The ORTHONECTIDA, *a* NEW CLASS *of the* PHYLUM *of the* WORMS.[1] By ALFRED GIARD, Professor in the Faculty of Sciences of Lille. With Plate XXII.

IN 1868, in an interesting memoir[2] on the marine Planarians of St. Malo, Keferstein figures an animal which he designates by the name "problematic parasite." The explanation of the plate (plate ii, fig. 8) indicates that this parasite has been found several times, and often in great quantity, in the digestive tube of the Tremellaria (*Leptoplana tremellaris*). The text gives us no information as to this curious organism, and it is chiefly by means of the rather rough figure of the second plate of Kerferstein's work that we are led to refer it to the group which we are about to study.

MacIntosh, in his beautiful monograph of the British Nemerteans, published in 1874,[3] recalls the observation of Keferstein in reference to a parasite which he met with in *Lineus gesserensis* (*Nemertes communis* of P. J. Van Beneden), and concerning which he gives the following details, accompanied by a few drawings:

"Another curious parasite is found burrowing in the body-wall of *Lineus gesserensis*, its presence being readily recognised by the perforated and honeycombed appearance of the dorsum of the affected animal, whose textures seem to be the seat of the workings of a microscopic *Tomicus typographicus*. When highly magnified, the affected region appears to be covered with a vast network of pale, minutely granular channels, which contain numerous opaque, ovoid, granular masses.

"On rupturing the body of the worm a large number of the peculiar structures (plate xviii, fig. 17) slide out of the channels, and swim through the surrounding water, generally, though not always, with the upper end (in the figure) first. Externally they are coated with long cilia, whose activity in the free state is of somewhat short duration, for after a time the animals remain quiet, and they drop off. The body is

[1] This memoir has been corrected and new matter, including previously unpublished figures, has been added by Professor Giard to the original memoir, which appeared in 'Robin and Ponchet's Journal,' for the present publication.

[2] Keferstein, 'Beiträge zur Anatomie und Entwickel. einiger Seeplanarien,' Göttingen, 1868.

[3] 'A Monograph of the British Annelids,' part i, Ray Society, p. 129, and pl. xviii, figs. 17, 18, 19.

distinctly segmented, and tapers slightly towards the posterior end; while the surface is marked by very fine longitudinal striæ, as in Opalina, though in a much more minute degree. Anteriorly is a conical portion (*a*), composed of three rather indistinctly marked segments. Two evident annuli (*b*) succeed, the posterior part of the last being narrowed, so as to cause a constriction of the body-wall. Behind are six nearly equal divisions (*c*), each often appearing double, that is, has a broad anterior and a narrow posterior annulus. The posterior region (*d*) consists of three indistinct segments. The body is minutely granular throughout, and an internal cavity is apparent from the fourth segment to the last, commencing in the former by a rounded end, and terminating just within the border of the latter. No aperture is observed at either end. The opaque, ovoid, granular bodies (plate xviii, fig. 18), scattered profusely throughout the infected portions of the Lineus, are evidently early stages in the development of this species, and they, too, are ciliated. On subjecting them to gentle pressure (fig. 19), transverse segmentation is apparent, the number of segments varying according to the degree of advancement. The parasites are very delicate structures, and in the free state soon break up into cells and granules, after discarding their cilia, as above mentioned. Transverse section of the affected worms shows that they occur both in the skin and in the walls of the digestive tract, their ravages in the pigmentary layer of the former tissue causing the curious appearances which led to their detection. It is a somewhat difficult point to determine whether the skin, muscles of the body-wall, or digestive canal, constitute the common area of this creature's depredations, whether it is piercing the former on its way to the surface, or passing to the alimentary cavity to be voided per anum. The characteristically segmented condition of the mature specimens and their internal structure exhibit a higher type of organisation than the ordinary Opalina. Professor Keferstein found a very similar parasite in the stomach of *Leptoplana tremellaris*, but he did not describe it further than simply mention, under the explanation of the plate, that it is an enigmatical structure. The centre of the body is occupied by a double row of large cells in his figure."

Such are the details, certainly rather incomplete, it must be conceded, which we have been able to find in earlier writers touching the curious animals which we have designated by the name of ORTHONECTIDA.[1]

[1] We published in the 'Comptus Rendus de l'Académie des Sciences'

II.—Species Observed.

