XIII SYSTEMATIC NOTES ON THE CTENOSTOMATOUS POLYZOA OF FRESH WATER

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In preparing an account of the freshwater polyzoa for the "Fauna of British India" I have had occasion to examine specimens of most of the ctenostomatous species as yet known to occur in the rivers, lakes and ponds of different regions. It may therefore prove useful to publish the following supplementary notes. I have received much assistance in the preparation of specimens from Mr. F. H. Gravely, Assistant Superintendent in the Indian Museum, and am indebted for many of these specimens to Dr. K. Kraepelin, Dr. W Michaelsen, Mr. C. Rousselet and Mr. R. Kirkpatrick. Full references to literature on the Indian species will be found in my volume in the "Fauna," only a few of the more important general works being cited in this paper.

Suborder CTENOSTOMATA.

Division *PALUDICELLINA*.

Ctenostomatous polyzoa in which the zoarium increases by a cruciform[1] system of budding, each zooecium giving rise normally to three daughter-zooecia (one on each side and one at its anterior end) and being connected posteriorly with its own mother-zooecium. No zooecium is ever connected by its base with more than four others. In the polypide that part of the alimentary canal which intervenes between the cardia and the main chamber of the stomach is always more or less modified but never forms an organ of compression or is provided with internal teeth.

All the Paludicellina are found in fresh or brackish water. Anatomically they appear to be related to the Alcyonellea rather than the Vesicularina,[2] to which many of them bear a certain superficial resemblance.

Family PALUDICELLIDAE.

Zooecia more or less tubular and at least partially vertical, often adherent by the base only or altogether free. In adverse

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[1] Rousselet (*P.Z.S.*, 1907 (i), p. 252) refers to such forms as "Cruciform Stolonifera" but includes with them certain marine genera that do not exhibit the same regularity in their method of budding.

[2] Waters, *Journ. Linn. Soc. London*—Zool., xxxi, p. 237 (1910).

circumstances resting buds with a hard chitinous coat are produced and lie dormant until the return of favourable conditions.

Key to the genera of the Paludicellidae.

1. No buds produced at the distal end of the zooecium.
   (*a*) Zooecia narrowly flask-shaped, semi-recumbent or at any rate with the dorsal surface clearly distinct from the ventral — *Paludicella.*
   (*b*) Zooecia tubular, upright; the dorsal and ventral surfaces identical — *Pottsiella.*
2. Buds produced at the distal end of the zooecia.
   Zooecia (when adult) tubular, nearly upright, more or less swollen at the base — *Victorella.*

Genus PALUDICELLA, Gervais.

Zooecia narrowly vase-shaped with the dorsal surface distinct from the ventral; the orifice situated on a tubular outgrowth from the former; no distal buds; collar without chitinous chaetae. No part of the alimentary canal of the polypide lined with chitin and only that part which surrounds the pyloric aperture of the stomach ciliated; no defined compressor muscle round the cardiac chamber, although separate fibres can be distinguished. The stomach connected with the zooecial wall by two funiculi, one of which bears the ovary, the other the testis, the former being situated nearer the pyloric orifice than the other. There are 16 tentacles.

Paludicella ehrenbergi, van Beneden.

(Pl. xiii, fig. 1.)

Syn. *Alcyonella articulata*, Ehrenberg; *Paludicella procumbans*, Hancock; *Paludicella elongata*, Leidy.

This is the only species I am able to assign to the genus. Its zoaria as a rule form upright branches consisting of zooecia arising directly one from another. Basal stolon-like tubules are never formed. The lateral basal buds are often suppressed, or only one of them is produced, so that budding is in linear series with only a few lateral branches instead of a cruciform figure. There is a slightly dilated but slender oval chamber between the cardia and the stomach proper. Its walls are glandular and not very thick.

P. ehrenbergi is common in Europe and America but probably does not occur in the Ethiopian and Oriental regions.

Genus POTTSIELLA, Kraepelin.

