Memories of the College of Science, Kyoto Imperial University Series B,
Vol. ix, No. 4, Art. 6, 1934

On the Structure of *Ctenoplana*

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With 8 Test-figures

(Received Oct. 20, 1933)

Introduction

The peculiar creeping ctenophore *Ctenoplana* was discovered first by Korotneff in 1885 in the sea close to the west coast of Sumatra. He found his unique specimen drifting in a sea current in company with a number of *Porpita*. His accounts of this novel organism were published in Z. W. Z. Vol. 43, and created a great sensation among the contemporatory zoologists. This was mainly due to the fact that the animal was thought to represent a connecting link between the radial and bilateral groups of the animal kingdom much as in the case of *Coeloplana* recorded six years previously. He named the animal *Ctenoplana kowalevskii* in honor of the discoverer of the latter animal. His observations on the specimen in the living state and in sections, although inevitably imperfect in some respects, were largely adequate and have often been quoted since. Ten years later, in 1896, Willey announced the discovery of the same animal in the sea in the Eastern Archipelago of British New Guinea. This time it was represented by four examples found attached to a drifting cuttlebone. He referred them to two species distinct from Korotneff's, namely, *C. korotneffi* and *C. rosacea*. His study of this material supplemented a good deal Korotneff's observations; especially noteworthy was the state of the male gonad which had been entirely unknown to the latter zoologist. *Ctenoplana* had never been found since until only recently. In the mean time our knowledge of the allied genera, *Coeloplana*, *Tjalfiella* and *Gastrodes*, had increased greatly, and a renewed study of *Ctenoplana* became highly desirable.

Fortunately in 1929 DOWYDOFF reported in C. R. Acad. Sci., Paris, Vol. 39, his rediscovery of *Ctenoplana* in the Bay of Nhatrang in Annam. His examples, ten in all, were assigned by him to three species all new, namely, *C. agniae*, *C. duboscqui* and *C. yuri*. He subsequently obtained more materials, and described in detail their external appearance and manner of life in papers published in 1930 and 1933. The internal features, however, remained entirely untouched, except some points observed from the outside.

Material

In the last part of August this year, I visited the Misaki Marine Biological Station where I carried out my studies on *Coeloplana* and *Gastrodes* more than ten years ago. The assistant of the station, Mr. N. YOSHII, brought me an organism which he had taken for a kind of *Coeloplana*. My past experience of *Coeloplana* enabled me to identify it with *Ctenoplana* at once. According to Mr. YOSHII, the animal, of which there were two examples, had been found attached to drift seaweed by Mr. T. FUKUDA, a student of zoology of the Tokyo Imperial University, and had been kept alive by himself for some days. A glance at the external appearance of the specimens brought strongly to mind WILLEY's figure of *Ctenoplana rosacea* which is often reproduced in textbooks. When attached to the substratum, the body is flattened, very thin and highly transparent. It is nearly rounded in outline, and has a slight concavity on either end of the axis in which a pair of long pinnate tentacles lie. As the center of the body is found the aboral sence-organ, and directly external to it in the sagittal plane, occurs a polar plate on either side. The plate is fringed with eight or nine finger-like processes which are highly characteristic of this genus. Eight ribs or combplate rows occupy the adradial positions. They are comparatively short, elongate-oval in contour, and consist of seven or eight plates each. The interradial area between the ribs of the same quadrant is marked with a conspicuous mass of whitish color. The mass is made up of two or three piriform bodies which are testes without any doubt. Each testis is provided with a duct which opens on the dorsal side. This opening was clearly visible even under a low-power microscope. The area external to the ribs is occupied by an anastomosing canal-system which presents an appearance in no way different from that of the corresponding area of *Coeloplana*.

So much for my observations of the living material. Mr. YOSHII

intends to publish his own observations on the material very shortly elsewhere, and I shall not go into it in any further detail.