I have had the opportunity of studying the species discovered by MacIntosh. *Lineus gesserensis* is very common at Wimereux, as also its variety *Lineus sanguineus*, under stones, in oozy spots, which are accessible every day even during the neap tides.

My attention was drawn to the parasite of this species, a rare one, on the whole, by my pupil and friend, J. Barrois, at the time when he was preparing in our laboratory his work on the Nemerteans. But I could then, in the absence of sufficient material, do no more than verify a part of the observations of MacIntosh, and rectify certain errors committed by this eminent zoologist, as I shall point out further on.

In vain I have sought, on several occasions, for the parasite discovered by Keferstein in *Leptoplana tremellaris;* and yet this Planarian is excessively common at Wimereux, in very nearly the same spots as *Lineus gesserensis*. Paul Hallez, Demonstrator in the Faculty of Sciences at Lille, who has dissected numerous examples of Leptoplana, has had no better luck than I in this search.

A happy chance made me acquainted, in 1877, with two new species of Orthonectida, which I have been able since to obtain in sufficient abundance to make a nearly complete study of them, although some gaps still remain to be filled up.

During the autumn of 1877 I had betaken myself to Wimereux in order to study the embryogeny of a species of Ophiura with condensed development. I had a choice between two species, *Ophiothrix fragilis* and *Ophiocoma neglecta,* both equally common, hermaphrodite, and viviparous. Reasons of an entirely technical nature caused me to prefer the second. In opening hundreds of Ophiocoma, to extract from them the embryos, I discovered two species of Orthonectida which have enabled me to undertake the study of the group. Both are excessively abundant in the animal infested by them, but it is quite a rare thing to find an Ophiurid thus infested. According to my notes, each species may be found once among about eighty specimens of Ophiurids, so that one has the chance of finding one or other species once in forty specimens dissected.[1]

(Seance du 29, Octobre, 1870), a short preliminary notice of these animals.

[1] Besides these two species of Orthonectida, *Ophiocoma neglecta* presents at Wimereux a certain number of other parasites, which are interesting.

1. A pretty Vorticella with a very short peduncle (*Vorticella ophiocomæ*,

In the month of June last I twice found the two species of Orthonectida associated in the same specimen of an Ophiurid.

It has appeared to me as though the Orthonectida were more common in the autumn than at any other season. But this perhaps depends on the fact that I had been able to give more attention then to my researches than during the academical session.

III.—Anatomy of Rhopalura ophiocomæ.

Nothing is easier than, with aid of fine needles, to separate the whole dorsal region of Ophiocomma from the ventral disc formed by the buccal plates and the arms. The animal deprived of its dorsal cupola, and consequently of its digestive and reproductive organs, lives nevertheless several days, walks, and conducts itself generally as though no injury had occurred to it.

In tearing open the dorsal cupola, in order to force out the embryos, the glass slip on which the operation is being conducted is sometimes seen to be covered by small white flakes, which, on examination with a low power of the microscope, are seen to be animated by a rapid movement of translation in a straight line, which is highly characteristic.

This movement, common to all the species of this group, has led me to give to these organisms the name of Orthonectida. These agile little animals resemble large ciliated infusoria of a porcellanous aspect and a generally cylindrical form. A certain number, however, have a somewhat shorter form, irregularly ovoid, and move more slowly.

In the one form or the other they are simple *Planulæ*,

nov. sp.), which is found even on the arms of young individuals still enclosed in the maternal incubatory pouch (very common).

2. An Urceolaria (*Ur. ophiocomæ*, nov. sp.), also very common.

3. A copepod crustacean of the family of the Ergasillidæ, or rather of a distinct family comprising the annelidocolous species. This crustacean, which is broad and provided with hooked limbs, attaches itself to the arm of the Ophiurid between the bristles. It recalls the form of the crab-louse. By a very natural association, I name it *Phthiriopsis Emilii*, and I dedicate this parasite of the star-fishes to M. Emile Blanchard, who teaches at the Museum of Paris the history of the Arthropoda. The Phthiriopsis is very rare.

