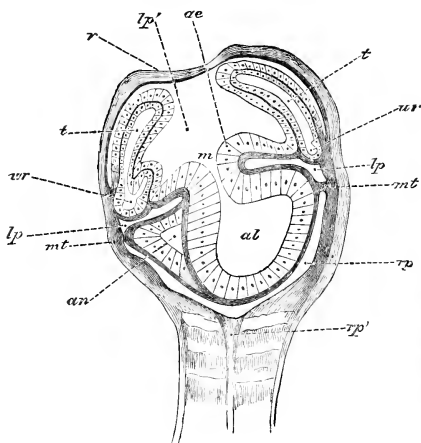
FIG. 220.—Longitudinal section through the cup of an *Antedon* larva, the vesti-
bule of which is still closed (after GOETTE, from BALFOUR's *Comparative Embryo-
logy*). *ae*, depression of the vestibular epithelium to form the mouth (*m*); *al*, intestinal
canal; *an*, region of the anus; *lp*, subambulacral body cavity; *lp'*, vestibule; *m*,
mouth; *mt*, transverse mesentery; *r*, roof of the vestibule; *rp*, visceral part of the
body cavity and its prolongation (*rp'*) into the stalk of the larva; *t*, tentacle; *wr*,
water-vascular ring.

this process. According to these authors, the lining of the vestibule
is not mesodermal, but ectodermal. The penetration of an enterocœlic
diverticulum into the stem, observed by GOETTE, PERRIER, and BURY, is
denied by BARROIS. According to him, these axial structures arise rather
by an accumulation of mesenchyma cells. On the other hand, according
to BARROIS, a process of the subambulacral body cavity penetrates axially
toward the stem. BURY's contention that, in addition to the right and

left portions of the body cavity, there is developed still a third part, was already mentioned in considering the hydrocœle (comp. p. 413).
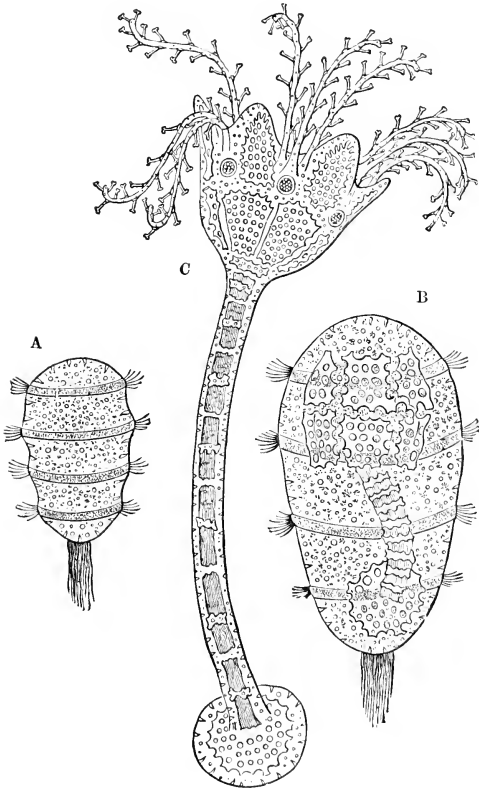
FIGS. 221 (and 222).—Pentacrinoid larva (C) and swarming larvæ (A and B) of *Antedon* (after THOMSON, from BALFOUR'S *Comparative Embryology*). The most anterior ciliated ring, described by BURY, is lacking on the swarming larvæ, which are placed in the positions in which they subsequently become attached (comp. Fig. 217, p. 444).

Hitherto we have learned of the intestinal canal of the Antedon larva only as a closed sac. The mouth and œsophagus do not arise until the formation—on the floor of the vestibule in the middle of the water-vascular ring—of a depression, which fuses with the intestine (Fig. 220 *m*). The intestine therefore does not even yet open directly to the outside world, but into the vestibule. Its interior at this time is not empty, but filled with cells (BURY) or with a kind of nutritive yolk (BARROIS). The entodermal mass elongates backwards (basal-wards) to form the intestine, and winds spirally about the axial part of the body cavity. Its end then moves in the transverse mesentery, at about the height of the upper margin of the basal plates, up to the body-wall (Fig. 220), with which it fuses, subsequently breaking through to the exterior. The anus comes to lie in the vicinity of the water-vascular pore. Subsequently it is shifted to its final position on the ventral wall of the cup. As in the rest of the Echinoderms, the anus seems to have no direct relation to the blastopore.

