

On Some Points in the Anatomy and Bud-Formation of *Limnocypris tanganicæ*.

By

Charles L. Boulenger, M.A.,

Lecturer on Zoology in the University of Birmingham.

With Plate 15 and 3 Text-figures.

CONTENTS.

	PAGE
1. Introductory	83
2. The Structure and Function of the "Nettle-ring"	85
3. The Nervous System	89
4. The Histology of the Manubrium	90
5. The Method of Nutrition	92
6. The Development of the Medusa-buds	94
7. The Phylogeny of the Medusoid Individual in the Hydro-medusæ	100
8. Summary	103
9. Bibliography	103
10. Explanation of Plate	105

1. INTRODUCTORY.

THE minute anatomy of the African freshwater jelly-fish, *Limnocypris tanganicæ* Böhm, was first described in this journal by R. T. Günther in 1893 (1); in addition to the account of the histology of this animal the paper includes a very complete description of the asexual development of the buds from the wall of the manubrium.

Since Günther's memoir numerous specimens of this interesting medusa have been brought back to this country by various collectors.

J. E. Moore's expedition to Lake Tanganyika added much to our knowledge of the life-history of *Limnocythidae*, and his book, 'The Tanganyika Problem,' contains a short account of the anatomy (2).

More recently the study of the excellently preserved specimens collected by the late J. S. Budgett in the Niger Delta, and by W. A. Cunningham in Lake Tanganyika, has led to a more complete understanding of the structure and arrangement of the tentacles on the umbrella edge. These two collections were described respectively by E. T. Browne (3) and R. T. Günther (4), the latter's report containing, in addition, a short account of some specimens from the Victoria Nyanza.

Whilst recently investigating the movements of the stinging-cells in the tissues of certain *Hydromedusæ* (5) my attention was drawn to some of Günther's figures of the "nettle-ring" of *Limnocythidae*, and it occurred to me that a detailed investigation of the structure of this characteristic organ might lead to an elucidation of the function of these thickened bands of ectoderm containing nematocysts, which occur with such regularity in the *Trachomedusæ* and *Narcomedusæ*.

Through the kindness of Dr. S. F. Harmer, F.R.S., and Mr. R. Kirkpatrick, I obtained permission to study the specimens of *Limnocythidae tanganicæ* in the British Museum collection, and was allowed to cut sections of one. The specimen selected was one from the large collection made by Dr. W. A. Cunningham during the Third Tanganyika Expedition of 1904-5, and was still in an excellent state of preservation, having been carefully fixed in weak osmic acid.

Sections were prepared by the ordinary paraffin method, and were stained with Grenacher's hæmatoxylin.

I purposely selected an individual bearing medusa-buds on the manubrium; Goette's recent paper on the development of the gonophores of the *Hydromedusæ* (6) has so completely revolutionised our knowledge of this subject that I felt that it was desirable to reinvestigate the process of bud-formation

in *Limnocnida*, in spite of the completeness of Günther's account.

I desire to take this opportunity of thanking Dr. Harmer and Mr. Kirkpatrick for their assistance in obtaining material for examination; my thanks are also due to Mr. R. T. Günther, of Magdalen College, Oxford, who very kindly read through parts of my manuscript.

The work in connection with this paper was carried out in the Zoological Department of the University of Birmingham.

2. THE STRUCTURE AND FUNCTION OF THE "NETTLE-RING."

The nettle-ring, or thickened band, containing stinging-cells, which occurs at the edge of the umbrella, is a very characteristic feature of the anatomy of *Limnocnida*. The minute structure of this organ was described by Günther as being similar to that of the peronium of other medusæ, and as consisting of modified stinging-cells. He considered its function as possibly skeletal as well as defensive.

In a recent paper published in this Journal (5) I endeavoured to show that the bulbous swellings which are so constantly present at the bases of the tentacles of *Craspedote* medusæ have a definite function besides that of bearing the ocellar sense-organs, serving to develop and store up the stinging-cells of the tentacle batteries, as these organs cannot be formed in situ owing to the absence of interstitial cells in the tentacular ectoderm. At the same time I suggested that in those forms which do not possess tentacle-bulbs (*Trachomedusæ* and *Narcomedusæ*) these organs are replaced by the thickened ring of ectoderm containing stinging-cells, which is so conspicuous a feature of their anatomy.

In order to investigate the structure of such a nettle-ring, sections, both radial and tangential, were cut through the umbrella edge of *Limnocnida*.

These sections show that this organ has identically the same structure as the ocellar bulbs which I examined in *Mœrisia lyonsi* (5, p. 768). The nettle-ring consists of

thickened ectoderm containing an enormous number of small irregularly shaped cells, the majority of which are obvious nematoblasts and contain nematocysts in various stages of development, many being quite fully formed. The latter are similar in every respect to the nematocysts of the tentacle-batteries, and I see no reason for considering them as modified in any way.

The nematoblasts of the fully formed stinging-cells in the nettle-ring are always without cnidocils, and, moreover, the capsules are orientated in such a way as to prevent their use as defensive organs. The characteristic elongated nematocysts are without any definite arrangement, and even at the edge of the nettle-ring none have their longer axes at right angles to the surface (figs. 2 and 3).

It is obvious from the above that the nettle-ring cannot be a functional stinging-cell battery, and some other use must be discovered for it. Examination of the structure of the tentacles reveals its proper function. The tentacles of *Limnocoidea* have been very carefully described by Günther (4) and Browne; the following account of their arrangement is quoted from the latter's recent description of the *R. Niger* specimens (3):

"The tentacles are very numerous and are very closely packed together round the margin of the umbrella. They are arranged in definite series showing a well-marked difference in size, which is due to growth. The four per-radial tentacles, opposite the radial canals, are the largest, and these are closely followed in size by the inter-radial and adradial tentacles. Then follow about five series of tentacles, decreasing rapidly in size. The tentacles in each series arise between the tentacles of the previous series, so that beginning with the four primary per-radial tentacles there come four inter-radial, eight adradial, and then sixteen, thirty-two, sixty-four, up to about 500 tentacles.

