XXX. THE HYDROIDS OF THE INDIAN MUSEUM.

II.—*ANNULELLA GEMMATA*, A NEW AND REMARKABLE BRACKISH-WATER HYDROID.

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(Plates XXX, XXXa.)

CONTENTS.

The hydroid described in the following pages stands in several respects by itself. It combines in its structure and life-history peculiar features which are either new or have hitherto been found isolated in different species. Among these peculiarities are to be reckoned the occurrence in the vegetative hydroid phase of an alternation of free and fixed stages, the adoption of such singular methods of multiplication as the setting free of planula-like buds

and of a mode of transverse fission associated with the basal-bulb, and the structural uniqueness of the tentacles and of the chitin-covered basal-bulb itself.

The examples of this minute but interesting species occurred in a valuable and extensive collection of Hydroids received from the Trustees of the Indian Museum for identification. It was first observed and collected by Dr. Nelson Annandale, during his investigation of the brackish water fauna of India ; and to the fortunate fact that some living examples were kept for a short period in an aquarium is due Dr. Annandale's record of the free-swimming medusoid generation.

PROVENANCE AND HABITAT.

So far the species has been found in only one locality—Port Canning, Lower Bengal; and in that locality it seems to be confined to a shallow brackish pond. At any rate careful search of material from other places in the neighbourhood of Port Canning has failed to reveal any trace of its presence. In the brackish water it occurs growing upon a delicate branched weed, the surface of which also bears many clusters of Acinetaria. The specimens were collected in the months of December, 1909 by Dr. N. Annandale, and in March, 1910 by Mr. F. H. Gravely and Dr. B. L. Chaudhuri, and the latter are registered in the Natural History collections of the Indian Museum under the number ZEV 3702/7.

DESCRIPTION OF THE HYDROID.

HABIT.

The individuals are solitary, growing as a rule far apart from, and independently of each other. In very rare cases two individuals may appear to be attached at their bases; but this is due to imperfect separation of their basal masses, which are held together in a common growth of mucus. There is no coenosarcal connection between such individuals, nor has any semblance to colonial development been observed.

Consideration of the structures of this curious hydroid leads me to believe that the attached stage is merely a temporary phase in the life-history. This stage is, however, repeated again and again, each two periods of attachment being separated by an interval during which the hydroid is free. Whether during the free periods it floats in the water of the brackish ponds, or creeps upon the bottom, I do not venture to guess; but the analogy of *Hypolytus peregrinus* suggests that the Indian species may yet be captured in a tow-net, floating at the surface. In such case its minuteness would render difficult its detection in a miscellaneous plankton collection.

The following facts point to the alternation of free and fixed stages. A hydroid individual in its attached stage consists of a

hydranth or polyp, with a long stalk-like extension of the body in older examples, and a unique basal development which I shall call the " basal bulb." The basal bulb, which alone is protected by perisarc, is the organ of fixation, actual adhesion being apparently due to a loose mass of debris-laden mucus which surrounds the bulb and spreads out upon the substratum. No part of the polyp, in its simplest condition, secretes perisarc or mucus. As will be found more fully described in a later section (p. 553) the bulb represents a method of vegetative reproduction, and is a temporary structure. Basal bulbs have been observed, both by Dr. Annandale and by myself, isolated and without any attached polyp. In such a case the polyp must either have disintegrated or have broken apart and become free. That the latter is the actual case is borne out by the condition of the isolated basal bulbs, which contain well-preserved coenosarc; and by the discovery of a polyp which has recently broken away from its base (pl. xxx, fig. 6).

Further, at the breaking-off period the released polyp possesses no means of attachment, although in course of time the lower end of the body secretes both perisarc and mucus, and gradually becomes modified into a new basal bulb. The details of these processes, so far as they have been traced, will be described in the paragraphs dealing with reproduction. The above more general observations, however, are sufficient to suggest that at certain phases the polyp is released from its old attachment, and that a period of freedom intervenes before a new organ of fixation has developed.

STRUCTURE OF THE HYDRANTH.

Form and Dimensions (see plate xxx, figs. 1-3).

An individual consists simply of an isolated polyp. There is no definite hydrocaulus, although the proximal end of the hydranth, especially in the more fully developed specimens, is extended into a stalk-like portion. Nor is there any stolon or hydrorhiza in the ordinary sense of the term, the functions of such being performed by the basal bulb.

In its living state, Dr. Annandale informs me, the hydroid is colourless.