Having considered the internal developmental processes, we turn again to the external shape of the larva, which in the meanwhile has essentially changed. These changes are partly due to the metamorphosis of the hydrocœle. Each of the

Fig. 223.—Diagram of a pentacrinoid larva of *Antedon rosacea* (after THOMSON, from BALFOUR's *Comparative Embryology*). *cd*, centrodorsal plate ; *or*, oralia ; 4, radialia ; 3, basalia ; 1, terminal plate.

five primary tentacles, which we have already seen to be an evagination of the water-vascular ring, splits into three

parts, so that fifteen tentacles can now be recognized. By the addition of two new tentacle-buds to each of the five groups, the number of tentacles soon increases to twenty-five, arranged in five radial groups. The tentacles (Figs. 219 and 220 t) project into the vestibule, the roof of which is stretched out between the upper margins of the oralia. This roof is at first thick, but gradually becoming thinner (Fig. 220 r), finally disappears entirely. The gradual disappearance of the roof is partly a result of growth, partly brought about by histolytic processes. According to BURY, such processes can also be recognized on the rest of the larval body, and cause a disappearance of the histological differentiation. Probably migratory cells make their appearance in this connection as *phagocytes*.

After the disappearance of the roof of the vestibule, the tentacles, on which papillæ subsequently bud forth, project free to the exterior (Fig. 221 C). The under-part of the larva has elongated into the stalk, and it now rests with its terminal plate on some support. The fundaments of the arms bud forth on the upper part of the cup as five projections (Fig. 221 C). The tips soon split into two branches corresponding to the permanent forking of the arms. One of the radial tentacles, each of which has likewise split into two, unites with the fundament of each of the arms. Surrounded by this, it grows out with it and becomes the ambulacral canal of the arm. By means of lateral budding it gives rise to the tentacles of the arm. The tentacle which is first formed always remains at the tip of the arm. The new tentacles arise at its base in groups of three. The mode of formation of the tentacles is therefore similar to that of the ambulacral feet of other Echinoderms. The development of the pinnules is the result of a forking of the arms, which occurs alternately to the right and to the left (W. CARPENTER, PERRIER). This explains the alternating position of the pinnules.

Important changes have taken place in the skeleton of the larva. Between the basal and oral plates, alternating with the latter, five new skeletal pieces, the *radialia*, have made their appearance (Fig. 223$_4$); these become greatly enlarged,

and serve for the support of the arms (Fig. 224 r_{I}-r_{III}). Through the vigorous growth of the radial pieces, to each one of which two other plates are added, the oral plates are crowded on to the oral surface, where they finally undergo resorption. In other Crinoids (*e.g.*, *Rhizocrinus*), on the contrary, the oralia are said to persist throughout life. Another change has taken place at the base of the cup: the centrodorsal plate has gradually overgrown the *basalia* and the lower *radialia*, so that nothing more remains visible of the chief pieces of the original cup. The basalia have fused into an unpaired piece, the so-called rosette. The
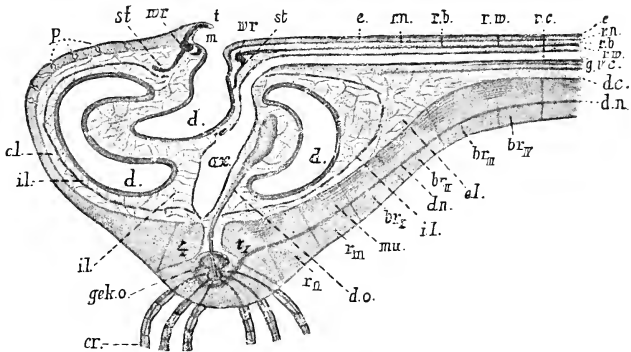
FIG. 224 —Vertical axial section through the disc and point of attachment of an arm of *Antedon rosacea* (with slight changes, after H. LUDWIG). At the left the section passes through an interradius, at the right through one of the radii. *av,* axial body cavity; *br*$_{\mathrm{I}}$, *br*$_{\mathrm{II}}$, *br*$_{\mathrm{III}}$, *br*$_{\mathrm{IV}}$, brachialia (skeletal pieces); *cl*, circum-visceral body cavity; *cr*, cirri; *d*, intestine; *dc*, dorsal canal of the arm; *dn*, dorsal nerve; *do*, dorsal organ; *e*, epithelium of the ambulacral groove; *g,* genital canal; *gek. o*, chambered organ; *il*, intervisceral body cavity; *m*, mouth-opening; *mu*, musculature of the arm; *p*, pores of the cup; *r*$_{\mathrm{I}}$, *r*$_{\mathrm{II}}$, *r*$_{\mathrm{III}}$, radialia (skeletal pieces); *rb*, radial blood-vessel; *rn*, radial (ventral) nerve; *rw*, radial water-vessel; *st*, stone canals; *t*, tentacle; *vc*, ventral canal of the arm; *wr,* water-vascular ring and the stone canal (*st*) proceeding from it.