4. A curious little annelid of the genus Sphærodorum, which presents the same relations to Ophiocoma which *Chlorhema Dujardinii* does to *Psammechinus miliaris*. I shall call it *Sphærodorum Greefii*, dedicating it to the learned Professor of the University of Marburg. About one Ophiurid in fifteen harbours a *Sphærodorum*.

All these parasites of Ophiocoma will be studied in detail in a special memoir.

that is to say, organisms composed fundamentally by two layers of cells, the one within the other—an ectoderm or external layer of cells, which are mostly ciliated, and an endoderm constituted by larger cells, which are more granular, and form the lining of a central cavity devoid of either mouth or anus.

The first ring terminates in a blunt cone anteriorly, which carries a bunch of stiff cilia. It is followed by a cylindrical ring of the same length, the whole surface of which is beset with papillæ, which are disposed in eight or ten longitudinal lines and in four or five transverse series; this ring is the sole part of the body which does not present vibratile cilia.

The third ring is larger by itself than the two first together; it gradually widens towards its posterior extremity.

The fourth metamere is of the same dimensions as the papilliferous ring; it is followed by a terminal ring provided with longer cilia, forming a brush at its posterior extremity. This last ring is conical and subdivided into two metameres, less distinct than those in front.

The last rings form a sort of club, with which the animal strikes the water, independently of the movement of the cilia, giving sharp strokes, which one is immediately led to attribute to the contraction of muscular elements. We shall point out below where these elements occur.

Such is the elongated variety. The ovoid variety differs from it only by being a third less in length and a greater breadth. It seems, at first sight, as though it had been derived from the former by a contraction along the long axis; but it is easy to assure one's self that this is not the case, and that it is, on the contrary, the elongated form which is the ultimate condition of the ovoid form, which latter is only the final embryonic phase of the animal.

For a more complete study of the anatomy of Rhopalura it is necessary to employ very high magnifying power, the objective 6 of Verick, or better, the objectif 9 (immersion) of Hartnack.

The ectodermal cells then appear very distinctly, except in the papilliferous zone where it is very difficult to determine their number and form. All the other metameres are made up by a single transverse row of cells, and the difference in the length of the metameres depends entirely on the difference in the length of the cellular elements which compose it. The terminal rings are formed entirely by four cells, as in the Dicyemida, the median rings comprise six or eight cells; it is very difficult to count with exactitude, since optical sections rarely present themselves, and it is impossible to make real sections.

The ectodermal cells present very long and very dense cilia. By using osmic acid, followed by picrocarmine, it is easy to preserve the ectoderm with its clothing of cilia. Preparations made a year ago give at this day an excellent idea of the living animal.[1]

The endoderm is primitively formed of larger cells than those of the ectoderm, but they undergo in the adult a very singular modification. The whole of this layer forms an oval sac, the anterior extremity of which is hidden by the papilliferous ring, and extends from the penultimate metamere until it is inserted, in the form of a sort of pedicle, between the four terminal ectodermal cells (Plate XXII, figs. 3 and 4). The swollen part of the endodermal sac presents, when examined with the immersion lens, fine muscular bands disposed in a finely granular matrix, and recalling the appearance of the endodermic muscular layer of certain nematoids.

I do not believe that these muscular elements are derived from the bodily transformation of certain endodermal cells; I consider them rather as a *part* only of such cells, which are thus called upon to play a double physiological *rôle*. They would thus be analogous to the epithelio-muscular cells described by Korotneff in Hydra, but with this difference, that in the present case it is the external part of the cell which becomes muscular, the internal part remaining epithelial.

I would draw the attention of histologists, more skilled than I am in technical methods, to this very delicate point. The question involved is one worthy of their skill.

Metschnikoff has recently put forward the opinion that the striated bands are formed by the tails of spermatozoa, the entire endoderm being nothing but a testicular gland.[2]

I am quite unable at present to accept the opinion of my learned opponent. These bands are chiefly visible in young individuals; their number is constant; they are always disposed obliquely, as I have figured them, on an ovoid endoderm; and this disposition is not, as I had at first supposed, the result of an accidental torsion. On changing the point of view, the continuation of the spiral is seen

[1] I have shown these preparations to various persons, and specially to Dr. Macleod, of the University of Ghent, who spent a few days at Wimereux during last April.