The zooecia differ from those of *Paludicella* in being entirely vertical and in being separated at the base by stolon-like tubules.

The anatomy of the two genera is very similar, but the whole alimentary canal (pl. xiii, fig. 2*a*) is more slender and elongate in *Pottsiella*, which has only 8 tentacles.

Pottsiella erecta (Potts).

(Pl. xiii, figs. 2, 2*a*.)

Syn. *Paludicella erecta*, Potts.

The zooecia are slender, elongate and somewhat constricted both at the base and at the tip. The orifice is pentagonal in cross-section. The basal tubules are often of considerable length; occasionally extra tubules are produced from the sides of the zooecium, but this is exceptional. Buds may, perhaps, be borne sometimes at the end of these adventitious lateral tubules.

This species is only known from the neighbourhood of Philadelphia, U.S.A. I have been enabled by the kindness of Mr. C. Rousselet to examine specimens from the type locality.

Genus VICTORELLA, Kent.

The adult zooecia are always nearly vertical but as a rule they pass through a stage at which they resemble those of *Paludicella* in form. They are separated by basal tubules resembling those of *Pottsiella*, and daughter-zooecia (distal buds), (with or without similar tubules intervening, are usually borne near the tip of the zooecium (pl. xiii, fig. 3) in addition to the basal buds.

The cardia closes off from the oesophagus proper an oval chamber lined with a thin chitinous coat and surrounded at its base by a stout compressor muscle. This muscle (pl. xiii, figs. 7, 8) serves to close off the chamber from the cardiac part of the stomach, which is produced upwards to meet it in tubular form. The arrangement of cilia in the alimentary canal is the same as that found in *Paludicella*. There is only one funiculus, attached to the base of the stomach, and the gonads are borne on the zooecial wall far from it. There are 8 tentacles.

Four "species" can be distinguished in this genus, but they are so closely allied that it might be better to regard them merely either as varieties or as subspecies (local races). They may be separated as follows:—

1. Parietal muscles present at the tip of the zooecium (pl. xiii, fig. 4). Young zooecium circular in cross-section at the tip, adult zooecium quadrate; distal buds only produced by adult zooecia; lateral basal buds rarely suppressed — *V. mülleri*.
2. Parietal muscles absent from the tip of the zooecium (pl. xiii, fig. 5).
   I. Both young and adult zooecia quadrate at the tip; basal tubules

elongate; distal buds produced in profusion by the adult zooecia; lateral basal buds rarely suppressed — *V. pavida.*

II. Young zooecia usually quadrate, adult zooecia quadrate or circular at the tip; basal tubules often short; distal buds produced, often sparingly, by both young and adult zooecia; lateral basal buds present or absent — *V bengalensis.*

III. Zooecia always circular at the tip; basal tubules short; distal buds often absent, never produced in profusion; lateral basal buds usually absent — *V symbiotica.*

Victorella mülleri (Kraepelin).

(Pl. xiii, fig. 4.)

Paludicella mülleri, *Kraepelin, Die deutschen Süsswasser-Bryozoen*, i, p. 159, figs. A, B (1887).

V. mülleri is the most distinct of the four forms and was originally described by Dr. K. Kraepelin as a species of *Paludicella.* I have, however, been enabled by the kindness of Dr. Kraepelin and Dr. W. Michaelsen to examine specimens from the type locality (Greifswald, Germany), in which they occurred together with examples of an undoubted *Victorella.* On a careful examination the latter were found to differ from specimens of *V. pavida* from the type locality in England and also from other German localities in having parietal muscles at the tip of the zooecium (pl. xiii, figs. 4, 5). A further search on the leaves to which the form *mülleri* was attached also revealed intermediate stages between that form and the *Victorella* associated with it. I have therefore no doubt that Kraepelin's types were merely young zoaria of a species of *Victorella* to which the specific name *mülleri* must be applied. In the young zooecium the cross-section of the distal part is almost circular, but in the adult zooecium it becomes quadrate. Apparently young zooecia in this species do not produce distal buds, which are borne in profusion by the zooecia of well-grown colonies.