"The basal portion of the tentacles is partly embedded in the jelly of the umbrella. The length of the portion which is embedded varies according to the size and age of the tentacle.

In the primary series it extends about 3 mm. up to the exumbrella, but in the seventh and eighth series of tentacles the attachment is not visible.

“The basal portion of the tentacle is hollow, and its cavity is in direct communication with the marginal canal.”

The structure of the tentacular ectoderm must be described in detail. This layer consists of large flattened cells, which appear polygonal in a surface view (Text-fig. 1). Interstitial cells are absent from the whole ectoderm.

The elongated nematocysts have a very definite arrangement, which differs in different regions of the tentacle. In the more distal parts these organs are arranged in groups of about thirty to forty on small projecting knobs of ectoderm, the latter forming transverse rings which are very conspicuous in a contracted tentacle. Each stinging-cell is provided with a cnidocil, and the longer axes of the nematocysts are perpendicular to the surface of the battery, the latter forming a powerful offensive organ (v. Text-fig. 1).

As already observed by Browne (3) and Günther (4) these nematocyst batteries are absent from the proximal regions of the larger tentacles. The reason for their absence is obvious to anyone familiar with the appearance of the medusa, the proximal embedded regions being protected by the overhanging distal parts of the tentacles which are carried in a downward position.

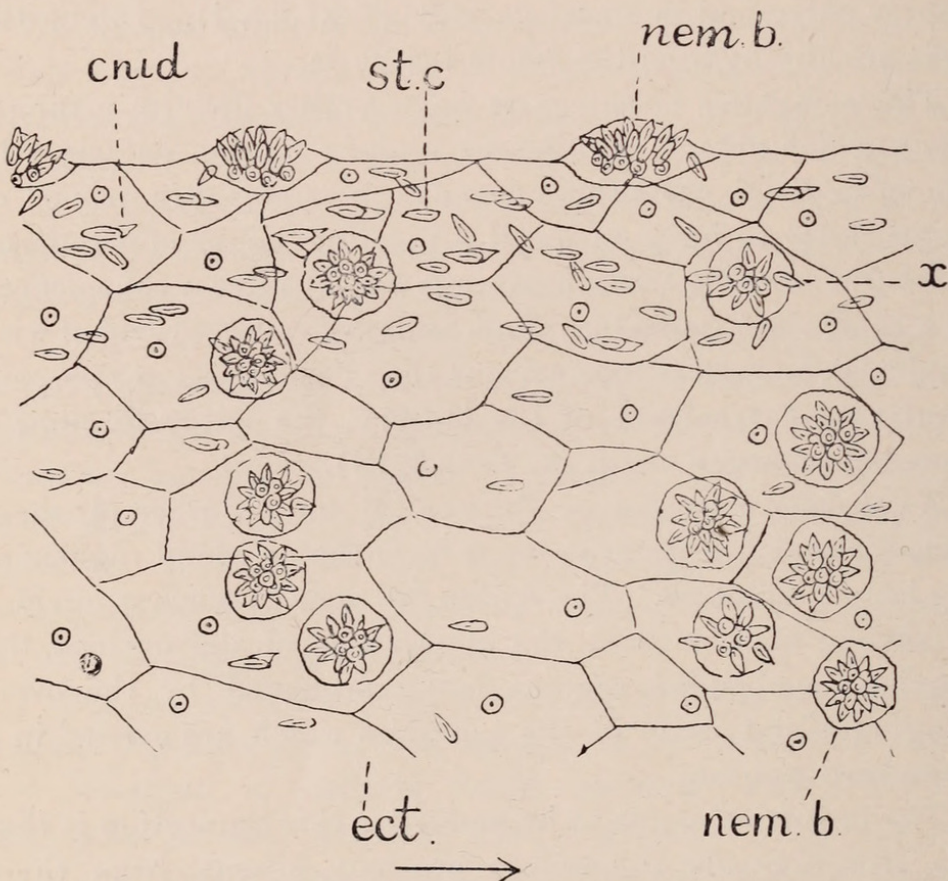
The important point to be noticed in this connection is that the stinging-cells themselves are not absent from these proximal portions of the tentacles; they merely do not form batteries in this position. This is most clearly seen by focussing with a high power on to the surface of a tentacle-base, when a number of nematocysts can be traced at the bases of the large ectoderm cells close to the structureless lamella (Text-fig. 1).

The orientation of these stinging-cells is very definite, the longer axes of the capsules being always parallel with the structureless lamella and the surface of the tentacles, not perpendicular to the latter as in the case of the functional

nematocysts of the batteries ; moreover, the slightly broader basal ends with the nematoblasts are directed away from the umbrella edge and towards the distal extremities of the tentacles.

The above-described orientation, which is even more con-

TEXT-FIG. 1.



Surface view of part of a large tentacle, showing the polygonal ectoderm cells and two rings of stinging-cell batteries. Below the large transparent cells are a number of migrating stinging-cells, all moving in the same direction towards the more distal parts of the tentacle ; in one place (*x*) they can be seen coming together to form a battery. *cnid.* Nematoblast of a migrating stinging-cell. *ect.* Ectoderm cell. *nem. b.* Battery of stinging-cells. *st. c.* Migrating stinging-cell. The arrow shows the direction in which the stinging-cells are moving. (Semi-diagrammatic.)

spicuous in longitudinal sections of the tentacles (Pl. 15, fig. 2), shows that the stinging-cells of the tentacle-bases are

migrating towards the more distal regions, and they form a regular stream moving towards the nematocyst batteries further along the tentacles. In the region of the first few rings of batteries the stinging-cells can be seen grouping themselves together to form these characteristic organs (Text-fig. 1, *x*).

The next point to consider is the origin of these wandering cells, and one's attention is naturally drawn to the nettle-ring; examination of longitudinal sections through the points where the tentacles are given off from the umbrella-edge shows that the stinging-cells are actually proceeding from this thickened ring of ectoderm (Pl. 15, fig. 2).