[2] 'Zoologischen Anzeiger,' II, No. 43, p. 619.

on the other side of the body, and the clear interspaces take the form of lozenges, just as one sees sometimes in looking through certain kinds of open basket-work. Finally, it will be seen below, that I have also found these elements in *Intoshia*, which Metschinkoff considers as the female form of Rhopalura, and where, consequently, there would be no spermatozoa.

Whatever may be the origin of these muscular elements, they unite, as I have pointed out above, into a sort of fascicle at the terminal part of the adult animals, and by their contraction give rise to those brusque movements, those strokes of the club-like tail, to which the name *Rhopalura* has reference.

If the interpretation above given is admitted, there would not be in the Orthonectida any true middle layer, but only a splanchno-pleural pseudo-mesoderm, comparable to the somato-pleural pseudo-mesoderm of the Hydra.

I give to the totality of these elements the name o *pseudo-mesoderm*, because it appears to me desirable to reserve the name of mesoderm, properly so called, for other structures which do not exist in the Orthonectida, and the homology of which in the various groups of Metazoa is very difficult to establish.

I distinguish :—(1) a *solid mesoderm*, formed very early at the expense of the endodermic cells of the embryo (rudiment of the notochord of the Tunicates and of the Vertebrates, skeletogenous cells of the embryo of Echinoderms, mesodermal cells derived from the four first spheres of the endoderm of Planarians, of Bonellia, according to the researches of P. Hallez and of Spengel, &c.). (2) A *cavitary mesoderm* formed by the diverticula of the endoderm (enterocœls), and appearing generally at a later epoch (aquiferous system of Echinoderms, enterocœl of the Tunicates, of the Brachiopods, of Sagitta, of Amphioxus, &c.). The solid mesoderm gives rise chiefly to the muscular system; the cavitary mesoderm forms principally the vascular organs.

The physiological *rôle* of a histological element has, be it noted, only a secondary importance for the determination of phylogenetic homologies. A muscular element, for example, will always be formed at that point where it is needed, sometimes in a rudiment having an endodermal origin, sometimes at the expense of ectodermic elements (Nemerteans). It may even be formed by a mere portion of a cell (plastidule), as we find in the Infusoria, in the Cœlentera, and in the Orthonectida.

The interior of the endodermic sac is filled, in certain individuals, by cellular elements, which give rise to the genital products. I am at a loss to understand why Metschnikoff refuses the name of endoderm to a cell-layer which arises absolutely in the same way and plays precisely the same part as the part called by this name by all embryologists in the other Metazoa.

I have seen in some Rhopaluræ a cloud of agile corpuscles issue from the sides of the body between the third and the fourth metameres. Are these corpuscles spermatozoa? It was not possible for me to get a distinct notion of their form, and I also am unable to affirm the presence of a natural opening at this spot on the body. It is possible that the specimens which presented this appearance of an emission of spermatozoa were really the victims of lacerations.

IV.—Anatomy of Intoshia gigas.

The second species of Orthonectida parasitic in *Ophiocoma neglecta* is much larger than *Rhophalura*. Its length is, in fact, two and a half times that of the latter. I name it *Intoshia gigas*.

Intoshia presents in swimming alternative movements of contraction and expansion in a transverse direction. It does not possess a papilliferous ring, but simply a ring devoid of cilia in its place. The body is of a more regular breadth and less tapering at the two extremities, which are blunt points, a little more conical than in the *Intoshia* parasitic in Nemerteans and Planarians.

Further, the anterior part of the body is strongly flattened in *Intoshia gigas*, and the non-ciliated segment presents on its inferior face, throughout its breadth, a transverse groove of some depth, so that the profile of the animal is that of a shoe with a heel to it (Plate XXII, fig. 5).

The metamerisation is less distinct than in Rhopalura. After the cephalic ring and a cervical ring corresponding to the papilliferous ring there follow three metameres of decreasing breadth (the third (γ) is about half of the first (α), the second (β) being of intermediate dimensions). To these follows a ring (δ) of much larger size, which seems sometimes to be divided into three, then follow two very small metameres (ϵ and ζ), which have about the same length as γ, and, finally, the terminal piece.