After the specimens had been kept alive for several days they were fixed with BONIN's mixture by Mr. YOSHII. One of them was lost unfortunately, and the remaining one was presented to me so that I might examine the internal structure. The fixation was excellent, and I was able to make out without difficulty the essential points of the organization of this curious animal which had remained obscure in spite of the investigations of previous authors. The only regret is that the male gonad which was such a conspicuous structure when I saw the living specimen, had entirely disappeared, evidently owing to the discharge of the ripe sperm meanwhile. However, I have been able to recognize the remaining gonoducts in sections and to locate the former position of the testes.

General Plan of Organization

As is shown in the diagrams (Fig. 1, 2), the general plan of the structure of *Ctenoplana* is essentially that of a ctenophore. However, the body is flattened and has developed a distinct dorsi-ventrality. This flatness and dorsi-ventrality, which the animal shares with other members of the Platyctenea, has been brought about, not through the simple reduction of the principal axis of the body of the ctenophore, but mainly through the extension of the external half of the pharynx. Hence, the ventral surface on which the animal crawls, is morphologically the internal surface of the external half of the pharynx.

At the center of this ventral surface, right under the sense-organ (*s*), is found the mouth-opening of this animal (*m*). This is originally the isthums lying between the external and internal sections of the pharynx of the ordinary ctenophore. The axis connecting the sense-organ and the mouth-opening determines the main axis of the body. The other organs are arranged in the biradial manner as in the ordinary ctenophore. The tentacles (*t*) lie in the transverse plane; the polar plates (*p.p*) in the sagittal plane, while the ribs (*r*) occupy the adradial planes. The whole tentacular apparatus takes the horizontal position instead of the vertical position of the ordinary ctenophore, and the tentacle sheath is divided into two distinct compartments over-lying each other, the one containing the tentacle proper (Fig. 2. *t. sh. d*), over the other enveloping the root and basis (*t. sh. v*). In the gastro-vascular system, the pharynx (*ph. i*), which corresponds to the internal portion of the pharynx of the ordinary ctenophore, is of a depressed form, and has its wall folded considerably. At the center of its roof occurs a slit

leading into the oesophagus (*oe*), an organ very inconspicuous in the ordinary ctenophore, but rather apparent in the Platyctenea. This forms a passage from the pharynx into the infundibulum (*i*). The latter is disproportionately large as compared with that of the ordinary ctenophore. From its sagittal wall on either side, starts an excretory canal