stem of the pentacrinoid stage now also degenerates. In place of it there are developed from the centrodorsal plate (according to PERRIER as evaginations of the chambered organ) at first five and later additional cirri, by means of which the young Rhizocrinus attaches itself (Fig. 224 *cr*).

Some internal developmental processes still remain for us to consider, in which, however, we must confine ourselves to the fundaments of the chief systems of organs.

We saw that the body cavity of the young larva consists of two separate spaces, namely the subambulacral and the visceral body cavities (Figs. 219 *Ls* and *Lv* and 220 *lp* and *rp*). In the development of the arms these two spaces are continued into them and give rise to their ventral and dorsal canals (PERRIER). The separation of the body cavity into these primitive spaces does not, however, persist long. The mesentery lying between the subambulacral and visceral body cavities partly disappears, and the two thus coalesce. On the other hand, a membrane, which marks off a central space (Fig. 224 *ax*)—lying approximately in the perpendicular axis of the body—from the rest of the body, makes its appearance as a new structure. Another such boundary is developed in the periphery of the intestine (Fig. 224 *il*); it is called the visceral sac. The part of the body cavity lying external to it is called by LUDWIG the circumvisceral, the inner part, on the other hand, the intervisceral, body cavity[1] (Fig. 224 *cl* and *il*). Enclosed in the latter lies the axial cavity (*ax*) already mentioned. After the disappearance of the primary mesenteries and the development of these spaces, the ventral canal of the arm coalesces with the axial, and the dorsal cavity with the circumvisceral cavity (Fig. 224).

The genital canal, which encloses the genital cavity, extends in the arms between the dorsal and ventral canals (Fig. 224 *g*). These structures also take their origin from the disc. According to PERRIER, the genital apparatus is established at an early period, even before the pentacrinoid stage is reached. It then consists of a thickening of the splanchnic layer of the visceral body cavity and occupies an axial position in the lower part of the cup. It remains here for a while, and so changes as to acquire a racemose appearance and, within, a cavity. After the development of the arms has taken place, it splits at the tip and sends a branch into each arm. This mode of origin of the genital apparatus agrees with the recent description of HAMANN (No. 21), according to whom there is in other Echinoderms also a central part of the genital apparatus, from which branches go off to the different radii. The additional branching of the genital tubes to the pinnules in the Crinoids is then homologous with the development of the genital sacs of other Echinoderms.

As regards the blood-vascular system, we have already learned that the chambered organ lying in the centrodorsal piece takes its origin from the outer enterocœlic lamella, which penetrates into the larval stalk (PERRIER). This splits into five cords, which acquire cavities and then

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[1] The presence of separate spaces of the body cavity is not admitted by HAMANN (*Histologie der Crinoiden*, Jena, 1889). We have followed the statements of LUDWIG, and as regards embryological questions have adhered to those of PERRIER.

form the five chambers of the organ. By means of an invagination each chamber gives rise to one of the five primary cirri. The dorsal organ (Fig. 224 *do*) is united with the chambered organ, in which, as in the latter, one is inclined to see the central organ of the blood-vascular system (LUDWIG).[1] According to PERRIER, the dorsal organ is composed of the genital fundament previously mentioned and a vascular plexus. The latter would also take its origin from the inner enterocœlic lamella of the visceral body cavity. A coalescence of the genital canals of the arms in the dorsal organ was conjectured even by W. B. CARPENTER and by LUDWIG. A number of other vascular plexuses are distinguished by PERRIER, and their development described. They are said to be directly connected with the ambulacral system. Inasmuch as portions of the body cavity also communicate with the so-called blood-vessels, the circulation is said to be general.

