On Ctenoplana.

By

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With Plate 21.

The discoverer of the remarkable genus Ctenoplana, which presents affinities both to the Ctenophora and to the Turbellaria, was, as is well known, Professor Alexis Korotneff, who obtained only a single specimen off the west coast of Sumatra, and described it in the 'Zeitschrift für wissenschaftliche Zoologie'[1] for 1886.

Korotneff found his specimen drifting in a current of the sea, in the company of a large number of Porpita. It was distinguished by its deep red or crimson colour, and was named C. Kowalevskii in honour of the discoverer of Cœloplana.

Since 1886 no second record of the occurrence of the genus has been made.

In January of this year (1896), while cruising among the islands which form the Eastern Archipelago of British New Guinea, in pursuance of zoological work, I was fortunate enough to pick up a cuttle-bone which had evidently been afloat for a long time, and was being carried along by the current off the group of the islands named on the chart the Conflict Group.[2] On the cuttle-bone were numerous minute

[1] Vol. xliii, pp. 242—251, Taf. viii.

[2] These islands surround a magnificent lagoon.

organisms, including young green-tinted Polychætes, young Planaria, Anthozoan larvæ, young Cirripedes in the Cypris stage, and four specimens of Ctenoplana. Three of the last were of a pronounced green colour, and the fourth was crimson.

The green Ctenoplana, both on account of its colour and its shape, is an entirely new kind, and I shall name it C. Korotneffi. The crimson variety may or may not be specifically identical with C. Kowalevskii; but as my sketches of the external form differ somewhat from Korotneff's figures, I think it will be well to give it a provisional name with the object of engaging the attention of any zoologists who may have future opportunities for studying the genus. I propose, therefore, to call my crimson specimen C. rosacea.

As I had no chance of getting ashore, I had to make the best of the limited accommodation supplied by a small cutter, in order to observe the appearances presented by the living animals and their movements. Although I omitted to make accurate measurements of the living expanded animals, their average diameter would correspond closely in length with that of C. Kowalevskii, which, as stated by Korotneff, measured 6 mm.

Many of the external features of Ctenoplana were correctly described and figured by Korotneff, but his specimen appears to have been not very active; and although, as he says, he had it under observation in the living condition for three to four hours, it did not once extrude its tentacles, so that he only became aware of their existence in section. The consequence of this was that Korotneff was completely wrong in localising the plane of the tentacles. He placed them in the plane at right angles to that in which they actually occur.

At the ends of one of the principal diameters of the disc-shaped body of Ctenoplana the margin of the body is incurved. Korotneff, without the smallest hesitation, describes these marginal bays as anterior and posterior in position, while, according to him, the tentacles were situated along the diameter at right angles to the "antero-posterior" diameter—that is to say, in what would correspond to the transverse plane. This, however, is quite wrong.

As will be seen later on, I agree with Korotneff in his identification of the antero-posterior axis (in comparison with bilateral animals), but it is along this axis that the solid tentacles lie.

Furthermore, Korotneff's specimen did not give him an exhibition of its swimming powers, so that he could not observe the movements of the ctenophoral plates, and the result was that he formed the opinion that these plates had become altered as to their function, and that they hardly appeared to serve for the progression of the body. This is a curious repetition of the old error with regard to the means of locomotion of the Ctenophores, as set forth in Chun's monograph. As a matter of fact, when Ctenoplana swims, the ctenophoral plates are its sole means of locomotion.

I now pass on to a systematic account of my own observations.

1. Shape and Movements of the Body.—Like the Planarians, the body of Ctenoplana comprises a thickened median ridge-like area and two lateral thin skirt-like areas, the "Seitenfelder" of Lang. In the attitude assumed when crawling, the body is nearly round with the exception of the above-mentioned marginal bays, from which I observed the muscular pinnate tentacles being constantly protruded and retracted while the animal was crawling (fig. 1). As also observed by Korotneff, Ctenoplana crawls with one of the rounded margins of the body directed forwards as a rule. The tentacles thus appear remarkably like transversely paired structures, and one would naturally at first describe them as such. But it must be remembered that the terms anterior, posterior, and transverse, as applied to bilateral animals, are not applicable to Ctenoplana.

The tentacles, when extruded, are found to be white structures, thus making a marked contrast to the green or red colour of the body. They are provided with small secondary tentacles or pinnæ, arranged somewhat irregularly, but in a single series. Like the tentacles of Cœloplana, described by Kowalevsky, they are strictly comparable with the tentacles of a Cydippid. Both the tentacles and their pinnæ are quite solid, being completely filled up with a muscular core. Within the body each tentacle is enclosed within a hollow sheath which opens to the exterior at the end of a small papilla at the base of the marginal bay. When retracted, therefore, the tentacles form a median axial skeletal support for the body, interrupted in the middle region of the body by the aboral sense-organ.

The aboral surface of the body may be at once called the dorsal surface, and the oral the ventral surface.