From the above considerations it is safe to argue that the nettle-ring of *Limnocrnida* is not a defensive organ, but has to be considered as the factory and storage-place of the tentacular stinging-cells.

3. THE NERVOUS SYSTEM.

Günther was unable to find any trace of a nervous system in *Limnocrnida*, although he made special search for a nerve-ring in the neighbourhood of the base of the velum. This was probably due to the state of preservation of his specimens. Radial sections of my own showed the nerve-ring in its usual position. It has much the same structure as in other *Craspedote medusæ*.

The ring of nerve-fibres is situated on the edge of the nettle-ring at the base of the velum and is double, the two parts being separated by the structureless lamella of that organ (Pl. 15, fig. 3). As in *Limnocrodium* (Günther [7]), the outer nerve-ring is much better developed than the inner ring, and in transverse sections is seen to be surrounded by a number of small cells which form a kind of sheath. The sense-organs are in close proximity to the outer nerve-ring, but I was unable to trace any definite nerve-endings in these organs. This was probably due to the very poor staining properties of the nerve-fibres. The inner ring of fibres is

considerably thinner than the outer and devoid of any kind of sheath; the nerve-fibres seem, however, distinctly separate from the bases of the overlying ectoderm cells.

4. THE HISTOLOGY OF THE MANUBRIUM.

Günther's account of the histology of this important organ is somewhat incomplete and, moreover, differs in several points from my own observations. I have, therefore, dealt with the subject somewhat fully, as it seems of considerable importance to solve (as far as is possible from the examination of preserved material) the interesting problem of the nutrition of Limnocoidea.

For the purpose of description the manubrium can be conveniently divided into three regions, which differ markedly from one another. These are—(1) an oral region in the neighbourhood of the mouth; (2) a middle region, from the ectoderm of which medusa-buds are formed; and (3) a proximal or basal region. It must be understood, however, that there are no definite boundaries to these regions, and that each one passes gradually into the next.

(i) The Oral Region.

The distal part of this region is somewhat contracted in the specimen which I examined, and is coiled up towards the subumbrellar surface of the manubrium (fig. 1); this, however, may be only a "post-mortem" phenomenon.

The structureless lamella of the whole oral region is somewhat thicker than elsewhere on the manubrium, but the chief peculiarity is to be found in the structure of the endodermal lining. The cells constituting the endodermal epithelium are of two kinds: (a) long narrow cells with finely granular protoplasmic contents and basal nuclei (fig. 4, *end.*), and (b) large goblet-cells wedged in between the former and occurring in large numbers (*gobl. c.*). These cells are very conspicuous, and resemble in every respect the goblet-cells of the alimentary

canal in the higher animals. Every condition of secretory activity can be distinguished in these goblet-cells, and they have, moreover, a very definite arrangement. The goblet-cells furthest from the mouth (fig. 4) stain very deeply with hæmatoxylin and have clear protoplasmic contents. Slightly distal to these (fig. 5) we find that these cells have elaborated large quantities of mucin, and contain large colourless and highly refringent granules of this substance. Finally, at the oral extremity of this region the goblet-cells have discharged the mucin, and have the characteristic cup-form typical of this kind of cell; except for the basal nucleus and a net-work of fine granules they do not stain at all, and thus become very conspicuous.

The ectoderm of the oral region consists of large, low musculo-epithelial cells with much vacuolated protoplasmic contents; interstitial cells, with occasional nematocyst-capsules, occur sparingly. I could trace no stinging-cell battery along the edge of the mouth.

(ii) The Middle Region.

The middle or gemmiferous region of my specimen agrees in structure with that described by Günther. The structureless lamella is very thin, and both ectodermal and endodermal linings high. The latter consists of more than one layer. The cells bordering on the cavity of the manubrium are elongated with fine granular contents, and obviously correspond to the similar cells in the oral region; I agree with Günther in thinking that these cells may be provided with flagella during life, although I could detect none in my sections.

One or two layers of smaller cells occur at the bases of the elongated endoderm cells; they are also finely granular, but roughly polygonal in shape, and provided with slightly smaller nuclei.

The ectoderm of this middle region consists of large vacuolated cells without definite cell outlines, between which

are numerous small, interstitial cells and stinging-cells in all stages of development. The fate of these stinging-cells is not very obvious; there are no functional nematocyst-batteries on the manubrium, and the cells do not seem in process of migration to other parts of the body; as far as I can make out the stinging-cells are for the supply of the medusa-buds in much the same way as in *Mœrisia*, where the developing medusa-buds receive a supply of nematocysts from the ectoderm of the parent hydroid (5).

(iii) The Proximal Region.

The proximal region or stomach proper consists of much lower cells than the other two, and therefore appears thin in sections. The ectoderm resembles that of the oral region, although interstitial cells occur less sparingly; the structureless lamella is distinct, although not of great thickness.

The endodermal lining resembles that described by Lankester (8) and Günther (7) as occurring in a similar position in *Limnocoedium*. It consists of a single layer of large, almost cubical cells (fig. 6), which are of two kinds—(a) large vacuolated cells, and (b) gland-cells. The former contain conspicuous food-balls (*f. b.*) and foreign particles in the vacuoles, and it is evidently in this region that the greater part of the digestion takes place. The gland-cells (*gl. c.*) contain coarse granular particles, the contents being very unlike those of the goblet-cells in the oral region, from which they also differ in being broader and in not tapering at the base.

The endodermal covering of the mass of jelly which projects into the manubrial cavity from the dorsal side consists of a simple epithelium of smallish cells.

5. THE METHOD OF NUTRITION.

The problem of the nutrition of *Limnocoidea* has given rise to some speculation. Günther, in his account of the anatomy of the medusa, described no gland-cells of any kind

in the lining of the gastric cavity; moreover, he was not able to observe any traces of intra-cellular digestion in any of the cells of the endodermal epithelium.