V. mülleri has only been found in Germany (Ryckflusse at Greifswald) in brackish water.

Victorella pavida, Kent.

(Pl. xiii, fig. 5.)

This species only differs from *V. mülleri* in the following characters:—

(*i*) There are no parietal muscles at the tip of the zooecium (pl. xiii, fig. 5);
(*ii*) both the young and the adult zooecia are quadrate;
(*iii*) *young* zooecia frequently bear stolon-like processes and buds near the distal end;
(*iv*) the growth of the zoarium is perhaps as a general rule somewhat more irregular, particularly as regards the production of lateral basal buds.

Victorella pavida occurs in brackish and occasionally in fresh water in England, Belgium and Germany. It has also been reported from the littoral zone of the sea in Europe and is stated to have been found in Australia.

Victorella bengalensis, Annandale.

(Pl. xiii, figs. 3, 7 and 8.)

This form is distinguished from *V. pavida* mainly by its more luxuriant and irregular growth and by the fact that the distal end of the adult zooecium is usually circular in cross-section. Its zoaria have as a rule the appearance of a thick fur coating the roots and stems of grasses, etc. The swelling at the base of adult zooecia is never very large.

V. bengalensis has been found at various places near the coast of Bengal and Madras, as a rule in brackish but occasionally in fresh water.

Victorella symbiotica, Rousselet.

(Pl. xiii, fig. 6.)

Rousselet, *P.Z.S.*, 1907 (i), p. 255. pl. xv, figs. 7, 8.

V. symbiotica is distinguished by the following characters:—
(*i*) The swelling at the base of the adult zooecium is very small and inconspicuous, the whole of the zooecium being almost cylindrical and practically vertical;
(*ii*) distal buds are produced very sparingly;
(*iii*) the distal end of the zooecium is always nearly circular in cross-section;
(*iv*) the lateral basal buds are very often suppressed.

V. symbiotica was originally described from Lake Tanganyika and has more recently been taken by Mr. C. L. Boulenger and Dr. Cunnington in the salt-lake Birket-el-Qurun in Egypt. I have examined specimens from both localities.

Family HISLOPIIDAE.

This family is easily distinguished by its flattened and adherent zooecia. The structure of the polypide differs considerably from that of any Paludicellid genus, its most characteristic features being the presence (*i*) of a relatively large and practically spherical

chamber lined with smooth chitin and covered externally by circular muscles (pl. xiii, figs. 10, 11), and (*ii*) of strong cilia round the cardiac orifice of the stomach as well as the pyloric. The spherical chamber is separated from the cardia by a cylindrical glandular tract and opens almost directly into the main chamber of the stomach, from which it is only separated by a ring bearing stout and very active cilia.

So far as is known, resting buds are not formed in this family.

The family is only known from Central Africa and Eastern Asia and only two genera can be recognized, namely *Arachnoidea* Moore, and *Hislopia* Carter; they may be distinguished as follows:—

1. Zooecia provided with an upright orificial tubule, separated from one another by stolon-like processes ... *Arachnoidea.*
2. Orifice little raised above the dorsal surface of the zooecia, which arise directly one from another .. *Hislopia.*

Genus ARACHNOIDEA, Moore.

Syn. *Arachnoidia*, Moore; *Arachnidium*, Loppens (*nec* Hincks).

The zoarium consists of flattened zooecia of irregular outline joined together in the typical cruciform manner by slender and elongate basal tubules. Each zooecium is provided on the dorsal surface with a relatively long but slender orificial tubule which projects almost vertically upright. The polypide has 8 tentacles. It possesses in its alimentary canal an almost spherical, strongly muscular chamber lined with chitin and similar in structure to that possessed by *Hislopia* which is described below. The collar is supported by chaetae.