The possession of a relatively wide Planarian-like skirt not only permits Ctenoplana to crawl about on firm surfaces, but enables it also to attach itself, in a highly characteristic manner, to the surface-film of water by its ventral surface. In this position it greatly resembles Planarians, which are also fond of assuming the same position. When lying thus attached to the surface of the water the round central oral opening can be seen. The mouth can be protruded so as to form a slight cone.

When swimming, Ctenoplana brings the two halves of the skirt together so as to form a bell-shaped, or better, a Pilidium-shaped structure which progresses very rapidly by means of the ctenophoral plates. In swimming, the aboral pole is directed forwards as it is in the Ctenophora.

The ctenophoral apparatus consists of eight small oval plates, placed four on each side of the tentacle axis.[1] Across each plate run six or seven shallow grooves, from which the long cilia arise (figs. 1 and 5). The cilia of each groove appear in section to be united usually for some distance from their base, and then to separate out into the individual cilia (fig. 5). The ctenophoral plates alternate with the lobes of the central gastric system (figs. 1—3). I only had a fleeting view of the

[1] *The line joining the bases of the tentacles may be called the "tentacle axis."*

peripheral anastomosing ramifications of the gastric system, and have not indicated them in the sketches of the external form.[1]

When Ctenoplana wishes to sink from the surface to the bottom it doubles itself up in the usual way, and so sinks apparently without employing the combs. This was also observed by Korotneff.

2. The Aboral Sense-organ.—As already described by Korotneff, the aboral sense-organ consists essentially of an otolithic mass, suspended by stiff processes from adjacent cells in a cupule, and surrounded by a ring of ciliated tentacles. Korotneff figures the latter in the form of a simple circlet. This, however, is not the case. The circlet of sensory tentacles surrounding the otolith consists of two distinct and separate halves, with about nine tentacles in each half. The one half is placed on one side, and the other on the opposite of the tentacle axis (fig. 1).

This is perhaps the most important observation that I was able to make on the living animal, and it is a crucial one for deciding upon the homologies of the axes of Ctenoplana with those of bilateral animals. The division of the circlet of sensory tentacles into two portions was remarkably distinct and unequivocal. The sensory or apical tentacles (as distinguished from the muscular or terminal pinnate tentacles) are usually carried extruded (figs. 2 and 3), but they can be completely retracted.

3. Cilia.—I cannot confirm Korotneff in his statement as to the general distribution of cilia over the surface of the body. The places where I have observed cilia (apart, of course, from the ctenophoral plates) are as follows: (i) on the sensory tentacles, (ii) on the cells lining the sheaths of the pinnate tentacles, and (iii) over a large area of ventral surface (fig. 5). I must deny the presence of cilia on the general dorsal surface.

[1] As Ctenoplana is semi-opaque, it is difficult to discern much of the internal structure in surface view.

4. Gastro-vascular System.—The central main portion of the gastro-vascular system presents the lobed appearance shown in the figures, the lobes being paired about the tentacle axis. The middle and largest pair of lobes belong to the stomach, and thus serve to mark out the stomachal plane (Magenebene of Chun). The stomachal plane, therefore, as in the Ctenophores, lies at right angles to the plane of the tentacles, which corresponds to the funnel plane (Trichterebene) of Ctenophores.

My identification of the stomachal plane in Ctenoplana is just the reverse of Korotneff's, who erroneously placed it in the true tentacular plane.

From the two opposed sides of the stomach a narrow median canal leads into the two terminal end-lobes of the central gastric cavity (cf. the schematic fig. 11). The two end-lobes are in open communication with the peripheral canal-system.

I do not find such definitely circumscribed peripheral canals as those figured by Korotneff, but they appear to me in section merely as the spaces partitioned off by the dorso-ventral trabeculæ, which Korotneff describes as dorso-ventral muscles (fig. 5).

The median funnel-vessel was correctly figured by Korotneff. It arises from the stomach immediately opposite to the mouth, and, proceeding aborally, embraces the sense-organ without opening to the exterior. It is very clearly shown in section.

5. Tentacle Sheaths and Musculature.—The tentacle-axis is occupied by the sheaths of the tentacles, which are hollow tubes lined by ciliated cells lying immediately beneath the dorsal surface, and completely separated from one another by the aboral sensory complex. The muscles of the tentacles form part of the voluminous musculature, which, so far as I can make out, effects the retraction of the aboral sense-organ and of the ctenophoral plates, which can be completely withdrawn into the body (cf. fig. 5). The tentacles were retracted in my preserved specimens, and so it was impossible for me to

analyse this very complicated longitudinal musculature. The musculature[1] on one side of the stomachal plane is completely separated from that on the other side; so that in sections parallel with the stomachal plane, passing through the region of the sense-organ, no muscles are visible. But at a short distance on either side of the median stomachal plane the sections in contracted specimens are almost entirely occupied by the convoluted bundles of muscles. Again, beyond the region of the ctenophoral plates the sections merely show the dorsally placed muscular tentacle lying in its sheath (fig. 10).