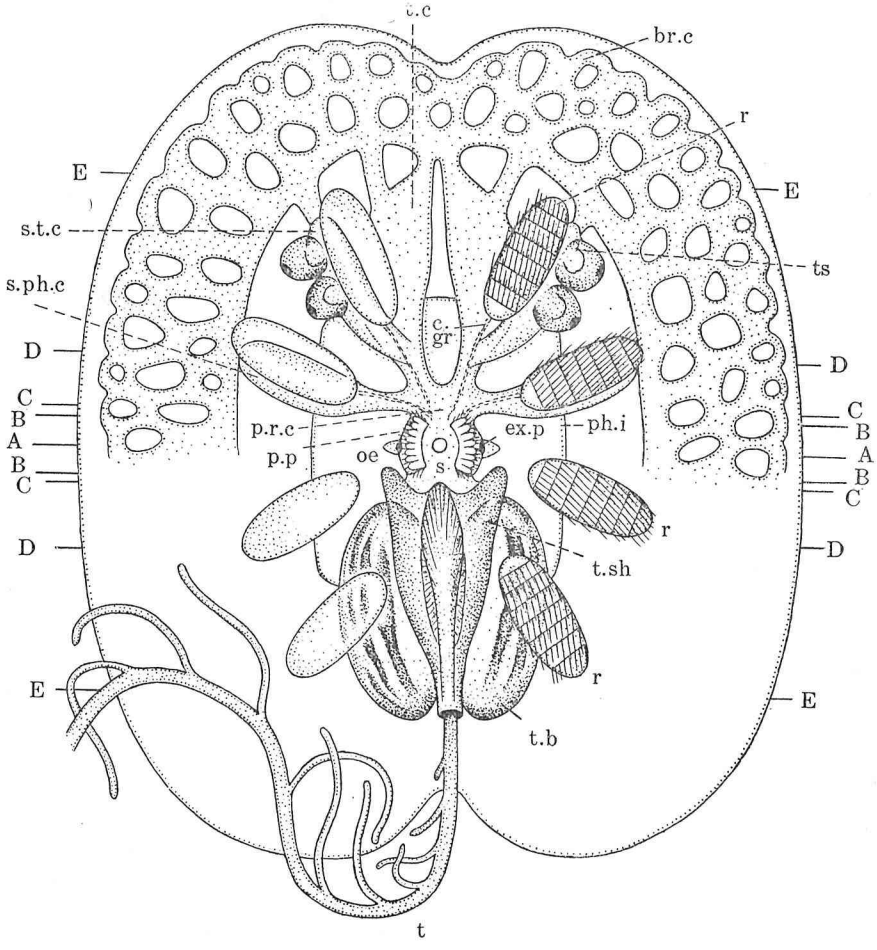

Fig. 1. Diagrammatic figure showing the structure of *Ctenoplana* in creeping attitude. In the upper half is shown the canal system, in the lower half, the tentacular apparatus.

(*ex. p*) which opens by an excretory pore (*ex. p*) on the external side of the polar plate (*p. p*). The infundibulum further gives off on either transverse side a perradial canal (*p. r. c*) which immediately divides into four canals, a pair of tentacular canals (*t. c*) and a pair of sub-

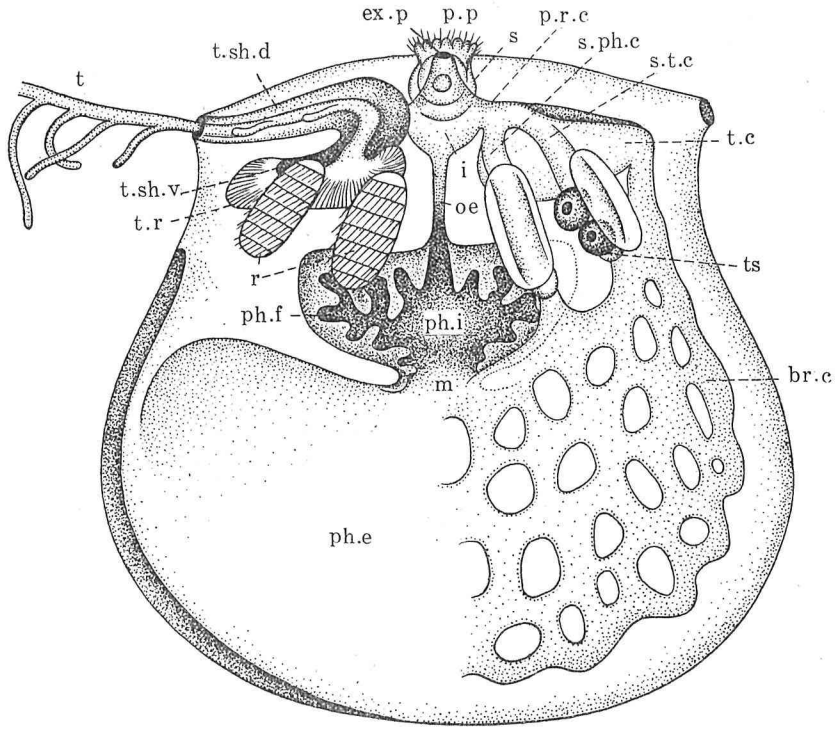

Fig. 2. Diagrammatic figure showing the structure of *Ctenoplana* in floating attitude. On the left side is shown the tentacular apparatus, on the right side, the canal system.

pharyngeal meridional canals (*s. ph. c*). The tentacular canal accompanies the tentacle-basis on its ventral side throughout its extension. Each tentacular canal further sends off the sub-tentacular meridional canal (*s. t. c*) from its proximal end. The sub-pharyngeal and sub-tentacular meridional canals run beneath the corresponding ribs as in the ordinary ctenophore. From various points in the main divisions of the gastro-vascular system mentioned above, are given off branch canals (*br. c*) which penetrate the peripheral region of the body and form the canal network very apparent in this animal as well as in *Coeloplana*.