Again, previous authors have commented on the shortness of the manubrium, and pointed out that the space which should be the central cavity of the stomach is occupied by a great mass of jelly which forms the roof of this organ and almost blocks up the whole of the cavity of the sub-umbrella (cf. fig. 1). Referring to this point E. T. Browne (3) remarks:

"A similar kind of stomach is found in *Mesonema pensile* (Browne, 1904), a large medusa belonging to the *Aequoriidæ*. In *Mesonema* the stomach has become quite rudimentary and the mouth cannot be closed. In *Limnocyclus* the abolition of the stomach is not carried quite so far, but to judge from the appearance of these specimens the mouth is incapable, owing to the shortness of the lower wall of the stomach, of completely closing up.

"In the case of *Mesonema* I have suggested that the function of the stomach has been transferred to the canal system, and that the animal lives upon organisms of microscopic dimensions, such as unicellular *Algæ* and *Protozoa*, which are driven by ciliary currents into the radial canals. Such organisms may also form the food-supply of *Limnocyclus*."

The histology of the manubrial endoderm, described in the previous section of my paper, clearly shows that the lining epithelium of the manubrium is well adapted for digesting and absorbing food material in a perfectly normal manner. Perhaps the most interesting point in the histology of the endoderm is the unusually great development of goblet-cells in the oral region.¹ These must secrete a large quantity of some mucous substance which no doubt entangles within itself any small organisms which enter the mouth with

¹ Similar mucus-secreting cells occur in the oral regions of the digestive cavities of the *Alcyonarians* *Xenia* (Ashworth [9]) and *Alcyonium* (Pratt [10]). Duerden's paper on the rôle of mucus in corals (11) is also of great interest in this connection.

the water taken in by the manubrium. These are probably carried by currents caused by flagella on the endodermal epithelium to the narrow cavity of the proximal part of the manubrium, where they are acted on by the secretion of the gland-cells, and the disintegrated particles are then taken up by the cubical vacuolated cells which occur in this region.

6. THE DEVELOPMENT OF THE MEDUSA-BUDS.

Günther's paper on the anatomy of *Limnocoidea* (1) contains a detailed account of the development of the asexual buds on the manubrium. His description of the process is briefly as follows:

The young medusa makes its first appearance as a small outpushing of both layers of the manubrium. The apical ectoderm of this bud next boldly invaginates into the endoderm and forms the hollow entocodon; the mouth of the apical invagination closes up and the whole of the entocodon becomes covered over by an overgrowth of ectoderm, and its cells become marked off from the cells of the peripheral ectoderm. At this stage the entocodon is a hollow sphere of ectoderm, one cell thick, enclosing a cavity which is really a portion of the exterior, which has been enclosed during the growth of the bud; meanwhile, owing to the invagination of such a comparatively bulky mass of ectoderm, the endoderm thins out so much as to be reduced to a single cup-shaped layer of cells enveloping the central entocodon.

A second ingrowth of ectoderm now occurs. The ectoderm cells at the apex of the bud grow down as a solid plug of cells into the apex of the entocodon, the effect of this second ingrowth of ectoderm being to push one wall of this organ into the other, with the result that the entocodon becomes a two-layered cup surrounding a plug of ectoderm cells; the lumen of the entocodon may even disappear altogether, in which case it always reappears at a subsequent stage. Later, the endoderm cells surrounding the entocodon grow further

over that organ, and at certain regions have begun to grow up into the mass of ectodermic cells at the apex of the bud, thus indicating the position of the future tentacles, four of which are considerably in advance of the others. Some of the cells of the apical ectoderm arrange themselves round the forecasts of the endodermal axes of the tentacles, others, more deeply seated, arrange themselves in a single tier along the outer wall of the entocodon; this causes a cavity to appear in the apical mass, separated from the cavity of the entocodon by the double row of ectoderm cells which becomes the velum of older medusæ. The circular canal appears as a split in the endoderm at the base of the tentacles, and is soon placed in communication with the enteric cavity of the parent by the four radial canals which arise one opposite to each of the four perradial tentacles. Between the radial canals and all round the entocodon the endoderm persists as the endoderm lamella.

A noticeable feature in the development of the medusa-buds of *Limnocythida* is the entire absence of any trace of manubrium and mouth in any of the stages examined. The mouth probably breaks through at the date of the setting free of the young medusæ.

The only other account of the bud-formation of *Limnocythida* is that given by Moore in his book, 'The Tanganyika Problem.' He also describes the formation of the entocodon by invagination, but his account of the later stages differs in some respects from that given by Günther. Thus, after describing the formation of the entocodon by a process of invagination he continues: "Still later a second shallower invagination takes place forming the mouth of the bell, and within this the four primary tentacles are at first folded inwards towards the centre of the velum. About this time the endodermal lining of the parental manubrium (which projects into the bud from its gastric cavity and forks into four radial canals) becomes thickened and folded, so as to form a rounded boss projecting into the cavity of the first ectodermal invagination of the bud, and quite visible from without. This is the rudiment of the manubrium of the bud.

About this time the velum becomes perforated in its centre, the four primary tentacles stand stiffly out, and each medusa, although still not fully formed and attached to the parental manubrium, pulsates with great vigour."

From the above accounts we see that the early development of the buds in this medusa is of a quite peculiar type, and Günther in 1894 remarked: "The method of invagination of the ectoderm to form the entocodon or 'Glockenkern' in *Limnocyda* differs from the method of formation in most other medusæ, in which the process has been described, and I am inclined to think that in this respect *Limnocyda* exhibits a more primitive condition."

Since that time our knowledge of the bud-formation in the *Hydromedusæ* has been completely revolutionised by Goette's monograph on the subject (6). He showed that, at any rate in all the forms he was able to examine, no double-walled cup of endoderm is present, even in the youngest stages, and that the four radial canals arise from four separate pouches of endoderm which grow out simultaneously from the cavity of the early bud. His results have been confirmed by J. Hadži (12) for Hydroids, by W. Richter (13) for the Siphonophora, and by myself (5) for the Egyptian *Hydromedusan* *Moerisia lyonsi*.

