Notes on the Hydroid Phase of Limnocodium Sowerbyi.

By

G. Herbert Fowler, B.A.Oxon., Ph.D.,
University College, London.

With Plate XXXII.

Though it is now nine years since the discovery of Limnocodium in the Victoria Regia tank of the Royal Botanic Society in Regent's Park, no certain knowledge of the course of its life-history has yet been obtained, owing to the peculiar circumstances under which it occurs, and to the briefness of its annual existence. For various reasons I have only attempted the problem from one side; with the view, namely, to determine whether an already known hydroid polyp occurring in the same tank with the medusoid bore any relation to it or not.

The medusoid reappeared on May 10th, 1888; débris of all sorts was at once collected from the tank, in which the hydroid was found in quantities. By great good fortune, in the course of the following day two specimens of the hydroid were found to be undoubtedly throwing off medusoids. Of these, the one isolated in order to undergo further development died shortly, and was not available for minute examination; the other was at once preserved. Further material, comprising several hundred specimens of the hydroid, was constantly examined till the end of July, 1888; but no further gemmation of medusoids took place. As, in spite of constant

and careful search during April, May, and half of June in this year (1889), neither hydroid nor medusoid could be found, I publish this incomplete account in the hope that the remainder of the life-history may be worked out in some future year, should this interesting form reappear.[1]

The hydroid was originally observed by Mr. F. A. Parsons ('Proc. Quekett Microsc. Club' (2), ii, p. 125), but was first described in a short note by Professor A. G. Bourne ('Proc. Roy. Soc.,' 1884, p. 9), who had discovered it independently, and regarded it as a probable stage in the ontogeny of Limnocodium. This remarkable polyp was in 1888 distributed over the whole of the tank, attached to stems and leaves, bits of dead wood, and algæ, generally in little permanent colonies of two or three individuals branching from a common base. It is a simple cylindrical tube, about 6 m.m. long, with a minute mouth, and is always devoid of tentacles; but, in spite of their absence, catches and swallows small Crustacea and free Nematoda. No perisarc is secreted, but it forms a loose case of vegetable detritus, beyond which the oral end always projects. The ectoderm is but little differentiated; a cap of cubic cells at the oral end passes into more flattened cells over the general surface, and at the base of attachment are longer columnar cells. The nematocysts, as in Hydra, are of two kinds, the one oval with an unbarbed thread, the other and larger flask-shaped, like that of Millepora, and barbed. The mesoglœa lamina is so thin as to be practically unrecognisable. The endoderm is divisible into two regions, which pass imperceptibly into each other; the cells of the upper third are highly vacuolated and clear, those of the lower two thirds are filled with very brilliantly staining spherical bodies of varying size. It is from this latter region alone that gemmation of a new hydroid takes place, and the endoderm of the bud consists only of these cells. As the bud when freed does not develop a mouth for some little time, and from their refringent and deeply-staining appearance, it is possible that these granules are a store of reserve nutriment. Besides the cells

[1] The medusa did not reappear at all this year.—November, 1889.

of undoubted endoderm and ectoderm already mentioned, there occurs, round the mouth of the adult polyp internally, a little mass of deeply stained non-vacuolated cells of which the outlines are only rarely distinguishable. They resemble the ectoderm more than the endoderm, but are not exactly continuous with either layer, and occur in all specimens of the hydroid all through the summer, except in the most recently budded examples; they possibly correspond to the "Glockenkern," or primary ingrowth for medusoid gemmation, but whether they are ectodermal or endodermal in origin there is no evidence to decide.

The gemmation of a new hydroid polyp presents no very special features; the bud differs from the parent only in the uniform cubic shape of the ectoderm cells, in the absence of a mouth, of nematocysts, and of the little mass of cells round the mouth just mentioned, and in the non-differentiation of the endoderm into two regions. The adventitious case of the parent is not continued on to the bud, but is acquired by it when freed. The bud may either remain attached to the parent, or may be nipped off and settle close by, its tissues in either case gradually undergoing the differentiations which characterise the adult.

On **the gemmation of the medusoid** I have unfortunately but few details to offer, for reasons already mentioned; the process is diagrammatically represented in fig. 8. In the sole specimen available for sections the medusoid was formed at the apex of a polyp, and measured about ·180 in diameter; in the first specimen its relations were not quite clear. The outer layer of ectoderm calls for no comment; at the apex it has apparently grown inwards to form (1) a solid plug of cells, which doubtless represents the præumbral lid of Lankester, and (2) separated from this plug by a thin line (? limiting membrane), and apparently composed of similar but more vacuolated cells, a somewhat globular mass, in which is already recognisable an excavation to form the subumbrellar cavity. Immediately over the surface of the manubrium these ectodermal cells show traces of differentiation into the flattened