Of the gonads, the ovary remains unknown; the testes (*ts*) develop as some separate compact bodies on the interradial side of the wall of the sub-tentacular meridional canals, exactly like in *Coeloplana*.

In the swimming attitude, as well as in the contracted state, *Ctenoplana* takes a shape not unlike that of a *Pilidium* (Fig. 2), the peripheral region of the body hanging down like a pair of lappets one on either side of the tentacular plane.

Anatomy and Histology

Before going into details of the structure of each organ, it may be mentioned that *Ctenoplana* bears a far-reaching similarity to *Coeloplana* in almost every respect, both anatomical and histological, so

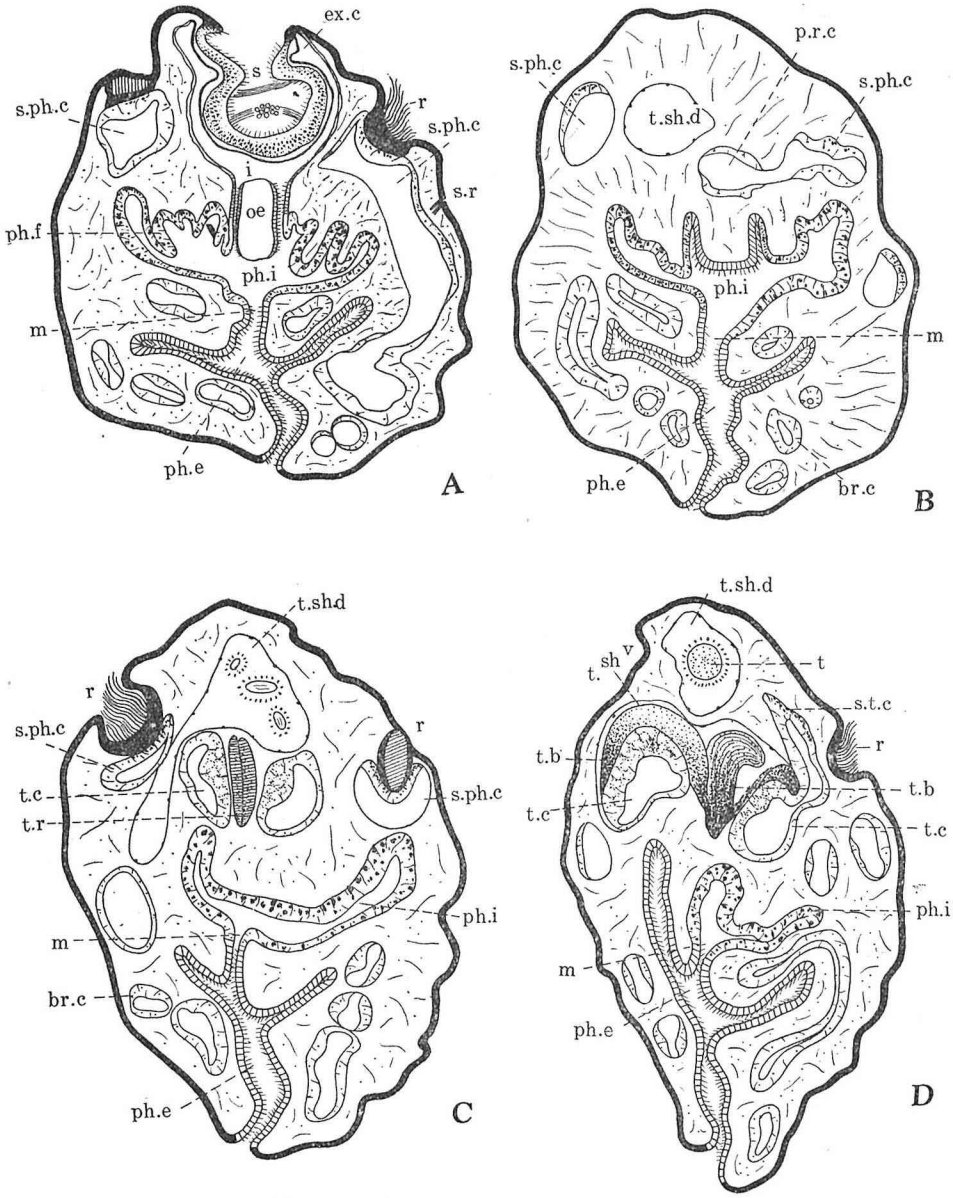

Fig. 3, A–D. Sections parallel to the sagittal plane on the levels A–D respectively in Fig. 1. ×70

that I shall confine myself mainly to the statements of the differences found between the two genera. The epidermis is very thin as compared with that of *Coeloplana*. It has, however, the same cell-components as the latter: two sorts (eosinophilous and cyanophilous) of gland cells and interstitial cells. The gland cells are smaller and fewer than in *Coeloplana*. The finger-like processes of the polar plates are formed by rather flattened ciliated cells. The ribs may be retracted