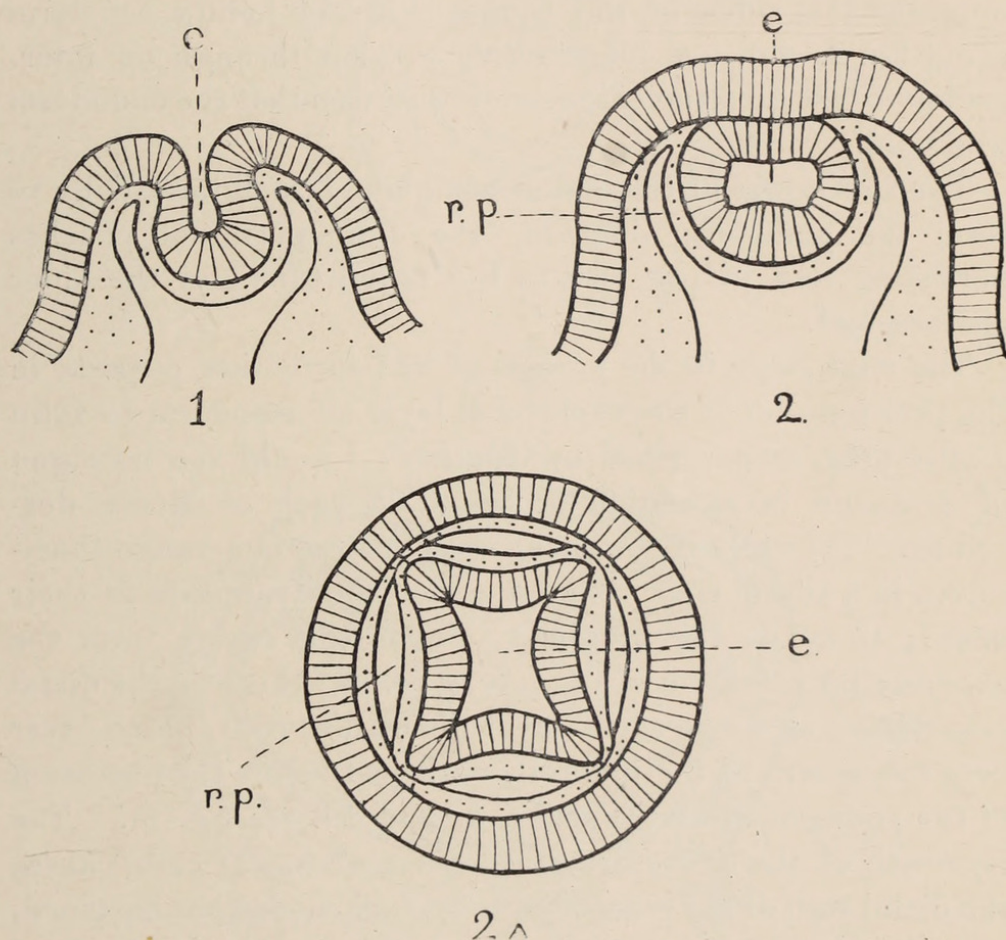
Goette's discovery has not only shattered the generally accepted views on the development of the medusa-buds in the *Hydromedusæ*, but has also led to considerable alterations in the existing theories on the relation between medusoid and hydroid individuals. I have, for this reason, carefully re-investigated the development of the buds of *Limnocyda*, not only with a view to clearing up the discrepancies between the accounts of Günther and Moore, but also in the hope of throwing fresh light on the subject of bud-formation in the *Hydromedusæ* generally.

My observations on the earliest stages in the formation of the buds of *Limnocyda* agree with those of previous authors; the ectoderm of the hollow two-layered bud invaginates into the endoderm to form the hollow entocodon, which

soon becomes completely separated from the superficial layer of ectoderm (Text-fig. 2, 1 and 2).

I do not, however, agree with Günther's further observation

TEXT-FIG. 2.



Outline sketches of three sections of young medusa-buds:

1. Longitudinal section showing the formation of the entocodon by invagination with the resulting double-walled cup of endoderm. 2. Similar section of a later stage; the apical invagination has now closed up. 2a. Transverse section of the same, showing the square entocodon and the constriction of the endodermal cup to form four perradial pouches. e. Cavity of the entocodon. r.p. Perradial pouch of endoderm.

that this process of invagination causes the endoderm of the bud to be reduced to a single cup-shaped layer of cells enveloping the entocodon. If a transverse section of a bud of this age be examined it will be seen that—(a) the endo-