Arachnoidea ray-lankesteri, Moore.

Rousselet, P.Z.S., 1907 (i), p. 255, pl. xiv, figs. 5, 6.

This, the only species, has the character of the genus, but its anatomy is imperfectly known and none of the specimens now in India or Europe appear to be in a sufficiently good state of preservation for its further elucidation.

A. ray-lankesteri is only known from Lake Tanganyika in Central Africa.

Genus HISLOPIA, Carter.

Syn *Norodonia*, Jullien; *Echinella*, Korotneff.

Hislopia differs from *Arachnoidea* mainly in two characters, (*i*) the fact that zooecia arise directly one from another without the intervention of basal tubules, and (*ii*) the absence of an orificial tubule, the orifice being raised above the dorsal surface merely on a slight eminence. The form of the zooecia is also more regular and each is surrounded by a thickened margin. The

number of tentacles is variable but is usually some multiple of four. The collar is unusually ample and is supported by delicate chitinous chaetae. Immediately below the cardia there is a short glandular portion of the alimentary canal, tubular in form, which lies at right angles to the main axis of the zooecium when the polypide is retracted. This opens into the spherical chamber, which is relatively large and bears a thick chitinous lining that has the appearance in optical section of a couple of vertical ridges. The compressor muscle (pl. xiii, figs. 10, 11) covers the whole of the chamber but only extends over the glandular region above it in the form of isolated fibres. In preserved specimens the chamber appears to open directly into the stomach but in living specimens the ring separating the two and bearing the cardiac cilia can be extended in a vertical direction to some length. The parietal muscles are reduced to three or four stout strands on either side of the zooecium and there is not a definite funiculus. The gonads are borne on the zooecial wall at each side of the polypide.

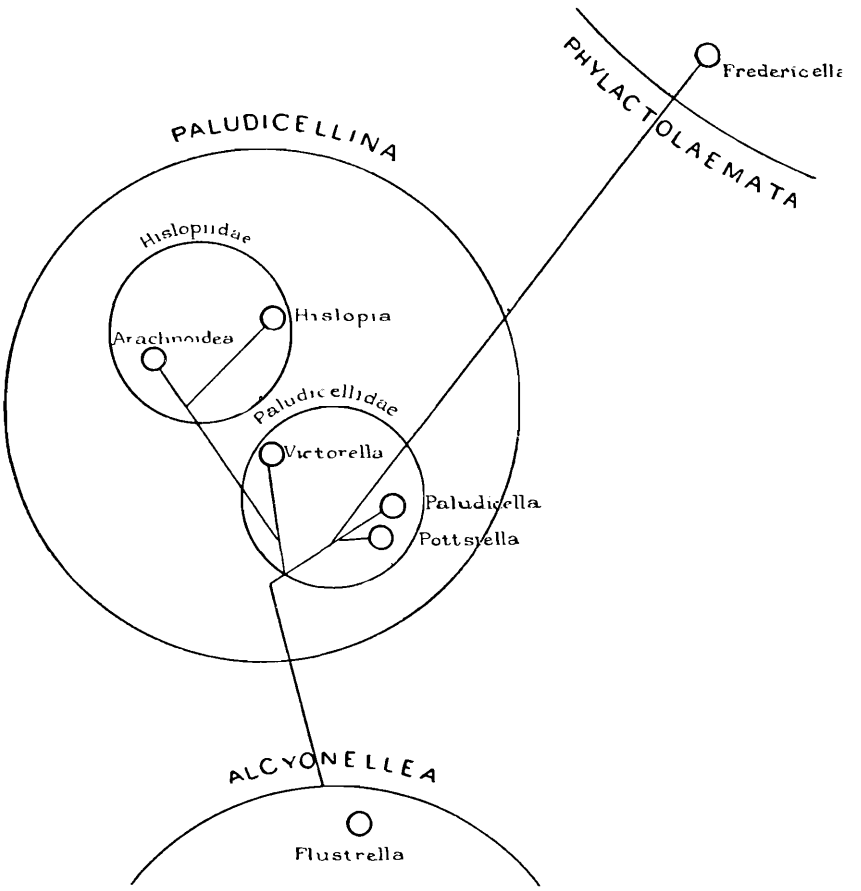
Hislopia lacustris, Carter.