epithelium of the adult. These two masses of ectoderm no doubt represent the "Glockenkern" or entocodon, "that important organ by means of which the cæcal bud becomes transformed into the medusa, the growth of ectoderm at the tip of the bud, already noted and described by so many authors under various names, which presses on the endoderm tube, and thus produces a hollow goblet-shaped reduplication of endoderm, from which proceed the endodermal structures of the medusan bell" (Weismann, 'Entsteh. Sexualzellen Hydromed.,' p. 16). In the endoderm the radial canals, the core of the manubrium and its cavity (œsophagus) are already differentiated. At the present apex of the medusoid is a slight depression, the edges of which are thrown into short conical processes, consisting of ectoderm with a solid endodermal core; these may represent either the folded edges of the velum, or more probably, since in the youngest free medusoids observed by Lankester the velum was not distinguished, the rudiments of the future tentacles; there are about eight of them. On each side of the œsophagus is a small blind tube in the substance of the manubrial endoderm, which was apparently natural. The mesoglœa lamina was indistinguishable.

With the certain knowledge that the medusoid is the product of a hydroid, the possible alternatives which the life-history of Limnocodium may present are reduced to three[1]: either (1), as Brooks suggests ('Mem. Boston Soc. Nat. Hist.,' iii, p. 385), the present stock is due to the introduction into the tank of hydroid individuals capable of budding only male medusoids, a process repeated year by year; or (2) female medusoids are formed on the hydroid stocks, but are never freed; or (3) Limnocodium may be an instance of some such reproductive method as the "sporogony" described by Metschnikoff in certain Cuninæ ('Embryologische Studien an Medusen'). In

[1] So many hundreds of medusoids have been examined at all times of the year, that it is most improbable that the existence of free females should have escaped notice.

three or four species of Cunina, Metschnikoff found that immature sexual cells separated themselves from the generative organs, both in males and females, and proceeded to multiply; that one of these cells became engulfed by another, and, thus protected, divided and re-divided to form a morula, which under certain circumstances developed into a medusa. Such a "male parthenogenesis" may occur in Limnocodium, and would account for several facts otherwise inexplicable.

The evidence on the matter is unfortunately but slight. Against the view of Brooks may be urged (a) that the hydroids, which have practically no power of locomotion, are to be found in the greatest numbers on the submerged sagittate leaves of various Nymphææ in the tank, which die down every year, a fact which seems rather to imply a free-swimming larva, and which is therefore somewhat in favour of one of the other hypotheses; (b) that the hydroid spreads into other tanks which are in connection with the water system of this one,[1] which seems to point in the same direction; (c) that the Victoria Regia tank is drained almost every winter, and lies nearly dry for a period varying from one to three months, which suggests that an ovum or gemmule with a cyst capable of resisting violent changes in the environment is necessary for the continuance of the species, the ordinary coating of the hydroid being obviously inadequate for the purpose. In favour of the third possibility is Bourne's statement that the genital sacs of the adult medusoids, after liberation of ripe spermatozoa, become nipped off, fall to the bottom, and live for some time at least without disintegration.

On the question of the systematic position of Limnocodium the foregoing observations do not throw much light. While Lankester assigned it to the Trachymedusæ, Allman and others regard it rather as belonging to the Leptomedusæ. On the one hand, no Trachymedusan has been observed to pass through a hydroid phase; on the other, the structure of the

[1] That no medusæ have been seen to live in these tanks is probably due to their lower temperature.

budding medusoid and of the minute free-swimming forms described by Lankester in 1881 differ somewhat from the ordinary Leptomedusan type; notably, the position of the budding medusoid at the end of a hydroid polyp is, I believe, unique. The processes of development of a medusoid by sexual and by asexual methods do not appear to me to be sufficiently alike to justify conclusions founded on this basis.

In conclusion, I have to express my thanks to Professor Lankester for his assistance, and to Mr. Sowerby, the Director of the Royal Botanic Society's Gardens, for many courtesies.

Note.—The observed appearances of Limnocodium, including the record of Professor Bourne ('Proc. Roy. Soc.,' xxxviii), are as follows:

1880. June 10th—July 31st.
1881. June 12th—June 25th.
1882. None.
1883. April 28th—July 25th.
1884. April 27th—(July ?).
1885. April 5th—(no record).
1886. August 7th—(no record).
1887. "End of May"—(no record).
1888. May 10th—? August.
1889. None.

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EXPLANATION OF PLATE XXXII,

Illustrating Dr. G. Herbert Fowler's "Notes on the Hydroid Phase of Limnocodium Sowerbyi."

FIG. 1.—Two hydroids with a common base of attachment, of which that on the right is budding a medusoid at its apex. Under the action of staining and clearing reagents the polyps have shrunk away from the casing of vegetable particles.

FIG. 2.—Colony of four individuals. At *a*, the gemmation of a medusoid was taking place. From the living specimen by reflected light.

FIG. 3.—Hydroids ingesting a Nematode worm.

FIG. 4.—Longitudinal section through a hydroid polyp, which is throwing off a completely formed bud on the right (cf. pp. 508, 509).