The form of a normal adult resembles an Indian-club. The head of the club is ovate with a broad median zone on which the tentacles are placed. On both sides of the tentacle-zone the hydranth tapers gradually away : distally into a large conical hypostome on the truncated summit of which a shallow depression marks the position of the mouth; proximally into the long almost parallel-sided handle of the club. The total length of a well-grown individual varies from 0·63 mm. to 0·98 mm., the length of the " head " from 0·28 mm. to 0·52 mm., and the diameter of the tentacle-zone (the greatest diameter of the hydranth) from 0·16 mm. to 0·28 mm. In the youngest examples I have seen there was no proximal extension of the hydranth, and the " head "

was sessile or rested upon the basal bulb (pl. xxx, fig. 1). In such cases the hydranths measured 0·15 mm. to 0·27 mm. in length, and their greatest diameter varied from 0·14 to 0·21 mm.

The following table showing the dimensions of various representative polyps gives at the same time an idea of the progressive development of an individual, the relative age or developmental stage being approximately indicated by the number of tentacles. All the polyps, with the exception of the first, were collected at the same place and time, and were killed under identical conditions. The measurements are in millimetres.

DIMENSIONS OF *ANNULELLA GEMMATA*.

Tentacles.		Polyp.		Stalk-like prolongation.		Basal Bulb.	
Number.	Maximum length.	Total length.	Maximum diameter.	Length.	Diameter.	Depth.	Horizontal diameter.
4	0·17	0·27	0·21	none		0·04	0·1
5	0·13	0·15	0·14	none			0·08 no perisarc
6	0·44	0·63	0·16	0·35	0·11	broken	
8	0·75	0·84	0·21	0·42	0·1	0·15	0·21
9	1·46	0·81	0·25	0·35	0·17	0·13	0·15
12	1·38	0·98	0·28	0·46	0·14	0·2	0·25

Tentacles.

The tentacles are confined to a somewhat prominent median zone on the hydranth. Over this they are irregularly scattered, at least three or four distinct levels being recognisable. Their number varies from 4 and 5 on the youngest individuals observed to 12 in the largest, but the average seems to centre about 6.

The appearance of the tentacles is characteristic and beautiful. They bear throughout their length, at fairly close and regular intervals, batteries of cnidoblasts aggregated in large projecting rings, or globular masses which resemble beads strung upon the axis of the tentacle (see pl. xxxa, fig. 7). These rings or globes have a diameter averaging three times that of the tentacle proper. Between the larger batteries there are occasionally smaller clumps of cnidoblasts in narrow rings or tiny circular groups. A globular battery terminates each tentacle, but since its size does not much exceed that of the cnidoblast rings the capitate condition is not always very evident, especially in contracted tentacles.

The detailed structure of the tentacles was examined in serial sections (see pl. xxxa, fig. 8). The typical cell-layers are repre-

sented by a solid endoderm, an exceedingly thin mesogloea, and an ectoderm of greatly varying thickness.

The *solid endoderm* is composed of many thin-walled cells, with sparse protoplasmic content which often simply lines the cell-wall and includes a small oval nucleus. The cells appear to be arranged, but somewhat irregularly, in four radial series of hexagonal cells, the bases of which rest upon the mesogloea, while the pyramids which form their apical regions interlock towards the centre of the tentacle. A longitudinal median section of a tentacle, therefore, generally exhibits a series of lateral walls of endoderm cells at right angles to the mesogloea, and in the centre a zigzag line representing the junctions of the pyramidal apices. Both in the character of its cells and in their arrangement the solid endoderm of this form differs very markedly from the solid endoderm of general occurrence in the tentacles of hydroids. Instead of thick-walled (" notochordal") cells arranged with great regularity in a single series lying along the long axis of the tentacle, as is the general rule, there are here delicate, thin-walled, multiserial cells.

The *mesogloea* of the tentacle-cells calls for no remark except that it is of extreme tenuity scarcely exceeding 1μ in thickness throughout the whole length of the tentacle.

The *ectoderm* of the tentacles falls into two distinct zones, the ring-like or globe-like swellings, which I shall designate *nodes*, and the spaces between them (see pl. xxxa, figs. 7 and 8). In the inter-nodes or inter-annular zones the ectoderm, even when the tentacle, in contraction, is at its stoutest, consists of a very thin layer of much flattened epithelial cells. In an extended tentacle this layer owing to its tenuity becomes scarcely visible. A rare cnidoblast, similar to the lesser variety in the nodes, forms the only inclusion in the internodal cells.

The nodes are composed of a zone of large oval cushion-shaped cells, closely appressed to each other laterally in a single row. Occasionally, however, incomplete zones or isolated individuals of these cushion-shaped cells occur in the inter-nodal areas. At the junction of nodes and inter-nodes the internodal ectoderm conforms to the outline of the nodal cells, being banked up against their curved walls with a gentle slope. The size of the nodal cells varies with the contraction of the tentacle, but the short diameter (parallel to the long axis of the tentacle) usually lies between 15μ and 27μ, while the height varies from 12μ to 22μ. Apart from inclusions the nodal cells contain little cytoplasm, the greater part of their interior being occupied by a large vacuolar space. Upon the base of the cell, however, there lies a thin layer of cytoplasm, and a median nucleus, 5μ by 3μ in diameter, containing a small nucleolus and surrounded by a sparse coat of cytoplasm whence delicate strands radiate outwards. The whole structure of the cell appears to be organised in relation to its function as a battery cell. I shall, therefore, discuss here the arrangement and structure of its cnidoblasts.