The variable dimensions of these metameres is no longer related, as in *Rhopalura*, to the size of the compound cells.

Each metamere is, in fact, formed by several rows of cells, the cells of each row being regularly placed over the corresponding cell of adjacent rows, so as to form a longitudinal series. It is to this disposition that the longitudinal striæ observed by MacIntosh are due, which led this naturalist to approximate the parasites of Lineus to the Opalinæ.

The ring α contains three rows of cells, the ring β comprises two, the ring γ only one, and the others only one.

The ectodermal cells of *Intoshia gigas* are, accordingly, much smaller and much more numerous than those of *Rhopalura*. All the cells, without exception, have long cilia. The head carries, as in Rhopalura, a bunch of straight cilia directed forwards. This character is, in fact, common to all known species of Orthonectida.

The endoderm forms a regularly ovoid sac, constituted in the adult animal by beautiful polygonal cells, and enclosing, in its interior, other cells of a rounded shape, more or less abundant.

The action of acetic acid is such as to detach the ectoderm (Pl. XXII, fig. 7), and then brings well to view the endodermic sac. The jerking movements of the caudal part are much less energetic in *Intoshia* than in *Rhopalura*. We should, therefore, expect to find the muscular system much reduced; and this is actually the case, and for a long time I in vain endeavoured to see the muscular bands at all. I succeeded, however, last summer by producing a gradual and very slight compression of the animal by allowing the water to evaporate from beneath the cover glass. The bands were rendered visible at the anterior part of the body, where the endodermic cells hinder observation the least. The bands have the same oblique direction as in Rhopalura.

V.—Gemmiparous Reproduction of the Orthonectida.

The oldest individuals of *Rhopalura* or of *Intoshia* present a considerable modification of the endodermal cell-layer. The cells of this layer are no longer visible, and the endoderm seems formed by a homogeneous membrane of granular aspect, very similar to certain tissues of the Nematoids. On the other hand, we have seen that the ectoderm can be detached in these animals with the greatest facility under the influence of reagents. As a result of the proliferation of cellular elements in the interior of the endodermal sac, this organ swells, becomes spherical, and bursting the ectoderm, which disappears, is transformed into a true "sporo-cyst" (Pl. XXII, figs. 14, 15, 16 and 17). In the interior of the sporocyst are seen buds, the cellular nature of which is extremely difficult to demonstrate. The same difficulty, it may be noted, is found with regard to the buds of the sporocysts of the Trematoda, and all zoologists who have occupied themselves with the study of these animals know how difficult it is to demonstrate the cells which form the bud-like embryo of a *Bucephalus* or of any Distoma.

Occasionally the primary buds produce secondary buds. When these buds have arrived at a certain size, they are composed clearly enough by a single layer of cells, which then proceed later to form an internal layer by delamination.

It appears, from what has been just stated, that the endoderm alone of the parent animal enters into the formation of the bud-like embryos, but it must not be forgotten that the papilliferous ring, or that which represents it in *Intoshia*, is characterised by great opacity, and that it is possible that at certain points ectodermal cells penetrate to the interior of the endodermal sac.

With their increasing development, the sporocysts lose their original form and become very voluminous. Often there are found several sporocysts in the interior of a specimen of an Ophiurid. This very active gemmiparous reproduction of the Orthonectida explains how it is that these animals are found in such great abundance in the Echinoderms infested by them. The phenomenon is one very similar to that occurring in the case of the Dicyemida; but with regard to these latter, it is almost impossible to find a Cephalopod which does not swarm with them, whilst the Orthonectida are comparatively rare.

VI.—Oviparous Reproduction.

Side by side with the sporocysts just described, we find in the infested Ophiurids a great number of cellular masses, which must be considered as eggs in various stages of segmentation.

In the case of *Rhopalura*, I have only been able to observe a small number of these embryonic stages (Pl. XXII, figs. 19, 20, 21). The little which I have been able to observe leads me to the conclusion that the segmentation is irregular, and that the planula is formed by epibolé, as in the Dicyemida. Each division of the cells in the mulberry mass gives rise to stellate figures, so well known at the present day by the name of *caryolitic figures* or *amphiasters*. The use of osmic acid enables one to observe them with the greatest facility.