6. The Gonads.—By the discovery of the male genital organs of Ctenoplana I have brought a welcome additional piece of evidence as to the adult character of the organism.[2] The testes are placed at the bases of the two end-lobes of the main portion of the gastro-vascular system. Their position is indicated by crosses in fig. 1. They thus consist of two pairs of organs, paired about the tentacle axis. They may be either simple or lobed and subdivided. They may contain practically nothing but mature spermatozoa as in fig. 7; or they may contain both mature and developing spermatozoa as in fig. 9. Finally, they may possess one or several ducts opening to the exterior on the dorso-lateral surface of the body below the level of the ctenophoral plates.

The male genital ducts are merely tubular extensions of the tunica propria which encloses each testis.

In the centre of that portion (always the ventral portion) of the testis in which the immature sperm-cells (spermatogonia and spermatocytes) occur there is usually to be observed a cavity surrounded by large clear cells exactly like those which line the cavities of the terminal gastric lobes; and, in fact, I have traced this cavity into communication with the gastro-vascular system (cf. figs. 5, 6, and 9).

[1] I do not include the dermal musculature described by Korotneff, about which I am at present in the dark.

[2] Unfortunately I can say nothing about the female reproductive organs. It seems unlikely that Ctenoplana should be unisexual. More probably it is a protandric hermaphrodite.

These central cavities in the immature testes may therefore be called the genital cæca, and the genital products appear to arise as proliferations of the walls of the cæca (figs. 5 and 6).

What is very puzzling is the fact that similar proliferations occur on the walls of the terminal gastric lobes themselves (fig. 5). On the dorsal walls of the terminal gastric lobes the cells of these proliferations appear to assume the properties of chloragogenous cells, and numerous yellowish refringent concretions occur in and amongst them. Somewhat similar refringent particles are to be seen in the cells of the subjacent true endoderm. Finally, in connection with this subject I can only mention the fact that as the median walls of the neighbouring terminal lobes fuse together on nearing the median canal which connects them with the stomach, the minute cellules which compose the greater part of the proliferations in question are replaced by long pyramidal cells which compose a compact gland, having a radiating structure due to the peculiar arrangement of the cells. I will call this a gastric gland, and hope that at some future date light may be thrown upon its nature.

What distinguishes the genital proliferations from the above-described gastric proliferations, apart from their different topographical relations, is the fact that the nuclei of the cellules of the former are of different sizes (fig. 9). The larger nuclei I interpret as belonging to spermatogonia and the smaller to spermatocytes. Unfortunately I am unable to make out any nuclear structure in my preparations, although they are otherwise well enough preserved.

The spermatozoa form dense clusters with characteristically deeply stained heads and unstained tails. The tails are directed both outwardly and mesially. When a testis contains only mature spermatozoa there is no longer any trace of the genital cæcum (fig. 7).

With regard to the ducts in one individual, I counted no less than twelve ducts, which were distributed equally between the four testes. Of these ducts I was able to see the actual opening to the exterior in six. In another individual I counted seven ducts altogether.

It should be added that the above description of the male gonads applies exclusively to C. Korotneffii, all three specimens of which possessed them.

7. Axial Relations—Comparison of Ctenoplana with Planaria and Ctenophora.—As already known from the work of Korotneff, Ctenoplana agrees with the Ctenophora in the possession of a main axis (Hauptachse) which connects the aboral pole with the oral pole, the mouth with the sense-organ, and that this main axis forms the line of junction of the two principal planes—namely, the tentacular plane and the stomachal plane.

Ctenoplana presents remarkable Planarian affinities in respect of its dorso-ventrally flattened body, in the possession of a definite dorsal surface, and a definite ventral or locomoter surface, in its habit of creeping, and especially in its habit of attaching itself to the surface-film of water.[1] This enumeration, to which may be added the partial ciliation of the ectoderm, nearly exhausts the list of its strictly Planarian affinities.

Besides the coincidence of the main axis and principal planes of Ctenoplana with those of the Ctenophora, the chief points of affinity are the possession of two pinnate tentacles which are each retractile within a sheath, the possession of the eight ctenophoral plates, and the presence of the median funnel vessel.