completely beneath the external surface; this is brought about presumably by the muscle-fibers that run lengthwise below the ribs. Each rib is connected with the sense-organ by a ciliated groove as is clearly shown by DAWYDOFF. This groove is formed by a row of ca. 15 rather flattened cells which contain compact eosinophilous plasm and bear short but strong cilia (Fig. 5). Parenthetically it may be added that this groove occurs in *Coeloplana* as well (KOMAI, 1922, Pl. 4 Fig. 6) although it is often hard to recognize and has escaped DAWYDOFF'S notice.

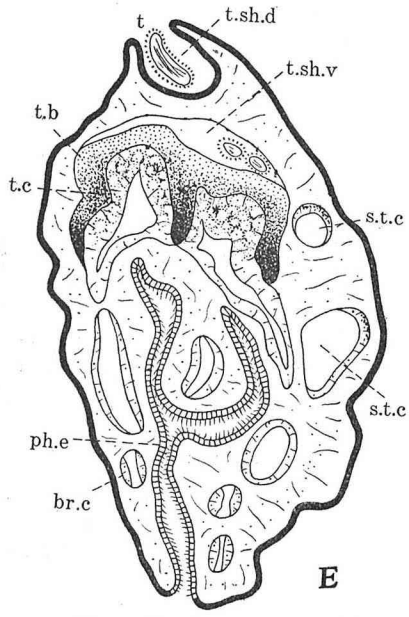

Fig. 3, E. Sections parallel to the sagittal plane on the level E in Fig. 1. ×70

The tentacular apparatus is identical in structure with that of *Coeloplana*, except that the tentacle appears shorter and stiffer than in the latter. The root and basis of the tentacle, which are the formative zones of the muscles and colloblasts respectively, are identical with the corresponding parts of *Coeloplana*. The tentacle sheath is lined with a thin epithelium in its deeper parts; the epithelium thickens gradually toward the opening, and shows ciliation at least in these thicker parts. The proximal end of the dorsal section of the tentacle sheath is prolonged into a caecum on either side (Fig. 3, B, C. *t. sh. d*).