In the study of the development of *Intoshia* I have been more successful. Here the segmented egg forms at first a perfectly regular *blastula*, the cells of which are at first very much elongated in a radial direction (Pl. XXII, figs. 8 to 13). This *blastula* very soon exhibits a very definite process of delamination; the internal part of each cylindrical cell gives rise to a spherical cellular mass, which detaches itself from the mother-cell, which is shortened by the process (Pl. XXII, fig. 10). This is absolutely the same mode of formation as that which can be observed in the production of the mesoderm in the Ophiurids with a condensed embryogeny (*Ophiothrix fragilis, Ophiocoma neglecta*). In the present case it is the endoderm which forms at the expense of the ectoderm, but we have seen that this endoderm contains potentially the mesodermic elements (the muscular bands).

Soon the ectodermal cells become covered with vibratile cilia, and elongate in a definite direction; then the embryo, which was spherical, becomes ovoid, the metameres show themselves little by little, and by insensible gradations we arrive at the adult condition.

VII.—Systematic.

According to what has been stated in the preceding pages, the Orthonectida may be defined in the following manner:—"Metazoa retaining throughout their existence the form of the *planula*, having a ciliated ectoderm (stiff cilia forming a bunch on the anterior cephalic region, vibratile cilia on the other regions of the body), presenting metameres, which do not correspond to any internal division of the body, with a sacciform endoderm, which gives rise to a muscular splanchno-pleural pseudo-mesoderm. Reproduction of two kinds: (1) gemmiparous in the interior of sporocysts, constituted by the development of the endoderm; (2) oviparous, dependent on the combination of male and female elements, formed in all probability in different individuals."

The class comprises at present two genera:

I. The genus Rhopalura, characterised by the presence of a papilliferous ring, by its ectoderm composed of large cells limited in number, and its definitely muscular endoderm.

Species unique. *Rhopalura ophiocomæ*. Length 0·108 mm.

II. The genus *Intoshia*, devoid of papilliferous ring; ectoderm formed of small, very numerous cells.

Three species:

1. *Intoshia gigas*.—Parasitic in *Ophiocoma neglecta*. Length 0·270 mm.

2. *Intoshia linei*.—Parasitic in *Lineus gesserensis*. Length 0·157 mm.

3. *Intoshia leptoplanæ.*—Parasitic in *Leptoplana tremellaris.* Length 0·135, breadth 0·03 mm.

This last species, like the preceding, is regularly cylindrical, and rounded at the extremities. According to the figure of Keferstein, it presents ten metameres, perfectly regular, in addition to the cephalic and caudal rings. The endoderm appears to be formed by large spherical cells.

The general form of the body, the regularity of the metamerisation in the two species parasitic in the Nemertean and the Planarian, lead to the supposition that there may be other differential characters present in them, which would lead zoologists probably to create a particular genus for these two types. Such a step in our present state of knowledge would, it appears to me, be superfluous.

Metschnikoff[1] has recently described, under the name of *Rhopalura Giardii*, a new species of Orthonectida, which he has since identified with *Rhopalura ophiocomæ.*

This species, which is parasitic in *Amphiura squamata*, was found abundantly at Spezzia. It presents itself in two different forms, which Metschinkoff thinks are probably identical with *Rhopalura ophiocomæ* and *Intoshia gigas*, which, according to him, are merely the male and female of one species.

I must confess that this idea has often occurred to me during my researches, and I do not entirely give it up even at this moment. The strongest argument in its favour is that the two forms, *Intoshia* and *Rhopalura,* exist in about the same quantity in *Ophiocoma neglecta ;* and that it would be curious to find in this little Ophiurid two different representatives of a group so rare as are the Orthonectida. At the same time, the difference between the two forms is greater than I had at first supposed. Further, we have not elsewhere any example of an animal in which some females produce eggs, giving birth to males exclusively, and others eggs from which only females issue. We might, perhaps, try to remove the difficulty by supposing that, in one or the other case, there was parthenogenesis (arrenotoky or thelytoky) ; but this would be, at present, pure hypothesis. However this may be, I have no fundamental objection to such a mode of explaining the facts, but I shall wait to make up my mind for the time when I shall have found in another species of *Intoshia* (*Intoshia linei,* for instance) an accompanying form analogous to *Rhopalura.*