The two series of sensory tentacles placed on opposite sides of the otolith, whose epithelium is directly continuous with the epithelium of the cupule of the otolith, are directly comparable with the polar plates (Polplatten) as described by Chun in the Ctenophores. In the first place they agree with the latter in lying in the stomachal plane, in so far that they are paired about the tentacle axis. This is the most important point of agreement morphologically, but they also agree in

[1] *According to the remarkable observations of Chun, some Ctenophores* possess this power, effecting it by spreading out the wall of the stomach,—sometimes, as in Lampetia Panceri, nearly everting the stomach as far as to the origin of the peripheral vessels.

some details. The relation to the otolith-bearing portion of the sense-organ is identical in both cases. The polar plates of Ctenophores are ciliated, as are the sensory tentacles of Ctenoplana. Moreover in the Beroidæ, according to Chun, the thickened margin of the polar plates does not form a simple ridge, but is raised up into a series of lappets. This is a very remarkable correspondence, and after my observation of the double, paired character of the sensory tentacles of Ctenoplana I think there can be no doubt that the latter are homologous with the polar plates of Ctenophores.

The comparison of the gonads of Ctenoplana with those of other forms is not such a simple matter. They agree with those of the Ctenophora in being developed about the walls of diverticula of the gastro-vascular system, and with those of the Polyclades in being enveloped in a tunica propria. But they differ from both in the possession of ducts opening directly to the exterior. In the Ctenophora the genital products fall into the meridional vessels, and are discharged through the mouth; while in the Polyclades, according to Lang, the tunicæ propriæ which envelop the innumerable testes open into a system of intra-cellular genital capillaries which eventually convey the sexual products to the vas deferens on each side, by which they are ultimately led to the ventrally placed external genital pore.

We now come to the critical consideration of the axial relations of Ctenoplana. The problem to be solved is the following:—To what do the planes of the tentacles and of the stomach respectively correspond in bilateral animals? Does the tentacle plane of Ctenoplana (Trichterebene of Ctenophores) correspond to the sagittal plane of bilateral animals or to the transverse plane?

We shall find, if it has not already appeared evident in the foregoing pages, that Ctenoplana unequivocally proves, as I think, that the tentacle plane or funnel-plane of it and the Ctenophores corresponds to the sagittal plane of bilateral animals, and not to the transverse plane.

At present there exist two interpretations of the axial relations of the Ctenophores, namely, that of Chun[1] and that of Lang.[2] These may be briefly tabulated as follows.

According to Chun—

1. Tentacle or funnel-plane of Ctenophores = Sagittal plane of Bilateralia.
2. Stomachal plane of Ctenophores = Transverse plane of Bilateralia.
3. Main axis of Ctenophores[3] = Longitudinal axis of Bilateralia.

According to Lang—

1. Tentacle or funnel-plane of Ctenophores = Transverse plane of Polyclades.
2. Stomachal plane of Ctenophores = Sagittal plane of Polyclades.
3. Main axis of Ctenophores becomes bent (geknicht) in Polyclades.

From the above it will be seen that, as regards the tentacle and stomachal planes, Lang's interetation is the exact reverse of that of Chun; and yet it is singular that there is no mention of such a fundamental discrepancy in Lang's monograph.

Selenka (quoted by Lang) held the view that the anterior end of a Polyclade corresponded to the aboral pole of the Ctenophore, and the posterior end of the former to the oral pole of the latter. Lang says he himself formerly held this view, but afterwards gave it up as being erroneous. It would, however, necessarily follow if the main axis of the Ctenophores corresponded to the long axis of Polyclades as stated by Chun. The latter view, however, is irreconcilable with Chun's own identification of the tentacle plane of Ctenophores with the sagittal plane of Bilateralia, and, in fact, it may be dismissed, once for all, as erroneous.

Chun's other homologies, however, in respect of the tentacle[4] and stomachal planes are fully confirmed by the conditions

[1] Carl Chun, 'Die Ctenophoren des Golfes von Neapel,' 1880.

[2] Arnold Lang, 'Die Polycladen des Golfes von Neapel,' 1884.

[3] Carl Chun, "Die Verwandtschaftsbeziehungen zwischen Würmern und Cœlenteraten," 'Biol. Centralblatt,' Bd. ii, 1882–3. In this paper Chun intimates that the main axis of Ctenophores becomes the long axis of Polyclades; but I cannot find out how he reconciles some of the views here expressed with the previous statements as to the homologies of the planes contained in his monograph.

[4] Chun denominated the plane in which the tentacles of Ctenophora lie the Trichterebene, because there are no tentacles in the Beroidæ.

observed in Ctenoplana. Chun was at first in doubt as to the criterion by which to homologise the planes of Ctenophores with those of Bilateralia, as the axes passing through these planes in Ctenophora were equipolar (gleichpolig).

The way by which he finally arrived at the conclusion that the tentacle plane corresponded to the sagittal plane was so remarkable that I will give a free translation of his description.

"Naturally," says Chun, "we must disregard all accidental conditions of asymmetry by which one of the axes (Kreuzachsen) becomes inequipolar. For example, one seldom finds a Cestus veneris in which the two band-like halves of the body are equal in length. . . . Should, however, one of the axes prove to be inequipolar in such a way that constantly an essential organ-complex failed to develop on the one half of the axis, then we should have a transition to bilateral symmetry which would enable us to speak of a dorsal and a ventral surface. . . . How surprised was I to find a larva which presented a remarkable axial disturbance in the funnel-plane [*i. e.* the tentacle plane]! I give it the provisional name of Thöe paradoxa, as I have not succeeded in associating it with certainty with any adult Ctenophore. It possesses, in fact, only a single tentacle apparatus and tentacle [Fangfaden]. Only in the course of the later development is a second tentacle apparatus differentiated at the other pole of the axis, so that the original disturbance becomes gradually levelled out."