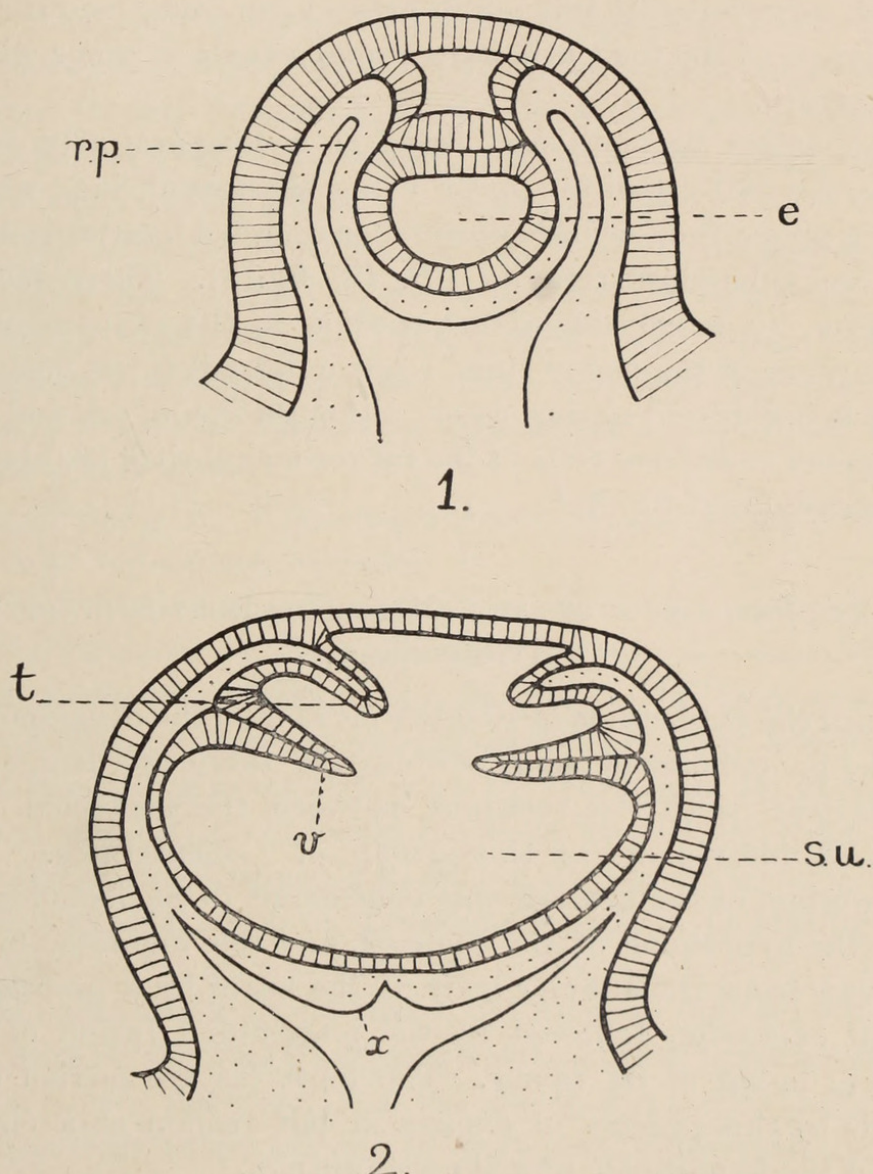
dermal cup is distinctly two-layered and (b) the entocodon is approximately square in section, and that this causes the walls of the double cup of endoderm to be brought into contact with one another opposite the four corners of this organ, thus leaving four distinct pouches in a perradial position opposite the sides of the square mass of hollow ectoderm (Text-fig. 2, 2a). A longitudinal section through an inter-radius would give the erroneous impression that the endoderm was solid.

The two layers of the endodermal cup fuse interradially to form the endoderm lamella, the four perradial pouches persisting and giving rise to the radial canals of the older medusa-bud.

The next stage in the process of bud-formation consists in the proliferation of the superficial layer of ectoderm to form a solid plug, as described by Günther; I could see no signs of a second invagination of ectoderm such as Moore described. The cells of this solid mass very soon arrange themselves in a single layer round a cavity which appears in their midst; those on the proximal side of this cavity form the exumbrellar ectoderm of the future velum; those on the distal side persist as a superficial layer of smallish cells, which cover over the mouth of the umbrella until just before the liberation of the young medusa (Text-fig. 3, and Pl. 15, fig. 8). The ingrowth of the above-described mass of apical cells causes the distal wall of the entocodon to become somewhat flattened, but I have never seen one wall pushed into the other so as to cause the organ to assume a cup-shape, with the consequent obliteration of the cavity; I cannot help thinking that Günther must have arrived at this conclusion from the examination of tangential instead of radial sections of the medusa buds.

The four perradial pouches, as mentioned above, form the rudiments of the radial canals; these grow out centrifugally and form the endodermal axes of the first four tentacles; the latter appear in the cavity on the distal side of the velum, and their axes are, of course, surrounded by the ectoderm

TEXT-FIG. 3.



Outline sketches of two longitudinal sections of older medusa-buds: 1. A cavity has appeared in the thickened ectoderm of the apex, into which the perradial tentacles are beginning to grow. 2. Almost fully formed medusa in which the velum is already perforated and the perradial tentacles well developed. In this specimen there is no sign of a manubrium, although the mouth and the manubrial endoderm (*x*) are indicated. *e*. Cavity of the entocodon. *r.p.* Perradial pouch of endoderm. *s.u.* Sub-umbrella cavity of the older bud. *t*. Tentacle. *v*. Velum.

cells of the superficial layer (Text-fig. 3). I was not able to observe the formation of the circular canal; there can be no doubt, however, that this organ arises as in other medusæ by the fusion of the four primitive radial canals at their distal extremities.

The velum becomes perforated at a comparatively early stage, the last organ to appear being the manubrium, which Moore correctly described as forming a rounded boss projecting into the subumbrella cavity (Pl. 15, fig. 8). There seems, however, to be considerable variation in the exact time of appearance of the manubrium, some quite advanced medusa-buds being devoid of this organ, although the mouth and the elongated endoderm cells of the future manubrium are always indicated (Text-fig. 3).¹

7. THE PHYLOGENY OF THE MEDUSOID INDIVIDUAL IN THE HYDROMEDUSÆ.

Until the publication of Goette's memoir on the development of the gonophores of the Hydromedusæ there was a general agreement as to the relations between the medusoid and hydroid individuals of this group of Cœlenterates. The manubrium of the medusa was considered to be homologous with the hypostome of the hydroid, and the umbrella to be derived from the tubular body of the latter by a process of radial expansion followed by the inter-radial fusion of the gastric lining of its cavity. The tentacles are carried outwards by this process of expansion but remain as a circlet round the hypostome, now the manubrium.

The development of the medusa-buds, as formerly understood, distinctly favoured this theory, and Weismann, in his classical monograph on the origin of the sex-cells in the Hydromedusæ (14), showed how the ontogenetic evidence could be made to fit in with such a phylogenetic origin of medusæ. To quote his own words²:

¹ Cf. also Günther's figure (1), pl. 19, fig. 14.

² The quotation is taken from Goette's memoir (6), p. 261.