Cnidoblasts of the nodal cells.

In surface view of a tentacle-node a regular arrangement of cnidoblasts is apparent (see pl. xxxa, fig. 7). Round an individual of large size circles a group of smaller cnidoblasts. The latter are set singly and more or less regularly on an imaginary circumference,
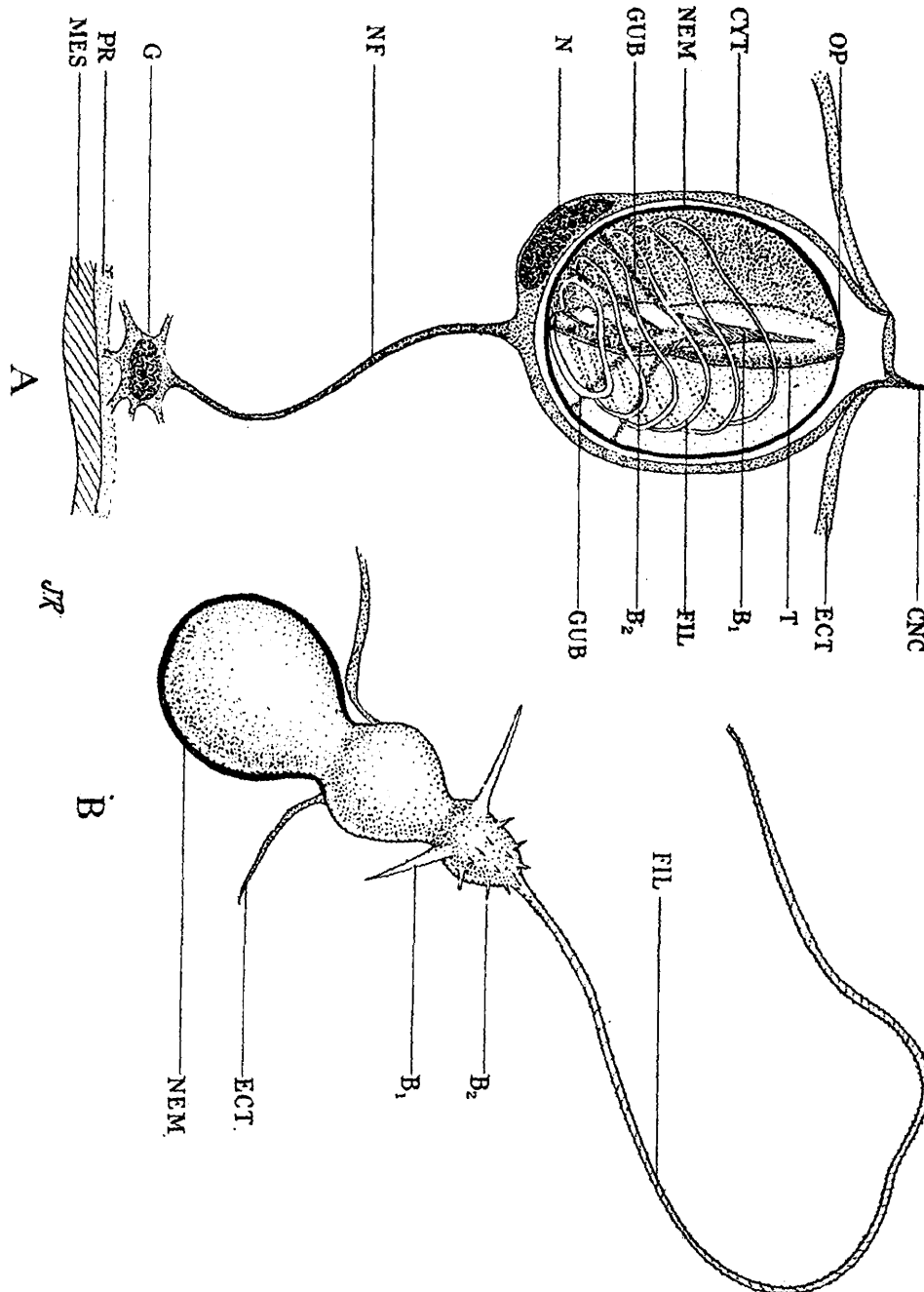
TEXT-FIG. I.

Large type of cnidoblast (*macrocnide*) from nodal cell.