In Ctenoplana the tentacle axis and the stomachal axis are equipolar; but if we consider about which axis the paired structures are situated, we are simply forced to acknowledge that the plane of the tentacles corresponds to the sagittal plane,—in other words, that the tentacle axis of Ctenoplana and Ctenophora corresponds to the longitudinal axis of Bilateralia.

Lang's theory of the origin of Polyclades from Ctenophores rests in the first instance on the assumption that the pinnate tentacles of Ctenophora and Cœloplana are homologous with the sensory tentacles of Polyclades; and his above-quoted interpretation of the axial relations is framed in accordance with this assumption.

In the first place the fact should be emphasised that under no circumstances and from no point of view are the tentacles of Ctenoplana bilaterally disposed, but they are biradially disposed.

As mentioned above, it cannot be denied that, in the creeping attitude, the tentacles of Ctenoplana present to the onlooker the appearance of ordinary transversely paired structures, and it may seem difficult to imagine an ancestor of bilateral animals with an unpaired tentacle in front and an unpaired tentacle behind. But the point is that we have not got to imagine this, because in the animals with which we are dealing there are no such relations as anterior and posterior, right and left.

As regards the particular homology of the pinnate tentacles (Greiftentakel) of Ctenophores with the nuchal tentacles of Polyclades, so strongly and, it must be added, plausibly upheld by Lang, I venture to think that my observations on Ctenoplana, especially as to the double character of the aboral circlet of sensory tentacles, justifies me in frankly denying its accuracy. From their close relation to the central sensory apparatus, and the fact that they are paired about the tentacle axis, which I regard as equivalent to the longitudinal axis of Polyclades, I suggest that it is much more probable, from their relations and function, that the paired multiple sensory tentacles of Ctenoplana and the polar plates of Ctenophora are homologous with the sensory nuchal tentacles of Polyclades, than that the latter are homologous with the pinnate tentacles of Ctenophora, whose chief function is that of seizing objects for food.

Moreover, from their structure and function, their extreme retractility within definite sheaths, and their worm-like mobility, it would appear that the pinnate tentacles of Ctenoplana and Ctenophora belong to a category of structures totally different from that of the nuchal tentacles of Polyclades. They belong, namely, to the same category of structures as the proboscis of Nemertines and of certain Rhabdocœle Planarians.

Finally, we may recapitulate the organs in Ctenoplana which are paired about the tentacle axis (cf. fig. 1). There are four pairs of ctenophoral plates, three pairs of gastric lobes, two pairs of gonads with their ducts, and one pair of multiple sensory tentacles.

From what has been said I regard it as proved that—

1. The tentacle axis of Ctenoplana = the longitudinal axis of Planarians.
2. The stomachal axis of Ctenoplana = the transverse axis of Planarians.
3. The main axis of Ctenoplana = according to Lang, the primary main axis of Planarians, which becomes bent as the ganglion is shifted towards the anterior end of the body.
4. The main axis of Ctenoplana and Ctenophores = the dorso-ventral axis of Bilateralia.

8. Synopsis of Species of Ctenoplana.

(i) C. Kowalevskii, Korotneff.—Colour crimson, body in swimming attitude shaped like a truncated pyramid; median dorsal surface concave; free margin of skirt frilled. Habitat, west coast of Sumatra.

(ii) C. rosacea, n. sp.—Colour crimson; body in swimming attitude of a quadrilateral form; median dorsal surface convex; free margin of skirt plain. May be merely a variety of preceding species. Habitat, Eastern Archipelago of New Guinea.

(iii) C. Korotneffi, n. sp.—Colour green; body in swimming attitude roof-shaped; median dorsal surface upraised with two upright end-knobs; free margin of skirt slightly frilled. Habitat, Eastern Archipelago of New Guinea.

In Korotneff's fig. 13 there are only eleven sensory tentacles figured for C. Kowalevskii,[1] while C. rosacea had

[1] Korotneff describes an aperture to the exterior on each side in the neighbourhood of the tentacles in C. Kowalevskii which leads into a "system of canals which branch in the body parenchyma." Korotneff himself says that after he had preserved his specimen in sublimate he was unable properly to orientate it. I have already shown that he completely misplaced the tentacles. The apertures in question are obviously the openings of the

about eighteen. But I should hesitate to insist upon this as a specific difference.