Without doubt sexual differences, such as exist in *Bonellia viridis,* and in other worms, such as *Bilharzia hæmatobia,*

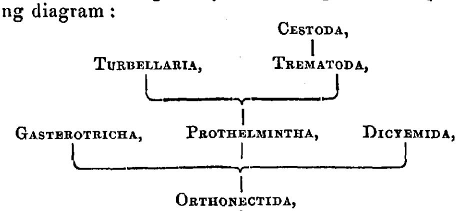
[1] 'Zoologischen Anzeiger,' II, No. 40, and No. 43.

are of a nature to make one very cautious on this subject; but, in addition to the special characters of the histological constitution of the ectoderm, I have recently observed new facts which still further separate *Intoshia gigas* from *Rhopalura ophiocomæ*.

It appears, as the result of an examination of many hundreds of adult individuals, that *Intoshia gigas* never has its non-ciliated segment provided with papillæ, nor even with refringent corpuscles. The "refringent corpuscles" of M. Metschnikoff form actual projections on the ring, which I call the "papilliferous ring" in Rhopalura. It must, then, be admitted that if such corpuscles exist in the supposed females of the parasite of *Amphiura squamata*, this parasite belongs to a new species (as is probable enough *à priori*), and that the sexual dimorphism is less accentuated in this species than in the other.

VIII.—Phylogeny.

With reference to the position of the group of the Orthonectida on the genealogical tree of animals, it is very difficult to make a definite statement. But there is no doubt that these parasites ought to be attached to the phylum of the *Vermes*, and take their place at the base of this phylum side by side with the Dicyemida. The phylum of the worms would then, according to my idea, be represented by the following diagram:



The Orthonectida must occupy in this scheme an inferior position to that of the Dicyemida. These latter are evidently much degenerated by parasitism. Their organisation must have been formerly much higher than it is to-day. The epiderm contains very clearly (*Dicyema* of *Sepia*) the rod-like bodies characteristic of the skin of the Turbellaria, and the embryo presents a very complex organ, the *urna*: nothing of this sort is seen in the Orthonectida.[1] One of the most

[1] See on "Dycyemida," the beautiful memoir of Edouard Van

characteristic features of the group of the Vermes thus limited is the existence, in all the animals of this group, of a gemmiparous reproduction (sporocysts, echinococci, &c.). This peculiarity only disappears in the higher worms, the Turbellarians, which are related to the rest of the group by so numerous and so important morphological features that no serious zoologist will entertain the idea of separating them from the Trematoda and Cestoda, in order to approximate them to the Annelids, as has sometimes been done.

Amongst the animals formerly classified with the preceding, some (Bryozoa, Annelida, and satellite-groups) are intimately related to the true Molluscs, with which I unite them to constitute the group of the *Gymnotoca,* whilst others form an assemblage which we may call the *Nematelmia,* including therein the *Nematoidea,* the *Echinorhyncha,* the *Desmoscolecida,* the *Gasterotricha,* &c. The Tunicata must be placed at the base of the phylum of Vertebrata. Budding from the interior of sporocysts is found, it is true, in other classes of the animal kingdom. Leaving aside the somewhat aberrant cases found among Arthropoda, we see in certain Rotifers (*Callidina*) an internal gemmiparity very similar to that of the Vermes. Further, the Gasterotricha, the parent-stock of the Rotifers and perhaps of all the Gymnotoka, appear to me to be readily connected with the Vermes by means of the Orthonectida.

We must not forget that the external resemblances between the Orthonectida, Gasterotricha, parasitic Rotifera, &c., are further increased by the similar manner of life obtaining in all these animals. *Ophicoma,* like *Lineus gesserensis* and *Leptoplana tremellaris,* inhabits muddy bottoms. The same is true of the limicolous Annelids and of Nebalia, on which we find as parasites certain degraded Rotifers (Balatro and Saccobdella). But the Orthonectida are in any case very inferior to the most degraded Rotifers, and represent, without any doubt, after the Gastræada, the first step of the sub-kingdom Metazoa.