A. Undischarged cnidoblast and its connections *in situ* (× approximately 4000 diameters).

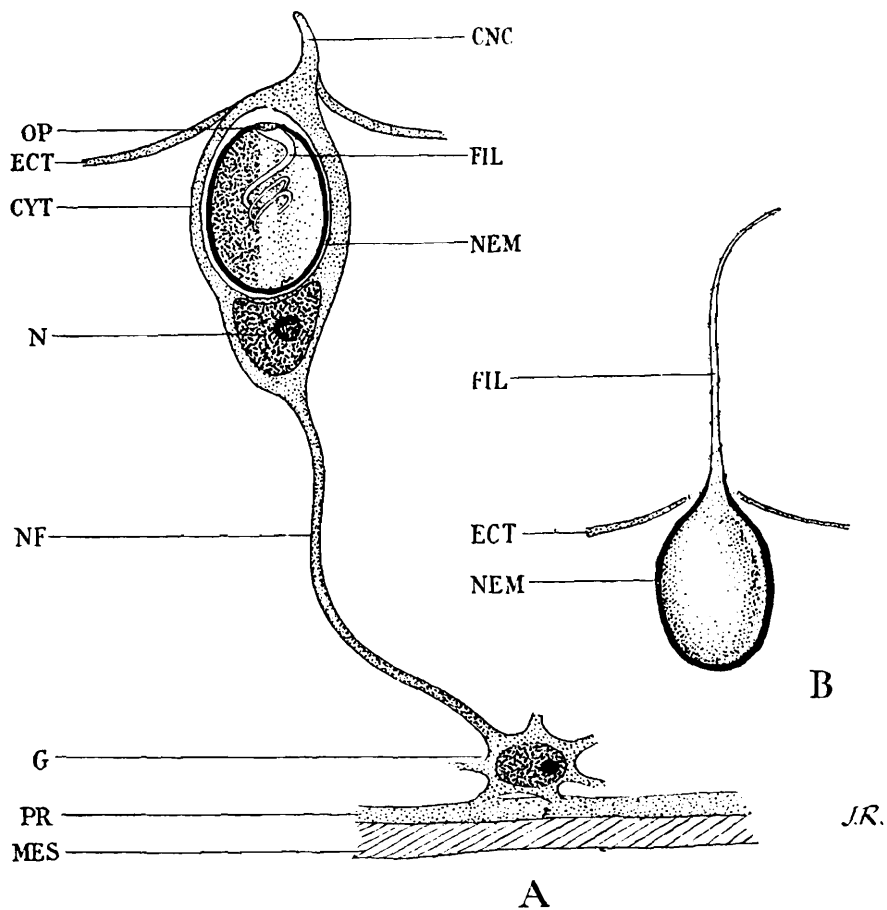B. Discharged nematocyst (× approximately 3000 diameters).

B_1, B_2, major and minor barbs; CNC, cnidocil; CYT, cytoplasm; ECT, external wall of ectodermal cell; FIL, filament; G, ganglionic mass, GUB, gubernaculum,—protoplasmic strand supporting central tube; MES, mesogloea of tentacle; N, nucleus; NEM, nematocyst; NF, nerve fibril; OP, operculum; PR, layer of protoplasm lining bottom of cell; T, central tube.

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with generally seven but sometimes as many as eleven examples. In a single node about 8 to 10 large cnidoblasts are present with their attendant satellites—a total of approximately 80 individuals. As a rule each cell contains only one complete group, but occasionally the cell-wall appears to become obliterated so that several groups come to lie within a cell's boundaries. In median longitudinal section of a tentacle (pl. xxxa, fig. 8) the nematocysts are seen to lie at the periphery of the cell, radially inclined outwards from the mid-point of its base. There are considerable differences in the structures of the two types of cnidoblasts.

The larger individuals (*macrocnides*) (text-fig. 1) consist of an almost spherical nematocyst, 7μ to 8μ long by 6μ in diameter, surrounded by a thin and uniform covering of cytoplasm which pushes up the cell-wall, and is produced into a short delicate cnidocil. At some point in the proximal portion of this cytoplasm lies an elongated nucleus the inner profile of which conforms to the outline of the nematocyst. Contrary to the experience of Schneider (1890, p. 332) as regards *Hydra fusca*, the nucleus contains a distinct nucleolus. At the proximal end of the cnido-blast a delicate thread, the nerve fibre, leaves the cytoplasm, and passing across the vacuolar space of the cell merges with the cytoplasm surrounding the nucleus that lies on the floor of the cell. The nucleus and its surrounding cytoplasm seem to constitute a ganglionic mass to which radiate the nerve filaments of many or all the cnidoblasts in a group. The ganglion mass is in its turn connected with the layer of cytoplasm which covers the floor of the cell. None of the macrocnides possessed a simple broad cytoplasmic peduncle such as forms an attaching structure in examples from several other species of Hydrozoa.