9. General Conclusions.—With regard to the systematic position of Ctenoplana, which we now know to be an adult animal, I am strongly of opinion that it is an ancestral form, and not, as some zoologists seem to suppose, a highly modified creeping Ctenophore. By ancestral form I simply mean a primitive archaic form belonging to an ancestral type, and of course I do not imply that it is the actual ancestor of anything in the world. That the Planarians and Polyclades in particular have close affinities with the Ctenophora there can be no doubt, but it is very much open to question whether the former are derived from the latter. The view that the Polyclades are so derived seems a reversal of the natural order of events, which point to the littoral fauna as the origin both of the pelagic and of the abyssal fauna.

Are we to regard the immediate ancestors of the Turbellaria as amorphous forms, like Trichoplax, or forms without any kind of symmetry, like Planulæ or the Mesozoa? Or, on the contrary, are we not rather to regard their immediate ancestors as forms with some kind of radial symmetry?

Having regard to the complete bilateral symmetry of the flat-worms, and more particularly their well-developed nervous system, with cerebral ganglion in even the lowest forms, I cannot imagine them to be derived directly from amorphous organisms, but rather from animals which possibly, like Ctenoplana, possessed a biradial symmetry.

Ctenoplana approaches more nearly to a condition of bilateral symmetry than the Ctenophores do, in that it possesses very clearly differentiated dorsal and ventral surfaces. And this is exactly what we should expect to find in the littoral or sublittoral ancestor of such purely pelagic forms as the Ctenophora, the pelagic habit, as is well known, often tending to produce a more or less radial symmetry.

tentacle sheaths, and the "system of canals" are the sheaths themselves, which do in fact send off occasional diverticula, possibly due to the contraction of their walls during preservation (cf. figs. 5 and 10).

On the other hand, a biradial form, like Ctenoplana, possesses the potentiality of assuming a strictly littoral life, in which the ventral surface is the permanent locomotor surface, such an existence leading to a condition of bilateral symmetry, according to well-understood physiological principles.

The ctenophoral plates must have put in their appearance for the first time in some form or other; and although it is at present beyond the limits of our knowledge to explain how they arose, yet it is not right to conclude that the ctenophoral plates of Ctenoplana are degenerate or reduced structures merely because they are smaller than the ctenophoral rows of the Ctenophora.

It is a groundless assumption to say that Cœloplana and Ctenoplana are modified creeping Ctenophores. Ctenoplana is an expert crawler, it is expert at hanging on to the surface film of water, and it is indeed an expert swimmer. Everything it attempts it does well in the old primeval fashion, and there is nothing degenerate about it.

If Cœloplana and Ctenoplana are neither Ctenophores nor Planarians, what are they? I think it is necessary to create a new order of Plathelminthes for their reception; and I propose to call the new order the Archiplanoidea, and to regard it as equivalent to the orders Turbellaria, Trematoda, Cestoda, and Nemertina.

Furthermore, I should look to the Archiplanoidea for the ancestors of all the Plathelminthes (including the Nemertines) on the one hand, and of the Ctenophora on the other.

The resemblance in form and shape, however superficial, between Ctenoplana and the Pilidium larva of Nemertines should not pass unnoticed; and it is a remarkable fact that the main axis of Pilidium passes through mouth and apical sense-organ as in Ctenoplana.

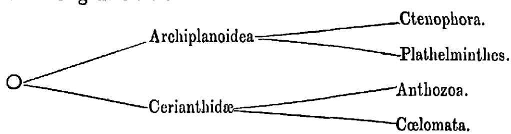
In the Archiplanoidea, therefore, we have organisms presenting a transition from radial to bilateral symmetry.

In the Cerianthidæ, as we know especially from the works of Carl Vogt[1] and Éd. van Beneden,[2] we have also forms belonging to the category of radial animals, which are undoubtedly physiologically radial, and nevertheless present a pronounced bilateral symmetry.

Van Beneden's views are clearly set forth in the following quotation from his memoir above quoted:—"Je partage entièrement l'opinion de Sedgwick et de Caldwell d'après laquelle le disque qui porte la bouche et les tentacles, chez les Actinozoaires, répond morphologiquement à la face neurale des Annéles, des Arthropodes, et des Chordés. Je pense, comme ces auteurs, que la bouche des Cnidaires est homologue à la fente blastoporique des Arthrozoaires. Les diverticules cœlomiques qui sont, ontogéniquement parlant, la cause de la segmentation, répondent aux loges mésenteriques des Anthozoaires et les cloisons intersegmentaires sont anatomiquement équivalentes aux sarcoseptes."

If we accept these conclusions side by side with those derived from the study of Ctenoplana, we are compelled to frame the hypothesis, which I believe to be highly probable, of the diphyletic origin of Bilateralia.

The following scheme will make this view clear, and will save a long discussion:



I believe this view will be found to be a natural one in every respect; and if it be regarded by morphologists as substantiated, it will certainly relieve the science of morphology of several burdens. For instance, Hubrecht's original speculations as to a relationship between the Nemertines and the Chordates, as well as Bateson's comparison of the Nemertines with Balano-

[1] Carl Vogt, "Des Genres Arachnactis et Cerianthus," 'Arch. de Biol.,' t. viii, 1888.