FIG. 5.—Longitudinal section through the medusoid represented in Fig. 1. The various parts are named on Fig. 3, with the exception of two circular groups of 4—5 cells in the apparent centre of the præumbral lid; these are the endodermal cores of two of the supposed tentacles.

In Figs. 5—9, the references are as follows.—*c.* Cæcal canals in the endodermal core of the manubrium. *ect*^{1}. Ectodermal ingrowth for subumbrellar cavity. *end*^{1}. Circular termination of the endoderm lamella, the site of the ring-canal. *man*^{1}. Endodermal core of the manubrium. *œs.* Œsophagus. *p. c.* Permanent ectodermal layer of the manubrium. *pr. l.* Præumbral lid. *r. c.* Radial canal. *s. c.* Excavation for the ultimate subumbrellar cavity.

FIG. 6.—Quadrant of a diagrammatic section along the plane **6** in Fig. 8.

FIG. 7.—Similar diagram of a section along the plane **7** in Fig. 8.

FIG. 8.—General diagram of the stage of medusoid formation, represented in Figs. 1, 5, 9.

FIG. 9.—The next section to that drawn in Fig. 5; it passes to one side of the præumbral lid. Camera drawing; diagrammatically tinted.

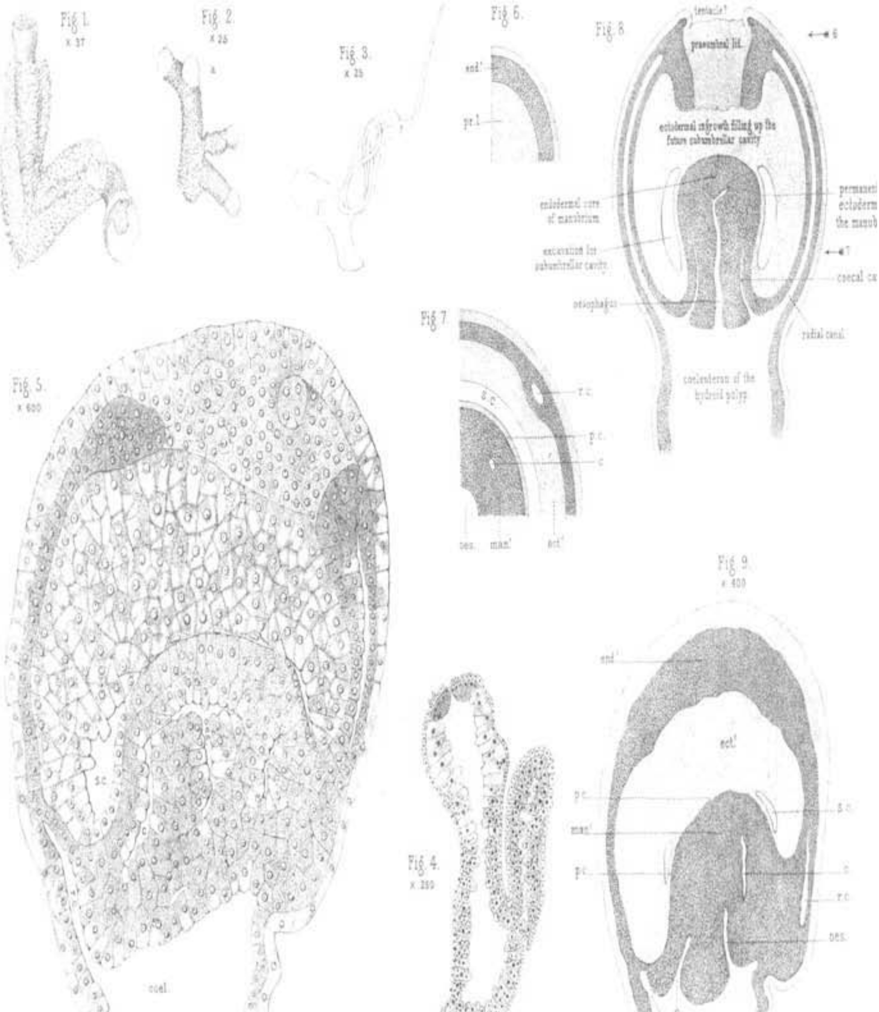
Fig. 1.
× 37
Fig. 2.
× 25
a
Fig. 3.
× 25
Fig. 6.
end'
pr.l
Fig. 8.
tentacle?
praeoral lid.
← 6
ectodermal ingrowth filling up the future subumbrellar cavity
endodermal core of manubrium
excavation for subumbrellar cavity
oesophagus
permanent ectoderm the manub
← 7
coecal ca
radial canal
coelenteron of the hydroid polyp
Fig. 7.
r.c.
s.c.
p.c.
c
oes.
man'
ect'
Fig. 5.
× 600
s.c.
c
coel.
Fig. 4.
× 250
Fig. 9.
× 400
end'
ect'
p.c.
s.c.
man'
p.c.
c
r.c.
oes.
c
r.c.