The interior of the nematocyst is filled with a highly refractive fluid, which renders accurate observation of the internal structures a matter of some difficulty. At the distal pole of the nematocyst is a circular area—the operculum—of consistency different from that of the nematocyst wall. From this area, whence the filament escapes on its discharge, a cylindrical tube of considerable diameter projects into the cyst, passing along its longitudinal axis almost to the proximal wall. In its upper half the tube contains a prominent opaque triangle pointing upwards and almost reaching the distal wall of the cyst, and this represents the single whorl of three major barbs which encircles the lower portion of the ejected filament. Similar smaller and less well-defined structures are sometimes apparent in the lower half of the tube. The lower section of the tube is kept in position by a series of exceedingly delicate gubernacula—protoplasmic strands which attach it to the wall of the nematocyst, and which are to be observed only under specially favourable conditions of staining and lighting. The proximal portion of the tube narrows rapidly and at its base is continuous with the filament which lies near to the wall of the cyst in an ascending spiral of some six loose coils.

The everted portion of a discharged nematocyst is some three to three and a half times the length of the nematocyst, and consists of a smooth-walled basal bulb, a second and smaller bulb furnished with about four whorls of barbs of which the proximal whorl contains three large individuals, while those of the distal whorls are more numerous and insignificant. From the second bulb proceeds the filament which throughout its length is armed by a close spiral of exceedingly minute barbules ascending in a contra-clockwise direction (see text-fig. 1B).

TEXT-FIG. 2.
Lesser type of cnidoblast (*microcnide*) from nodal cell.
A. Undischarged cnidoblast and its connections *in situ* (× approximately 4000 diameters).
B. Discharged nematocyst (similarly magnified).
Lettering as in text-fig. 1.

The second and smaller type of cnidoblast—*microcnide*—is of simpler structure. The nematocyst is similar in shape but is approximately half the linear dimensions of that of the large type, 4μ or 5μ by 3μ. The cnidocil is stouter and longer than in the macrocnides, and although the general arrangement of cytoplasm is the same the cytoplasmic coat is drawn out into an elongate oval shape to include a very large nucleus which lies against the proximal wall of the nematocyst. The nucleus varies in shape, but its inner surface is always closely moulded upon the nematocyst wall,

and it frequently assumes the deep helmet-shape shown in section in text-fig. 2A.   It contains a large nucleolus.   The cytoplasm is connected by a long delicate nerve fibre with the ganglionic mass on the floor of the cell.   Occasionally, however, the connection becomes a comparatively broad protoplasmic strand resembling the peduncular attachment of some cnidoblasts.

The internal structure of a microcnide differs much from that of a macrocnide.   The former contains only the filament, which proceeds directly from the operculum at the distal pole of the cyst in a loose descending spiral of about three small coils.   These appear to encircle a central pillar of delicate consistency which may, however, be simply one of those phenomena of refraction which render so difficult the exact observation of the contents of nemato-cysts.   In a discharged microcnide (text-fig. 2B) three points strike one as characteristic : the shortness of the simple filament, the length of which is only twice that of the nematocyst ; the directness with which the filament projects from the nematocyst, for it invariably lies in line with the long axis of the nematocyst and is straight, except for a very regular curve towards the tip ; and, lastly, the openness of the spiral of minute barbules, which performs only about ten revolutions in its contra-clockwise ascent.

Hydranth Body.

The *ectoderm* of the hydranth-body consists of a layer of irregular epithelial cells, between which lie small interstitial cells. The bases of the epithelial cells are produced into longitudinal muscle fibres which rest upon the mesogloea.   The ectoderm averages in thickness some $7\cdot5\mu$, but especially in the lower prolongation of the hydranth is arranged in slight horizontal ridges.   The cells contain large rounded nuclei, and in parts a large number of cnidoblasts, but only some of the latter possess cnidocils and are functional, the remainder being under process of formation.   The cuticle, if present, is of extreme delicacy, and no perisarc is secreted.   At certain stages of development, however,—when a new basal bulb is being formed (see p. 555)—a number of hydranth cells take part, along with the cells of the basal bulb, in the secretion of a thick coating of hyaline mucus.   In portions of this secretion masses of diatoms and other debris become entangled, and it is interesting to note that in this condition the diatoms appear to have continued a symbiotic existence, for the greater number show evidence, in their well-preserved protoplasm, of recent active metabolism.   A similar state of symbiosis has been noted by Schaudinn in the case of the diatoms and algae which surround the body of *Haleremita* (Schaudinn, 1894, p. 226).

In the neighbourhood of the tentacle-zone and around the margin of the mouth the ectoderm is thickened.   In the latter region it contains a close array of functional cnidoblasts, similar to the macrocnides of the tentacles.   In the tentacle-zone, however, the majority of the cnidoblasts—macro- and micro-cnides— lie some distance below the surface and are in process of formation.