[2] Ed. van Beneden, "Recherches sur le développement des Arachnactis," ibid., t. xi, 1891.

glossus and many other such like theories, which at the time no doubt appeared to be logical necessities, will be quite ruled out of the field of possibilities.

The descendants of the Archiplanoidea have no cœlom and no præoral lobe. The descendants of the Cerianthidæ have a cœlom and also a præoral lobe (excluding the Anthozoa).

It is an interesting parallelism that the criterion for the antero-posterior axis, both in the Cerianthidæ and in the Ctenophora (Thöe paradoxa), was provided by what may be called a directive tentacle. It may, indeed, be something more than a mere parallelism.

10. Summary of Principal Results.—(1) Discovery of one very distinct new species of Ctenoplana, and of another somewhat doubtful new species.

(2) Observation of the movements and of the pinnate tentacles of the living Ctenoplana.

(3) Accurate localisation of the pinnate tentacles.

(4) Discovery of the double character of the circlet of sensory tentacles surrounding the otolith.

(5) Discovery of the male genital organs and ducts of Ctenoplana, thus proving that Ctenoplana is an adult animal.

(6) Description of the tentacle sheaths.

(7) Account of the genital cæca of the gastro-vascular system, about whose walls occur the genital proliferations.

(8) Chloragogenous tissue and gastric gland.

(9) The tentacle axis of Ctenoplana corresponds to the longitudinal axis of Planarians, the stomachal axis of the former to the transverse axis of the latter, and the main axis of the former to the dorso-ventral axis of the latter.

(10) The solid pinnate tentacles of Ctenoplana are not disposed bilaterally, but biradially.

(11) The ctenophoral plates, gastric lobes, gonads, gonaducts, and aboral sensory tentacles are paired about the tentacle axis.

(12) The aboral sensory tentacles of Ctenoplana are homologous with the polar plates (Polplatten) of Ctenophora, and with the nuchal tentacles of Polyclades.

(13) The testes of Ctenoplana are enclosed within a tunica propria.

(14) The pinnate seizing tentacles (Greiftentakel) of Ctenoplana and Ctenophora, retractile within definite sheaths, belong to the same category of structures to which the proboscis of Nemertines and certain Rhabdocœle Planarians belong.

(15) Creation of a new order, the Archiplanoidea, for the reception of Cœloplana and Ctenoplana. The order will thus contain two families, the Cœloplanidæ and the Ctenoplanidæ.

(16) Hypothesis of the diphyletic origin of Bilateralia.

In conclusion, as I am about to leave Sydney, I wish to repeat my thanks to Professor W. A. Haswell for his kindness and hospitality to me.

SYDNEY; June 29th, 1896.

EXPLANATION OF PLATE 21,

Illustrating Mr. Arthur Willey's paper "On Ctenoplana."

N.B.—My material was preserved in sublimate and in a sublimate-acetic mixture, and stained with alum-cochineal.

FIG. 1.—Ctenoplana rosacea, n. sp., from dorsal aspect. The two pinnate tentacles are extended, the ctenophoral plates alternate with the gastric lobes, the two middle large gastric lobes mark the stomachal plane; in the dorsal centrum is seen the otolith, surrounded by an incomplete circlet of ciliated sensory tentacles paired about the tentacle axis; the spots round the margin of the skirt represent crimson pigment spots. From living specimen. N.B.—The crosses indicate the positions of the male genital organs.

FIG. 2.—C. rosacea. In swimming attitude. From living specimen. Tentacles retracted. *t. o.* Opening of tentacle sheath.

FIG. 3.—C. Korotneffi, n. sp. In swimming attitude. The space indicated by dotted line below the aboral sense-organ was dimly seen through the body, and probably represents the space into which the sense-organ is withdrawn on retraction, although it might represent the funnel vessel.

From living specimen. Tentacles retracted. *t. o.* Opening of tentacle sheath.

FIG. 4.—Sketch of Ctenoplana as it may be seen when attached to the surface-film of water. In the centre is seen the mouth. The two end-lobes of the central gastric system show up white.

FIG. 5.—C. Korotneffi. Section parallel to stomachal plane (i.e. transverse to tentacle axis) to show the origin of the genital cæcum, &c. The section is somewhat oblique. *cil.* Ciliated epithelium of ventral surface. *cæ.* Genital cæcum. *ch.* Chloragogenous cells. *c. p.* Ctenophoral plate, retracted. *d. e.* Dorsal spongy vacuolar non-ciliated epithelium, with mucous granules at external surface. These cells would seem to be comparable to the so-called "Glanzzellen" of Ctenophora. *ent.* Cœlenteron. *ep.* Digestive epithelium, nuclei placed near free end of cells. These are clear faintly staining cells with indistinct cell outlines, and with a sharply defined non-ciliated free margin. *gen.* Genital proliferation on the wall of the genital cæcum. *g. p.* Gastric proliferation. *mes.* Mesenchymatous tissue. *t. o.* Opening of tentacle sheath. *t. s.* Tentacle sheath with its ciliated epithelium; the tentacle itself is retracted further back. *v. e.* Non-ciliated glandular epithelium of the ventral surface.