The views on the development of the nervous system are not yet clear enough to admit of a brief description. When PERRIER derives parts of the nervous system from mesenchymatous elements, he is in opposition
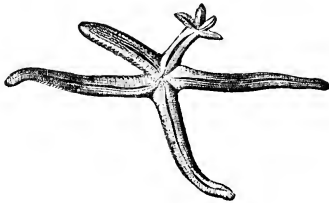
to the prevailing views. [To supplement what is stated here, reference is made to the work of SEELIGER (No. XXVI.), which gives a very thorough account of the embryology of Comatula.—K.]

Regeneration and Division.—Starfishes possess to a high degree the power of replacing lost arms. Single arms, which have become detached from the disc, are again made good; in fact, a detached arm is able to develop an entirely new disc with the normal number of arms. The so-called comet form of the starfish (VON MARTENS, HAECKEL) is due to the newly formed parts, which at first are relatively small, being appended, as it were, to the large arm. The mere replacement of lost parts seems here to merge into a reproduction by division. Such really takes place in those forms in which the disc constricts spontaneously

[1] In the recent work of HAMANN mentioned in the preceding note, the connection of the dorsal organ with the chambered organ is denied, and likewise the important relation of the former to the blood-vascular system is regarded as being without evidence.

through the middle and produces two parts, which again grow into new individuals (Kowalevsky, Simroth). Each part acquires a new mouth and the complete organization of the normal animal. A division of this kind, such as is found, for example, in *Asteracanthion tenuispinus* and *Ophiactis virens*, may be called *schizogony*.

An interesting form of regeneration, which can scarcely be called by that name, since it transcends the meaning of that word and appears to approach non-sexual reproduction, is described by P. und F. Sarasin (No. 46). They saw new arms budding forth on the stump of an arm of *Linckia multifora* in such a way as to seem to form a new star, which remained attached to the stump of the arm (Fig. 225). P. und F. Sarasin look upon this process as a budding of the starfish, and it is not to be denied that it would merit this term, if a mouth-opening could be demonstrated on the young starfish.

General Considerations.—The development of the various divisions of Echinoderms offers many common features, in which a close relationship of the five divisions can be recognized. We saw that cleavage was always total, tolerably equal, and its result a ciliated blastula. A typical invagination gastrula arises from it. The mesenchyma cells detach themselves from the invaginated part (*Antedon, Astropecten, Synapta*). The fact that the development of the mesenchyma in other forms (*Echinoidea, Ophiuroidea*) takes place even before gastrulation is completed does not seem to constitute an important distinction, because in such cases it is from the same region—namely, the entodermal part of the blastula—that the detachment of the mesenchyma cells takes place, and because in another case (*Holothuria*) this occurs during the beginning of gastrulation. The mesenchyma is doubtless to be traced to the same origin as the mesodermal structures, which as cœlomic sacs detach themselves from the archenteron. This assumption gains in probability from the fact that in a later stage of development another separation of cells takes place from the epithelium of the entero-hydrocœle. Enterocœle and hydrocœle are the derivatives of the two cœlomic sacs, which are constricted off together from the apex of the archenteron. They then separate into the two enterocœles and the hydrocœle, which latter enters into communication with the outside world by means of the dorsal pore.