The great numbers of developing nettling organs in this region clearly indicate it as a localised manufacturing area whence migration of fully developed nematocysts to the tentacles takes place, conditions apparently of general occurrence in the Hydromedusae (see Hadzi, 1911).

The *mesogloea* is colourless and of almost uniform thinness of 2μ.

Endoderm.—The endoderm cells present more variety in their shape and in their inclusions than the ectoderm. As in many other hydroids they fall into three indefinitely bounded regions, in all of which, however, a few longitudinal ridges of elongated cells project into the coelenteron.

The hypostome endoderm consists of a series of regular, elongated, narrow, palisade cells resting upon the mesogloea and lacking inclusions. Between the distal ends of these cells are inserted many clavate gland cells, with a large nucleus resting in the wedged-in narrowing portion of the club, and a content of finely granular cytoplasm.

In the region of the tentacle-zone the endoderm is considerably deeper. The palisade layer of the hypostome is replaced by several irregular rows of small highly-vacuolar cells. Upon these rest large clavate nutritive cells, containing oval nuclei and coarsely-granular secretory products, as well as foreign bodies the recognisable portions of which consist mainly of the frustules of diatoms. Throughout the endoderm in this region there are scattered dark oval cells containing excretory products.

Lastly in the prolonged basal portion of the hydranth the cell-varieties of the former regions disappear, and the endoderm consists of a network of regular, highly vacuolar cells in which the cytoplasm and nuclei are ranged along the cell-walls. Here the cells are almost devoid of inclusions, only a rare individual with excretory products being observable; and although a narrow central lumen penetrates the region it is clear that the cells lining it take little part in the secretory or digestive functions.

The structure of the basal bulb will be discussed in the section dealing with reproduction (p. 553).

METHODS OF REPRODUCTION.

I. SEXUAL REPRODUCTION.

There is no conclusive evidence of the occurrence of a sexual type of reproduction in the specimens which I have examined, although in one there is present, arising from the tentacle-zone, a very small globular bud (0·045 mm. in diameter) composed of ectodermal and endodermal elements, which might possibly have developed into a sporosac or medusoid gonophore. Its position within the tentacle-zone agrees with the position rather of the sexual bodies than of the simple buds of most other hydroid species.

But Dr. Nelson Annandale, who kept examples of the hydroid alive in an aquarium for some time wrote in a note accompanying some of the specimens : " The gonosomes, which develop into free medusae, are borne in a circle round the hydranth, below the tentacle"; and again, in reply to a request for examples of the medusa or for further information " I am sorry that I have not any specimens of the medusae of the little Hydroid from Port Canning. The only one I have seen escaped in my aquarium. It was so small that I could only just see it with a very powerful hand lens. "

In view of the minuteness of the structures concerned it is possible but unlikely, that a naturalist even of Dr. Annandale's acumen and experience, might have mistaken one of the planula-like buds to be afterwards described, for a medusa.

In any case the elucidation of the sexual phase must be left to new collections of material gathered possibly at a different season of the year.

II. ASEXUAL REPRODUCTION.

Lateral Budding.

A few hydranths possess lateral buds in various stages of development. The buds arise from the region below the tentacle-zone, and between it and the gentle narrowing which indicates the beginning of the stem-like basal prolongation. But they are not common on my specimens which were collected in the month of March, few hydranths possessing even a single bud, and two being the greatest number on any one hydranth.

The buds are of the simplest structure (see plate xxx, fig. 4). They arise as small hollow projections of ectoderm and endoderm, which increase in length much more rapidly than in breadth. So there is formed an elongated hollow sac with thin walls of single-layered ectoderm and endoderm. The base of the sac becomes much constricted at its point of junction with the hydranth, but the internal cavity retains connection with the coelenteron of the hydranth by a narrow passage. In due course the connecting neck of the bud becomes ruptured, and the bud, which is now vermiform and closely resembles the planula of many hydroids (except that it lacks cilia), breaks away and commences a free life.

A released and therefore mature bud contains no traces of sex cells, and it must be assumed that it gives rise directly to a new hydranth. The only free example which I have observed seems recently to have broken loose from the hydranth (plate xxx, fig. 5). It is almost cylindrical in shape, 0·30 mm. in length by 0·085 mm. in maximum and 0·065 mm. in minimum breadth, slightly narrower in its median region and widening gently to its rounded extremities   The resemblance in shape to the planula of *Cordylophora lacustris*, as figured by Allman (1871, pl. iii, fig. 5*a*) is very marked. The proximal extremity still retains an opening representing the lumen which connected the bud cavity

with that of the hydranth, and as a slight ridge well furnished with nematocysts surrounds the opening, it is possible that here is foreshadowed the adult mouth.