The body-parenchyme is more diffuse than in *Coeloplana*: it contains much fewer muscle fibers and other elements. The problematical eosinophilous mass which is very characteristic of the parenchyme of *Coeloplana* is entirely missing in *Ctenoplana*. The pigment cells are apparently of the same type as in *Coeloplana*. The opaque pigment cells which are made up of granules appearing yellowish by transmitted

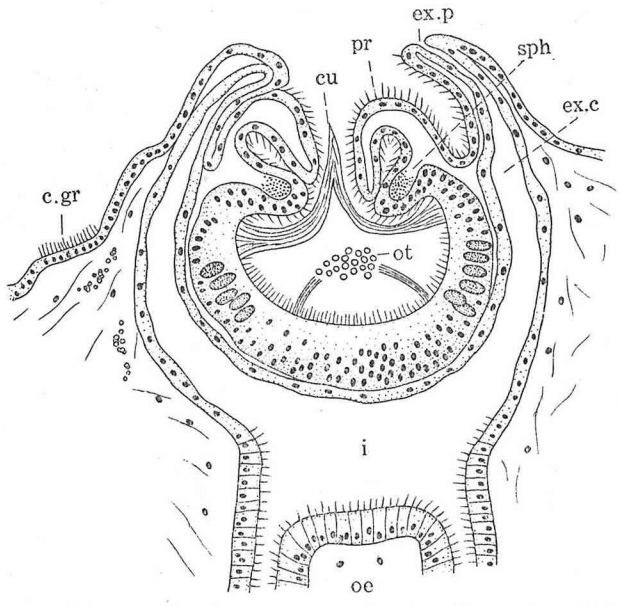

Fig. 4. Aboral sense-organ and surrounding parts. ×200

light and milky white by reflected light, are comparatively numerous. They are aggregated into rather conspicuous spots arranged with fairly regular intervals between them at some distance from the periphery. These spots are depicted faithfully in in WILLEY's figure (1896, Fig. 1).

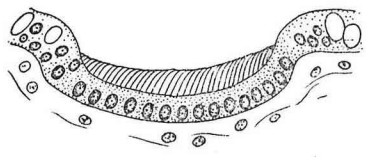

Fig. 5. Transverse section of ciliated groove. ×550

Of the gastro-vascular system, the external half of the original pharynx which forms the creeping sole (Fig. 3, *ph. e*) is formed for the greater part of ciliated cells dispersed sparsely with gland cells. The gland cells are comparatively well developed in the marginal parts of the sole. The internal half, the pharynx proper (*ph. i*), on the other hand, contains far more numerous gland cells, while the ciliation here is much thinner than in the external half. One kind of gland cell stands out very conspicuously in sections owing to the strong acidophily of the contained granules. The oesophagus (*oe*) which is the innermost part of the stomadaeum, is lined with cells bearing very strong cilia.

The infundibulum (Fig. 4, *i*), as well as the excretory canals (*ex. c*), has rather thin walls. The meridional canals may be distinguished from other canals by having a thick wall on the external side adjoining the rib (Fig. 3, *s. ph. c*, *s. t. c*). In the tentacular canals (*t. c*) the wall

on the dorsal side which lies directly beneath the tentacle basis is thickened enormously, and encloses a quantity of food material. It appears that the digestive activity of the animal is monopolized by the endoderm of this part. The branching canals (*br. c*) have comparatively thick walls on the ventral and dorsal sides. The so-called rosette, characteristic of the endoderm of the ctenophore, is here a rather conspicuous element. Obviously, it performs some important function, possibly the passage of water from the canal into the body parenchyme. The striking appearance of the cilia borne by the component cells supports this view (Fig. 6).

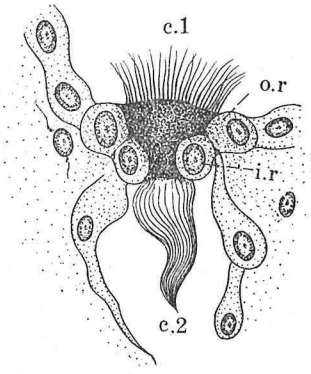

Fig. 6. Ciliated rosette. ×1500
i. r. ..... inner ring.
o. r. ..... outer ring.
c. 1.....Cilia of outer ring in the canal lumen.
c. 2.....Cilia of inner ring in a lacuna of mesogloea.