“Während sie (die Glocke) im Beginn der Phylogenese der Medusen auch in der Ontogenese als Kreisrunder Kelch im Umkreis der Basis des Manubriums mit freiem Rande emporwuchs, fand nun derselbe Prozess gewissermassen in umgekehrtem Sinn statt, indem die Kuppe der Knospe den Glockenrand dadurch bildete, dass sich das Ectoderm hier nach innen einstülpte.

“Bei weiterer Verkürzung der Ontogenese wurde diese Einstülpung zu einer blossen soliden Einwucherung ohne Einstülpungspforte und damit sind wir beim heutigen Glockenrand angelangt, der seine Abstammung von einer Einstülpung des Ectoderms auch heute in einzelnen Fällen noch erkennen lässt.”

According to Weismann's views sessile gonophores are merely degenerate medusæ.

Goette's studies on the development of the gonophores of a large number of Hydroids have led him to very different and somewhat startling conclusions. He considers that medusoid and hydroid individuals are not truly homologous, and takes a quite opposite view to Weismann, believing that the medusæ have not arisen from any kind of polyp-form, but represent completely new structures formed as the culminating points of long series of sessile gonophores of increasing complexity.

In a short preliminary paper, published in the 'Zoologischer Anzeiger' (12), Hadži subjects Goette's theoretical conclusions to a severe criticism, and (in my opinion) very justly condemns them as erroneous; he very clearly demonstrates that the medusa-form in the Hydromedusæ can be derived directly from the polyp-form, even in the light of the recent investigations of the development of gonophores.

Hadži revives and modifies an old theory of Allman's (15), and would derive the medusoid individual from some such polyp as that of *Laomedea* or *Campanopsis*, in which the tentacle bases are joined together by a web-like, solid duplication of ectoderm. He points out that if we consider the umbrella to have arisen from such a double fold of ectoderm

the radial canals prove to be nothing more than the hollow bases of the tentacles which have grown out centrifugally from the stomach in much the same way as the accessory radial canals of *Aequorea* have been known to do.

This theory would thus explain the independent origin of the four radial pouches from the endoderm of the young medusa-buds.

The development of the buds of *Limnocoidea* throws considerable light on the difficult problem of the relationship between the medusoid and hydroid individuals in the *Hydromedusæ*; I heartily agree with Hadži in considering these forms as strictly homologous structures, but can see no necessity for abandoning Weismann's old-established theories on this subject.

There can be no doubt that Günther was right in considering that in *Limnocoidea* the formation of the entocodon by invagination is a primitive feature, and that the solid ingrowth of ectoderm which occurs in the young buds of the majority of the *Hydromedusæ* merely represents a modification of such a process of invagination.

In my opinion the formation of a two-layered cup of endoderm is another primitive feature in the development of *Limnocoidea*; even in this genus it persists only for a very short time and almost simultaneously with its formation becomes constricted at the interradii to form the endoderm lamella, leaving four distinct and comparatively large perradial pouches, which are obviously homologous with those of other medusa-buds.

In the development of all types of gonophores in the *Hydromedusæ* we meet with a considerable shortening of their ontogeny, and it seems to me that where, as in the majority of forms, the four radial pouches arise independently from the endodermal cavity of the young bud we are dealing with a process of this nature, and that the primitive two-layered cup stage has been suppressed.

If this argument be accepted we can still retain Weismann's views on the phylogeny of the medusoid individual, in spite

of the fact that some of the observations on which his theories were based have been proved to be erroneous.

The late appearance of the manubrium in *Limnocrnida* is obviously a secondary feature, connected no doubt with the comparatively small dimensions of this organ in the adult.

8. SUMMARY.

(1) The stinging-cells on the tentacles of *Limnocrnida* are not developed in situ but in the ectoderm of the "nettle-ring," whence they migrate to the tentacular batteries. The "nettle-ring" is to be regarded merely as the factory and storage-place of these stinging-cells, and is not itself a functional nematocyst battery.

(2) *Limnocrnida* possesses a well-developed, double nerve-ring at the base of the velum, it is similar in most respects to that of *Limnocrodium* and of other medusæ.

(3) The manubrium is undoubtedly functional as a digestive organ. The gland-cells and digestive cells are restricted to the more proximal regions, the oral endoderm being characterised by the presence of an unusually large number of mucus-secreting goblet-cells.

(4) The development of the medusa-buds presents several interesting features, some of which are undoubtedly primitive. As originally described by Günther, the entocodon is formed by simple invagination; this causes the endodermal walls of the bud to assume the shape of a double-walled cup, which, almost simultaneously with its formation, becomes constricted at the interradii, leaving four large perradial pouches of endoderm, which give rise to the radial canals of the adult medusa. The manubrium appears very late as a rounded boss projecting into the umbrella cavity.

BIBLIOGRAPHY.

A complete bibliography of *Limnocrnida tanganicæ* up to 1907 will be found in E. T. Browne's memoir in the 'Budgett Memorial Volume' (3).