Serial sections reveal the fact that at the place of origin of a bud considerable activity is shown by the endoderm of the hydranth, which is crowded with finely granular protoplasm and engulfed food particles. These features are carried into the endoderm of the developing bud, the cells of the proximal portions of which contain much secretory and food material. The mesogloea of the bud is somewhat less developed than that of the hydranth, and the ectoderm is remarkable for the regularity and high, narrow palisade-like structure of the cells at both extremities. These contain spherical nuclei similar in size to those of the endoderm (3μ in diameter), and many nematocysts of both types undergoing development. As the bud increases in size some of these approach the surface of the ectoderm and lie in position for functioning, although in none of the buds, attached or free, are cnidocils present. An extremely thin cuticle is excreted by the ectoderm. I have seen no indication of the presence of an external coat of cilia.

The neck joining bud to hydranth is formed of ectoderm, mesogloea and endoderm, and in spite of the narrowness due to increasing constriction there is no sign that rupture is preceded by the disappearance of the endoderm, as in the case of the hydroid of *Gonionemus murbachii* (see p. 561), or of the ectoderm, as in the cases of the basal bulb described below, or of the sporosac buds of species of *Dicoryne*.[1]

Longitudinal fission.

In a single specimen longitudinal fission appears to be in progress (see pl. xxx, fig. 3). From the neighbourhood of the tentacle-zone of a well-developed hydranth with in all eleven tentacles a secondary hypostome branches out as if due to the division of the original hypostome. Both hypostomes are normal in character and the mouth of each is connected in the usual way with the common coelenteron of the hydranth. The endoderm layer between one hypostome and the other is of uniform thinness and regularity, and shows no prolongations or other abnormalities in the neighbourhood of the fission angle. The smaller hypostome has appropriated some of the tentacles of the original hydranth, and new smaller ones are arising at its base. Whether this process is to be reckoned as a normal mode of reproduction or whether the instance described is rather an abnormal case of budding or duplication than an example of true fission, I have no means of deciding.

The Basal Bulb.

Reference has already been made to the significance of a structure which I have termed the basal bulb. To judge by the

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[1] *See* Ashworth and Ritchie, 1915.

frequency of its occurrence this structure is of first importance in the propagation of the species, for every hydranth examined (except one) bore one and often two bulbs at varying stages of development. The solitary exception was a young individual with 5 tentacles, in which the proximal extremity ended in a sucker-like disc without perisarc, the equivalent of the basal disc or "Fussplatte" of *Hydra* and other forms. The universal presence of at least one basal bulb or its antecedent on these specimens can be readily understood by the fact that all the hydranths examined were growing upon a seaweed ; and that as the basal bulb is the only means of attachment its presence was postulated by the stage of growth of the hydranths discovered. The only hydranths likely to be found lacking the basal bulb are individuals belonging to the unattached, probably planktonic, stage.

Position and General Structure of the Basal Bulb (pl. xxx, figs. 1-3). The basal bulb is situated at the lower free end of the hydranth in the position generally occupied by the hydrorhiza. Resemblance to a hydrorhiza is further to be found in the fact that it seems to be the habit of the basal bulb to lie with its long axis parallel to the substratum and at right angles to the hydranth. Basal bulbs have been found in the youngest hydranths as well as in the oldest individuals examined ; in the former, the hydranth body springs directly from the bulb, in the latter the bulb terminates the stalk-like proximal prolongation of the hydranth.

At all stages the character of the bulb is obscured by masses of organic debris which adhere to it in a dense coating and spread from it for a short distance upon the hydranth. Within this debris, except in the very earliest stages, lies a more or less globular shell of chitin, thin, delicate, and colourless at first, but later becoming strong, immobile and tinted. During its impressionable stages the chitin of the bulb may be moulded upon the particular substance whereon it lies, and this produces considerable modification in the typical rounded form. The chitinous shell contains and protects a simple cellular sac, which in its more mature stages lies loosely within. This sac, the essential portion of the basal bulb, consists of a single layer of ectoderm and of endoderm. In its advanced stages it is connected with the proximal end of the hydranth by a narrow protoplasmic neck which passes through a small circular opening in the chitinous shell—the only aperture connecting the interior of the shell with the exterior.

Detailed Structure of Mature Basal Bulb (pl. xxxa, fig. 9). Well developed basal bulbs were examined in serial sections. In these specimens the cellular sac did not lie in contact with the chitinous investment ; but since the chitin showed many regular growth-lines and could only have been secreted by the sac, the hiatus may be artificial, due to shrinkage in preservation.

No special features mark the single layers of ectoderm and endoderm which form the walls of the sac : the latter contains

small round nuclei and here and there groups of excretory products ; the former contains many large nematocysts in process of formation, especially in the upper region near the aperture in the chitinous investment. It is curious that nematocysts should develop in an enclosed sac the ectoderm of which has no contact whatever with the exterior, but a similar condition has been observed in the hydrorhizal portion of *Myriothela cocksii* (Hardy, 1891, p. 512), and of *Corymorpha* (Torrey, 1907, p. 279), and I have noticed it in the case of some gonophores. In *Annulella* the history of the layers of the sac (see p. 555) offers a simple explanation. The walls of the sac are thin and leave a moderate space for a central cavity which is in direct communication with the coelenteron of the hydranth.