The gonad is evidently the most interesting part in the whole organization of *Ctenoplana*. The female gonad has never been found. In the specimen before me also, there is no trace of ovary, except the occurrence of some very small cells, possibly primordial egg cells, found in the outer wall of the meridional canals. However, there are a few tubular invaginations from the epidermis opposite the subpharyngeal canals (Fig. 7), and this structure reminds one strongly of the duct of the seminal receptacle occurring in *Coeloplana*. At any rate, it is highly probable that the ovary develops from the meridional canals on their perradial walls, the same as in *Coeloplana* and ordinary ctenophores. The testes in the present material were observed only in the living state as mentioned above. Fortunately, however, they are described in detail by WILLEY. His account of the male gonad seems to be largely adequate, since it comforms very well with the condition found in *Coeloplana*. The most noteworthy feature of this organ in these two genera consists in the facts that it forms some separate compact masses instead of a continuous series of testicular cells, and that each mass has a duct leading the sperm to the dorsal surface of the body. The opening of the duct may be seen clearly in living material, as already men-

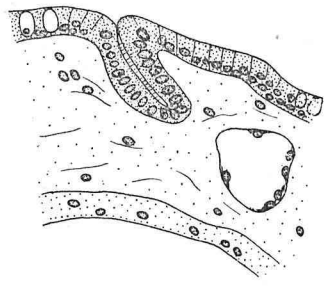

Fig. 7. Seminal receptacle? ×500

tioned. Of the meridional canals, the subtentacular canals alone seem to develop testes. In *Coeloplana* also, the testes arise mainly from the wall of these canals. However, the subpharyngeal canals may give rise to a few testes; and it is possible that the same thing holds for *Ctenoplana* as well.

Remarks

As already pointed out by MORTENSEN (1912), both KOROTNEFF and WILLEY failed to form an exact idea of the configuration of the tentacular apparatus. KOROTNEFF describes the tentacles enclosed in the sheath simply as 'Längsmuskel' and takes it to be of an enigmatic nature. WILLEY calls the tentacle basis 'gastric gland' and the primordia of colloblast 'chloragogenous cells', without any idea of their true nature. As to the gastro-vascular system also, neither of these authors has been able to identify individual canals adequately. KOROTNEFF states that there is 'keine bestimmte Konfiguration, wie es bei den Rippenquallen der Fall ist'. WILLEY recognizes no meridional canals. These canals however are by no means hard to recognize, by the characteristics that they accompany the ribs closely, and that they are lined by tall cells on the dorsal side only; besides they develop the gonad from their wall. The existence of the excretory pore in *Ctenoplana* is questioned by DAWYDOFF. However, the pore is easy to find in sections. Mr. YOSHII has observed even the actual discharge occur through the pore in the living material.

The testes belonging to the same quadrant are situated so close to one another, that they may appear as a single irregular-shaped body furnished with more than one duct. Thus, WILLEY states that the testes 'consist of two pairs of organs paired about the tentacle axis. They may be either simple or lobed and subdivided' and 'they may possess one or several ducts (1896, p. 329). DAWYDOFF, however, recognizes the duplicity of the genital mass of each quadrant. As a matter of fact, the condition of the testes is apparently identical with that in *Coeloplana*, where each meridional canal may develop one to several testes, and each testis is furnished with one duct. The testes have been observed by WILLEY, DAWYDOFF and myself; the ovary, however, has never been found. This is a rather striking fact which is hard to understand. The state of the female gonad thus awaits further discovery.