FIG. 6.—The same. Succeeding section to preceding through gonad to show the conversion of the genital cæcum into a canal. *cæ.* Genital cæcum. *s.* Genital proliferation broken up into polygonal groups of sperm mother-cells.

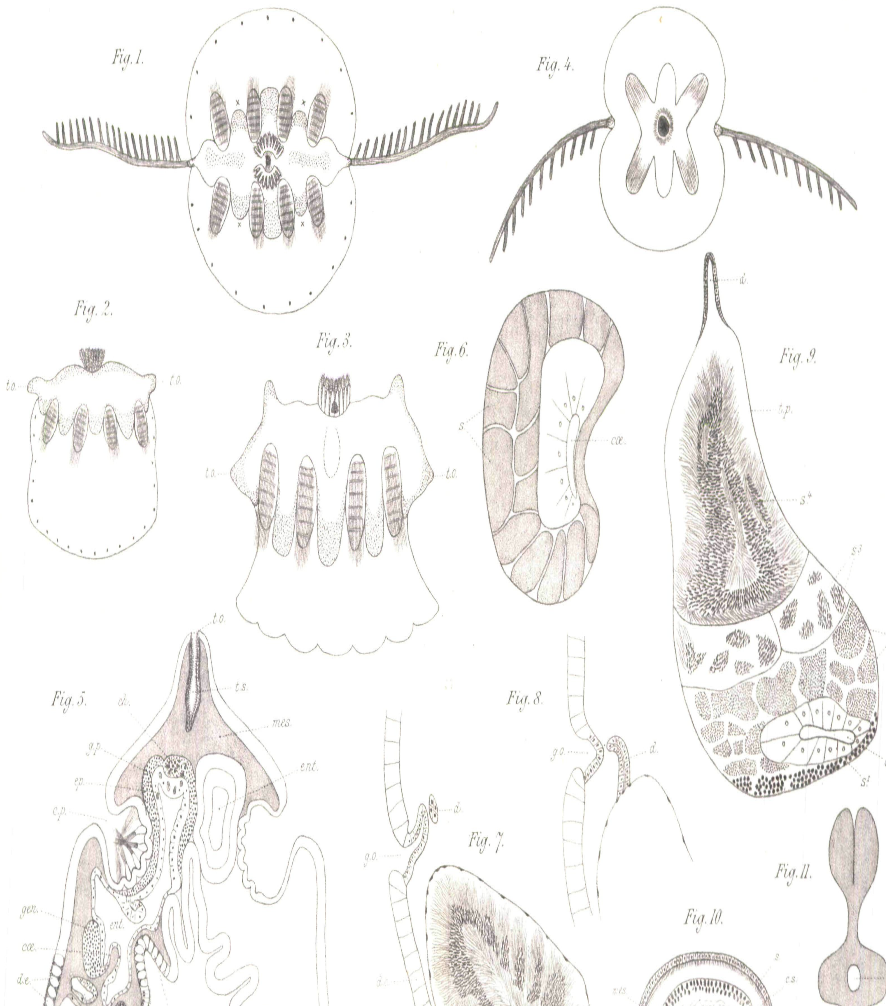
FIG. 7.—C. Korotneffi. Section through the region of the gonad of another individual to show the testis full of mature spermatozoa and the opening of the genital duct. *d.* Tangential section of portion of duct. *d. e.* Dorsal epithelium. *g. o.* Genital aperture. *t. p.* Tunica propria with flattened nuclei in its walls.

FIG. 8.—The same. Succeeding section to preceding to show junction of genital duct with tunica propria.

FIG. 9.—Section through a gonad of same individual as that from which fig. 5 was taken, to show subdivision of the testis. *cæ.* Genital cæcum. *d.* Genital duct. s^1. Spermatogonia. s^2. Spermatocytes. s^3. Spermatidia. s^4. Spermatozoa. *t. p.* Tunica propria.

FIG. 10.—Section through tentacle and its sheath. *c. s.* Cavity of sheath. *s.* Wall of sheath composed of ciliated epithelium. *t.* Tentacle with peripheral nuclei and central muscle-fibres. In the centre of the tentacle runs a core of mesenchyme-cells, *mes.* *p.* Branch or pinna of the tentacle.

FIG. 11.—Schematic figure to explain connections of the lobes of the central portion of the gastro-vascular system. *f.* Position of funnel vessel.



A. Willey del.

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