I must add here that, according to a letter from Leuckart, the embryo of Distoma resembles the Orthonectida in a most astonishing manner, a fact which tends to confirm the position which I have assigned to this group among the Vermes.

Beneden, 'Bulletins de l'Acad. de Belgique,' 2e serie, t. xli and xlii, No. 7, 1876; also Abstract, with Plate, in 'Quart. Journ. Mic. Science,' vol. xvii, 1877, p. 132.

IX.—General Reflections.

At first sight it seems as though the discovery of the Orthonectida would bring a very solid support to the Planula theory of Ray Lankester, or, still more, to the Parenchymula theory of Metschnikoff, and I do not doubt that more than one zoologist will interpret, in that sense, the observations I have recorded.

I persist, however, for my own part, in considering the *invaginate Gastrula* as the prototype of the Metazoa. I base this opinion on the following arguments:

1. The Orthonectida are parasitic animals, and we must take into account the retrogression which this kind of life may have brought about in their structure. An organisation which we consider as one of primitive simplicity is very possibly simple only in consequence of degeneration, if we have to deal with a parasite, and especially an internal parasite.

2 We have seen that the *Planula* is formed by epibolé in Rhopalura; in this case we have, then, at any rate, momentarily, a real gastrula, which closes up and does not reopen, because the mode of life of the animal does not require the existence of a permanent digestive tube.

3. The forms which present the embryonic phase termed *parenchymula* by El. Metschnikoff cannot be considered, as that naturalist would wish, as the lowest among the Sponges and Hydroids.

The forms known as *Halisarca* are not *low* sponges, but sponges which have undergone a degeneration of their skeletal apparatus. From the point of view of general morphology I have shown that we may compare them to the *Botrylli*, and must assign to them a very high grade among the Fibrosa, analogous to that which the Botrylli occupy among the Synascidiæ or the Leucones among the Calcispongiæ.

The Siphonophora, we may remember, are very far from being Cœlentera of inferior position, and it is by no means astonishing that they present a condensed embryogeny. The typical embryonic form is found among the Coralligena and certain Actiniæ.

The Echini and the Ophiurids with pelagic embryos have a small nutritive vitellus. They present a gastrula formed by invagination, and it is only when this gastrula is thus formed that the mesoderm takes origin, at first by partial delamination of the ectoderm, and later by lateral thickenings of the endoderm.

In the Ophiurids with condensed embryogeny, the egg presents an enormous nutritive yelk, and the mesoderm is formed by abbreviation at the same time as the endoderm by a general delamination of the ectoderm, which leads us to Metschnikoff's form dubbed *Parenchymula*. This I have established most clearly in cases of *Ophiocoma neglecta* and *Ophiothrix fragilis*.

It is clearly impossible for me to discuss here the important questions of general embryogeny which are raised by the study of the Orthonectida. I will merely say that, according to my observations, a large number of calcareous and siliceous sponges present what one may well call a *biconvex archigastrula*. Quite recently Keller has shown that *Chalinula* possesses an *amphigastrula*. Kowalevsky has described, in the most exact manner, the existence of an archigastrula in a variety of *Actinia mesembryanthemum*, in Cereanthus, and in various Medusæ. I am able to confirm his statement in reference to *Actinia equina*. Finally, Ed. van Beneden has described and figured an amphigastrula in the Dicyemida, so closely related in many respects to the Orthonectida.

These examples will suffice, I think, to justify my opinion that the *gastrula* by invagination is the primitive mode; the gastrula by delamination (*Planula* or *Parenchymula*) a secondary mode of embryonic development.

I would also direct attention to the metamerisation which is so remarkable in the *Orthonectida*.

We have seen that this metamerisation only affects the ectoderm, and I believe that this was primitively the case also in the Annelids. What proves this to be the case is the highly differentiated form of the digestive tube of the Chætopods in which metamerisation is only well marked in those organs derived from the ectoderm, such as the bristles, the parapodia, and the segmental organs (nephridia).

It is obvious enough that I am not alluding to that kind of metamerisation which is observed in *Salmacina*, *Syllis*, &c., which is merely the result of gemmiparous reproduction. This last kind of metamerisation is only comparable to what one finds in the Cestoidea and the Rhabdocœla.