(Pl. xiii, figs. 9, 10, 11.)

Owing to rapid lateral and terminal budding at the base of the zooecia and to the absence of intervening tubules, well-developed zoaria constitute, in the typical form of the species, an almost uniform flat layer which has much the same appearance as that of many Cheilostomata (*e.g Membranipora*) and also of certain Ctenostomata of the division Alcyonellea (*e.g.*, *Flustrella*). A careful analysis of the method of budding, however, shows that it is always of the cruciform type, whereas in *Membranipora* more than one lateral bud is produced at each side of the zooecium and in *Flustrella* the method of budding is radiate, numerous linear series of zooecia radiating out from a single parent-zooecium but pressed so closely together as to be practically parallel to one another. The form of the zooecium, especially in luxuriant zoaria, is very variable; it is typically oblong but may be oval, triangular or almost circular or even square. The dorsal surface is usually flat and always has a hyaline transparency, but if the zooecia are closely crowded together on a narrow support such as the stem of a slender water-plant they are often arched above and of a considerably greater depth (pl. xiii, fig. 9) than if they have plenty of room for expansion. In such cases the thickened margin is often practically obsolete. The orifice is surrounded by a thick chitinous rim which usually has a quadrate form and bears a spine at each corner; but sometimes it is circular, and the spines not only vary in length but are often reduced in number or altogether absent. The tentacles vary in number from 12 to 20.

The structure of the cardiac region of the alimentary canal has a certain resemblance to that found in *Bowerbankia* (Vesicularina), the spherical chamber having the same position as and

a certain similarity in structure to the gizzard of that genus (pl. xiii, figs. 12, 13). Its function is however totally different, and it differs structurally in not possessing horny internal teeth. Moreover, the walls do not contract automatically with the retraction of the polypide as they do in the gizzard of *Bowerbankia*.



The spherical chamber in the alimentary canal of *Hislopia* is not a crushing organ but serves as an antechamber in which food may be stored until it is wanted for digestion. In it also the flagellate organisms that seem to form the greater part of the food undergo a process of encystment in the course of which food-material is pressed out from their bodies and apparently absorbed by the polyzoon. Further details as regards this process are given on pp. 200—202 of my volume in the "Fauna of British India."

Two forms which I believe to be merely varieties or at most local races (subspecies) of *H. lacustris* have been described as distinct species. They are—

Norodonia sinensis, Jullien, from China;
Norodonia cambodgiensis, Jullien, from China, Cambodia and Siam.

Echinella placoides,[1] Korotneff, from Lake Baikal in Siberia also appears to belong to the genus.

I have not seen any of these forms, but apparently *N. sinensis* is distinguished by having narrow zooecia with circular orifices, while in *N. cambodgiensis* the zooecia are nearly circular but constricted posteriorly. In both these forms the growth is less luxuriant than in the typical form of the species. *E. placoides*, which may be a distinct species, is distinguished by the great length of the spines at the four corners of the orificial rim.

A fourth form, for which the name subspecies *moniliformis* is proposed, occurs in Calcutta and is distinguished by the shape of the zooecia and the method of growth. The former are practically circular but truncated, not constricted posteriorly and surrounded by a flat membranous fringe. The lateral basal buds are very often suppressed and both are rarely produced, so that a linear zoarium with occasional side-branches is formed.

The diagram on p. 200 represents the relationships of the Paludicellina, as they appear to me.

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[1] *Biol. Centralb.*, xxi, p. 311, fig. (1901).