The blastopore, in those cases where it persists, becomes the anus. The mouth arises by the union of the archenteron with the ectoderm. Certain differences occur in regard to the formation of mouth and anus as the result of differences in the mode of life and the consequent alteration of the shape of the larva. The larvæ are quite different in shape in the different groups of Echinoderms, although common features are not lacking. Apart from the internal organization already mentioned, in regard to which they are entirely comparable with one another, the external characters can also be compared, in spite of the differences in the shape of the body and, above all, the ciliated band, which, together with the shape of the larva, is derivable from a common fundamental larval form. Even the cask-shaped larva of *Antedon*, differing as it does from the other larval forms of the Echinoderms, resembles in shape the so-called pupa of the Holothurians, which, like it, possesses five ciliated bands.

The further development must in turn present differences corresponding to the variations in shape of the larvæ; but, on the other hand, it also exhibits certain resemblances, as the usual similarity of structure in the different systems of organs demands. Thus not only the fundament, but also the further development, of the water-vascular system recurs in nearly the same way in all cases. The development of the nervous system, as far as it is known, also shows many things in common, and the same is true to a still greater extent for the musculature. The early development and union of the ambulacral and subambulacral surfaces of the starfish and the Ophiuran in the *Brachiolaria* and *Pluteus* larvæ, which differ so much from each other in shape, takes place in a strikingly similar way. In the larvæ of Crinoids and Holothurians, a certain resemblance in regard to the development of the tentacles at the bottom of the vestibule or oral funnel cannot be mistaken.

As regards the development of the skeleton, it is not possible from what is at present known to discover any positively established relations between the different divisions of Echinoderms. To be sure, reference has been made to the position of the forming plates in relation to the internal

organs (H. P. Carpenter, Bury), but these relations are
quite uncertain still. Even the conception of the homology
of the plates founded by Lovén and championed by Car-
penter, especially those which in the different groups of
Echinoderms lie about the apical pole, is not to be considered
as assured.

All Echinoderms have a radial structure; the larvæ, on the
contrary, are bilaterally symmetrical as regards both their
internal and their external organization. It has been shown
by different examples how the radial structure arises onto-
genetically from the bilateral; but the question now presents
itself, How is the shape of the Echinoderms to be explained
phylogenetically? A reply to this involves another question,
namely, whether the different groups of Echinoderms are
derived one from the other, and in that event which of them
stands the highest and which the lowest. Recently the
Holothurians, and especially the apodal Holothurians
(*Synapta*), have been looked upon as the lowest forms, and
transitions have been sought from them to the Crinoids on
the one hand and to the Echinoids on the other, because certain
Holothurian characters were found on the one hand in the
(fossil) *Cystidæ*, on the other hand in the soft-shelled *Echino-
thuridæ* (P. und F. Sarasin, No. 47). Additional transitions
to the Asteroids and Ophiuroids are also demonstrable.
This theory, to be sure, traces the Echinoderms back to
simple forms, but gives no explanation of the origin of the
radial structure. Even the apodal Holothurians are still
radially constructed, and it does not seem at all impossible
that the simplicity of their structure is only a phenomenon
of degeneration. The Echinoderms, however, as we may con-
clude from their ontogeny, are to be referred to bilateral
forms as their source.

Another theory is that which traces back the different
divisions separately to a common ancestral form known as the
Pentactæa (Semon, No. 55). This ancestral form corresponds
to that stage in the ontogeny in which the larva had already
passed from the bilateral to the radial form by the closing
of the water-vascular ring, and by the putting forth of
five evaginations. Semon finds such a Pentactula stage in

the ontogeny of all five groups, and from this argues for a
common ancestor having that form. This theory encounters
the difficulty that the five groups, if they had assumed such
an independent development, would scarcely show so great
a resemblance in their organization as they in fact do. It
seems to us more justifiable to search for the ancestral forms
of the Echinodermata among the existing material which is
offered to us by palæontology. In this, however, the other
difficulties arise that the material is not complete, since
delicate forms have not been preserved, and that it allows
only the external shape to be recognized.