1. Günther, R. T.—“A Further Contribution to the Anatomy of *Limnocyclus tanganyica*,” ‘Quart. Journ. Micr. Sci.,’ vol. 36, 1894, p. 271.
2. Moore, J. E. S.—‘The Tanganyika Problem,’ London, 1903, p. 298.
3. Browne, E. T.—“On the Freshwater Medusa, *Limnocyclus tanganica*, discovered in the River Niger by the late J. S. Budgett,” in ‘The Work of John Samuel Budgett,’ Cambridge, 1907, p. 471.
4. Günther, R. T.—“Zoological Results of the Third Tanganyika Expedition conducted by Dr. W. A. Cunningham, 1904–1905: Report on *Limnocyclus tanganica*, with a Note on the Subspecies from the Victoria Nyanza,” ‘Proc. Zool. Soc. London,’ ii, 1907, p. 643.
5. Boulenger, C. L.—“On the Origin and Migration of the Stinging-cells in Craspedote Medusæ,” ‘Quart. Journ. Micr. Sci.,’ vol. 55, 1910, p. 763.
6. Goette, A.—“Vergleichende Entwicklungsgeschichte der Geschlechtsindividuen der Hydropolyten,” ‘Zeit. f. wiss. Zool.,’ Bd. lxxxvii, 1907, p. 1.
7. Günther, R. T.—“Some Further Contributions to Our Knowledge of the Minute Anatomy of *Limnocyclus*,” ‘Quart. Journ. Micr. Sci.,’ vol. 35, 1894, p. 539.
8. Lankester, E. R.—“On the Intra-cellular Digestion and Endoderm of *Limnocyclus*,” ‘Quart. Journ. Micr. Sci.,’ vol. 21, 1881, p. 119.
9. Ashworth, J. H.—“The Stomodæum, Mesenterial Filaments, and Endoderm of *Xenia*,” ‘Proc. Roy. Soc.,’ vol. lxiii, 1898.
10. Pratt, E. M.—“The Digestive Organs of the Aleyonaria and their Relation to the Mesogloal Cell Plexus,” ‘Quart. Journ. Micr. Sci.,’ vol. 49, 1905, p. 327.
11. Duerden, J. E.—“The Rôle of Mucus in Corals,” ‘Quart. Journ. Micr. Sci.,’ vol. 49, 1905, p. 591.
12. Hadži, J.—“Bemerkungen zur Onto- und Phylogenie der Hydro-medusen (I Mitt.),” ‘Zool. Anz.,’ Leipzig, vol. xxxv, 1909, p. 22.
13. Richter, W.—“Die Entwicklung der Gonophoren einiger Siphonophoren,” ‘Zeit. f. wiss. Zool.,’ Bd. lxxxvi, 1907.
14. Weismann, A.—‘Die Entstehung der Sexualzellen bei den Hydro-medusen,’ 1883.
15. Allman, G. J.—“Monograph of the Gymnoblasic or Tubularian Hydroids,” ‘Ray Society,’ 1871–2.

EXPLANATION OF PLATE 15,

Illustrating Mr. C. L. Boulenger's paper "On Some Points in the Anatomy and Bud-Formation of *Limnoccnida tanganicæ*."

LIST OF REFERENCE LETTERS.

circ. c. Circular canal. *ect.* Ectoderm. *end.* Endoderm. *end. l.* Endoderm lamella. *end. p.* Perradial pouch of endoderm in the medusa-bud. *ent.* Ectoderm of the entocodon. *ex. ect.* Ectoderm of the exumbrella. *f. b.* Food-ball in a nutritive cell of the endoderm. *gl. c.* Gland-cell. *gobl. c.* Mucus-secreting goblet-cell of the oral endoderm. *int. end.* Interradial constriction of the double-walled cup of endoderm in the young medusa-bud. *man.* Manubrium. *med.* Medusa-bud. *mes.* Mesogloea. *nem.* Stinging-cell in the nettle-ring. *nem.¹* Stinging-cell migrating through the tentacular ectoderm. *net.* Nettle-ring. *nr.¹ nr.²* The two divisions of the double nerve-ring. *tent.¹ tent.²* Sections of a tentacle. *tent. per.* Perradial tentacles of the medusa-bud. *vel.* velum.

Fig. 1.—Radial section through the periphery of *Limnoccnida* passing through the manubrium (*man.*) and the base of a large tentacle (*tent.¹*). The distal part of the same tentacle is cut transversely at *tent.²* The manubrium bears two medusa-buds on the middle region (*med. b.*); the oral region is coiled up towards the periphery. The umbrella is considerably shrunk. The ectoderm (*ect.*) is more deeply shaded than the mesogloea (*mes.*) and the endoderm (*end.*)

Fig. 2.—Radial longitudinal section of the nettle-ring (*net.*), and the basal embedded region of a large tentacle. The section does not quite pass through the centre of the latter, and therefore shows only part of the tentacle-cavity. The ectoderm on the exumbrellar side of the tentacle consists of large, low cells, with stinging-cells (*nem.¹*) migrating from the edge of the nettle-ring.

Fig. 3.—Radial section through the velar edge of the nettle-ring showing the double nerve-ring (*nr.¹* and *nr.²*) near the base of the velum (*vel.*)

Fig. 4.—Longitudinal section through the oral region of the manubrium some distance from the mouth. The endoderm consists of finely granular cells (*end.*), and goblet-cells (*gobl. c.*); the latter have clear contents, and stain deeply in this position.

Fig. 5.—A similar section, but through the distal extremity of the oral region. The goblet-cells have elaborated large quantities of mucin.

and contain large, colourless and highly refringent granules of this substance.

Fig. 6.—Longitudinal section of the proximal region of the manubrium. Here the endoderm forms a low epithelium, with gland-cells (*gl. c.*), and vacuolated cells, containing food-balls (*f. b.*)

Fig. 7.—Transverse section of a young medusa-bud just after the formation of the entocodon by invagination. The latter (*ent.*) is almost square and at its four corners constricts the double cup of endoderm interradially (*int. end.*). This leads to the formation of four per-radial pouches of endoderm (*end. p.*), from which the radial canals of the adult are derived.

Fig. 8.—Longitudinal section through an old medusa-bud. The velum (*vel.*) is already perforated, and the manubrium (*man.*) projects as a rounded boss into the umbrella cavity. Three of the four perradial tentacles are shown (*tent. per.*). Note that the manubrial endoderm is already differentiated from that of the rest of the gastric cavity; it is always indicated at this stage, even if the manubrium itself has not yet been evaginated.



Boulenger, Charles L. 1911. "Memoirs: On Some Points in the Anatomy and Bud-Formation of *Limnocyclus tanganicae*." *Quarterly journal of microscopical science* 57, 83–106.

View This Item Online: <https://www.biodiversitylibrary.org/item/192743>

Permalink: <https://www.biodiversitylibrary.org/partpdf/201136>

Holding Institution

American Museum of Natural History Library

Sponsored by

BHL-SIL-FEDLINK

Copyright & Reuse

Copyright Status: Public domain. The BHL considers that this work is no longer under copyright protection.

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.