As to the systematic position of *Ctenoplana*, there is no doubt that it belongs to the Platyctenea and represents a stage standing

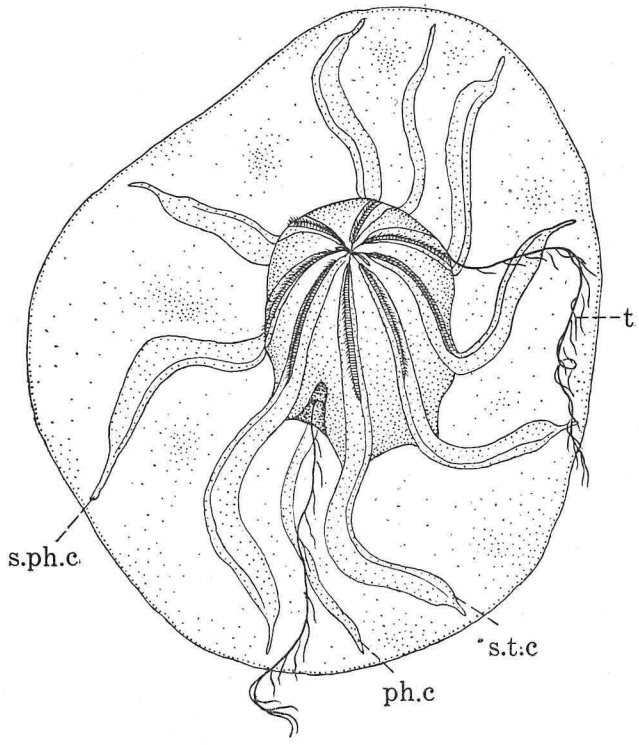

Fig. 8. *Lampetia pancerina* CHUN crawling. ×1.5
Author's sketch made in March 1919.

between the cydippid ctenophores especially like *Lampetia* (Fig. 8) and *Coeloplana*. It shares with *Coeloplana* among other things, the creeping sole, pigment, branching canals, compact testes, spermiducts, processes of polar plates and the absence of pharyngeal canals. Points in which it differs are that the body is much smaller; the ribs are persisting; the musculature is far less developed; the sense-organ and the finger-like processes of the polar plates are differentiated better than in *Coeloplana*. All these differences seem to be correlated with the fact that *Ctenoplana* is both a swimming and creeping animal, while *Coeloplana* is limited to creeping life in its adult stage. The close resemblance between *Ctenoplana* and the larva of *Coeloplana* has been pointed out by DAWYDOFF. However, differences may be found between the two in the gastro-vascular system, which is far better differentiated in *Ctenoplana*, and in the disposition of the tentacular apparatus—vertical in *Coeloplana* larva and horizontal in *Ctenoplana*.

Finally, as to the systematic position of the whole group Platy-

ctenea, I have nothing to add to the statements in my paper on *Coeloplana* and *Gastrodes*. In short, they are highly specialized but genuine ctenophores, and their resemblance to the Turbellaria is no more than a fine instance of parallel adaptation.

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Abbreviations used in text figures

br. c, branching canals; *c. gr*, ciliated groove; *cu*, 'cupule' of aboral sense-organ; *ex. c*, excretory canal; *ex. p*, excretory pore; *i*, infundiblum; *m*, mouth-aperture; *oe*, oesophagus; *ot*, otolith, *ph. c*, pharyngeal canal; *ph. e*, external portion of pharynx (when extended, forms creeping sole); *ph. f*, pharyngeal folds; *ph. i*, internal portion of pharynx; *p. p*, polar plate; *pr*, marginal process of polar plate; *p. r. c*, per-radial canal; *r*, rib; *s*, aboral sense-organ; *sph*, sphincter muscles of sense-organ; *s. ph. c*, sub-pharyngeal meridional canal; *s. r*, seminal receptacle; *s. t. c*, sub-tentacular meridional canal; *t*, tentacle; *t. b*, tentacle basis; *t. c*, tentacular canal; *t. r*, tentacle root; *ts*, testis; *t. sh. d*, dorsal compartment of tentacle sheath; *t. sh. v*, ventral compartment of tentacle sheath.

Postscriptum: While this paper was in press, Mr. YOSHII's note, "*Ctenoplana* from Japan", appeared in Proc. Imp. Acad. 9, 539-540 (1933). In this he has given the name of *Ctenoplana maculomarginata* to the specimen dealt with in the present paper. Further, he describes from the same locality another new species, *C. maculosa*.