At all events, it will be the stalked forms among which
we are to search for the ancestors of the Echinodermata;
for at any rate it was the influence of the attached mode of
life which in the Echinoderms, as in other groups of animals,
called forth the radial structure. Such forms as the *Cystidæ*
—which are in part stalked and in part without stalks, and
of which one part obviously led an attached life, while the
other part, on the contrary, led a free existence—seem best
fitted to stand as the ancestral forms of the Echinodermata
(comp. also NEUMAYR, No. 43). Their shape is spherical,
not yet being prolonged into arms. In many of them the
plates are irregularly arranged, and then no trace of a radial
arrangement is noticeable. On the other hand, five radial
furrows may extend out from the mouth, similar to the
ambulacral furrows on the disc of a Crinoid or Asteroid.
However, it is the relationships which exist between the
Cystidæ and the other groups of Echinoderms that seem
to be especially important. The Cystidæ, by means of tran-
sitional forms, are said to stand in relation to the Crinoids,
the Asteroids, and the Echinoids (NEUMAYR, No. 43). Since,
however, the Echinoids have been placed nearer to the Holo-
thurioids by P. UND F. SARASIN, and since evident relation-
ships between the Cystidæ themselves and the Holothuri-
oidea have been discovered by the same authors, this latter
group can also be compared with the rest of the Echino-
dermata. To us it seems probable that the Echinoderms
established their radial structure by an attached mode of
life long continued, and only later returned again to a free

life, which to-day characterizes the most of them. The shape of the larva seems to have been produced independently of this course of development.

As regards the question what may have been the nature of the bilateral progenitors of that radial ancestral form, we are altogether in the dark. Ontogeny gives no answer to this question, since, on the one hand, the larvæ are much changed, owing probably to phenomena of adaptation, and since, on the other hand, no true relationships to other larval forms—*e.g.*, those of the worms—can be recognized. One would most naturally compare the larvæ of the Echinodermata with those of the *Turbellaria* and *Nemerteans* or with the *Trochophore*, but the difference in the distribution of the ciliation and the absence of the apical plate make this difficult. Such larvæ as that of *Antedon*, the Holothurian pupa, and the vermiform larva of the Asteroidea (Joh. Müller) recall segmented forms; but they may quite as well represent secondarily acquired stages of development. This is especially difficult to determine in the case of the larva of Antedon, for it is not impossible that larvæ of the typical form of the Echinoderm larvæ make their appearance in the development of the Crinoids, which is still little known. The larva of Antedon even is modified, as the disappearance of the blastopore shows. Nevertheless, the resemblance to the Holothurian pupa is striking, the latter certainly representing a secondary stage of development.

The Echinoderm larvæ, as far as regards their internal organization, resemble most closely such forms as the Annelida, owing to the occurrence of cœlomic sacs. We are inclined to refer the formation of such a body cavity as takes place in the Annelida to a like origin with that of the Echinodermata, and accordingly to regard the mesoderm of the Echinodermata and that of the Annelida as homologous structures. Indeed, indications which point to relationships of the Echinodermata with segmented forms are not lacking.

An internal segmentation would find expression in the body, if the condition described by Bury (No. 8)—the development of two pairs of

enterocœles—should be confirmed. This would indicate an approach to segmented forms. But in this connection one is involuntarily reminded of the condition of the larva of *Balanoglossus*, in which, according to BATESON, an internal segmentation is expressed by the establishment of three pairs of cœlomic sacs (comp. Fig. 167, p. 380). Even in its external shape the *Tornaria* of *Balanoglossus* seems to possess a certain resemblance to the Echinoderm larvæ. Added to this is the fact that the so-called water-vascular vesicle of Balanoglossus may exhibit a bipartite fundament. Also the water-vascular vesicle of the Echinoderms in certain cases (especially in the Ophiuroidea, and occasionally in the Asteroidea) is said to be begun as a paired structure (METSCHNIKOFF). Should this statement (hitherto held to be insufficiently authenticated) be confirmed, then one would be able to compare the fundament of this system of organs—so important for the Echinoderms, but so obscure as regards its phylogenetic origin—with an embryonal excretory apparatus (primitive kidney). This view is supported by the discoveries of P. UND F. SARASIN (No. 47), who explain the glandular structure, which opens to the exterior at the same time as the stone canal—the so-called heart of the sea-urchin—as an excretory organ communicating freely with the body cavity by means of an open ciliated funnel. The assumption of the SARASINS that the excretory system is the more primitive, and the water-vascular system, with its locomotor function, is only an organ derived from it, seems to be one that is required by the natural course of events.

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