It is a remarkable fact that in the mature bulb there is no direct connection between the ectoderm of the hydranth and that of the basal bulb. At the constriction or neck uniting the two, the ectodermal layer disappears and the chitinous investment abuts against the mesogloea. This may be a preliminary to the severing of the neck at the time when the hydranth escapes from its holdfast; as such at any rate it would fall into line with the well-defined process which precedes the release of the free-swimming sporosacs of species of *Dicoryne* (*see* Ashworth and Ritchie, 1915).

An unusual feature distinguishes the mesogloea of the basal bulb. It is continuous with the mesogloea of the hydranth, but just beneath the neck and within the aperture of the chitinous shell, it forms a very much thickened rim deeper than either endoderm or ectoderm. From the proximal margin of this ring the mesogloea suddenly tapers away, and throughout the remainder of the bulb forms a layer of extreme tenuity.

The chitinous investment of the basal bulb is of rudely spherical form, sometimes greatly modified by its contact with the solid substratum. The chitin is of very different densities, but the upper portions are always the more solid and deeply tinted. Round the small but very definite aperture through which the neck of the basal bulb passes there is a thickened ring slightly incurved. While the perisarc is well defined in the distal portions and there exhibit definite growth lines, in the central area of the floor of the bulb it gradually loses its compactness and merges into an amorphous gelatinous mass of much greater thickness (pl. xxxa, fig. 9a). In this mass are included, along with other debris, large quantities of diatom skeletons in some of which the protoplasm is so well preserved as to indicate that the algae continued to live after their inclusion. This unconsolidated basal area may add to the efficiency of the basal bulb as a hold-fast, or may provide for the expansion of the perisarc-shell during the growth of the sac within.

The secretion of perisarc is confined to the basal bulb, at the neck of which the chitinous covering ends abruptly. Yet masses of gelatinous material containing much debris not only surround the bulb but are continued for a short distance on the lower exposed portion of the hydranth.

Origin and Development of the Basal Bulb (see pl. xxx, fig. 6). The basal bulb is a modified portion of the hydranth body. This is clearly shown by a hydranth which has recently broken away from a former basal bulb, and is in process of forming a new one. The history of this specimen (fig. 6) may be taken as indicating the general development of a basal bulb, and appears to have been as follows.

The hydranth tapers away at its basal end almost to a point, and here the tissues are ruptured. This narrow portion is the neck of a former basal bulb, and the damaged tissues show where the narrow neck, already prepared by increasing constriction and by the disappearance of the ectoderm layer, has broken asunder, allowing the hydranth to escape from its former anchorage. The final rupture of the neck is no doubt due to mechanical strain brought about by the swaying of the hydranth in the water currents.

So far as one can judge the free stage of the hydranth must be of very limited duration, for even before the traces of rupture at the neck of the old basal bulb have disappeared, a new basal bulb is in process of formation.

Four modifications mark the development of a basal bulb. Its origin is first indicated by a slight constriction in the lower portion of the body of the hydranth. This constriction affects all the cell-layers: the endoderm and mesogloea are simply indented, but even at the early stage figured, there is already a disruption in the ectoderm, which, although not yet severed, is reduced to very thin dimensions at the level of the future neck. A second characteristic regards the differentiation of the ectoderm of the basal bulb. Distal to the constriction, that is on the unaltered hydranth, the ectoderm is of the normal ridged type with rather elongated cells, but proximal to the constriction the cells are smaller, more regular and flattened. In the third place, copious masses of mucus in which debris becomes entangled begin at once to be secreted by the ectoderm of the basal bulb; and lastly the formation of mucus is succeeded by the secretion of a chitinous investment, the perisarc, which at the stage figured had only begun to form in the lower regions. The folding over of the bulb until its long axis lies at right angles to that of the hydranth must be a subsequent development.

While the above mode of development of the basal bulb happens to have come to my notice and is, on account of its uniqueness, described in some detail, it probably represents only one of several methods by which a basal bulb may arise. It can hardly be doubted that the original basal bulb of a hydranth develops directly from the basal-disc or "Fussplatte" of the larva, and development from a lateral bud seems to be hinted at by the following facts.

In many cases there are two basal bulbs at the base of a single hydranth (see pl. xxx, figs. 2 and 3) and in such case they arise not in linear succession but one terminally and one laterally.

The latter may have originated as a bud. Of the two the terminal bulb possesses thicker perisarc and more contracted coenosarc and appears, though not the larger, to be the older individual.

Significance of the Basal Bulb. There is no direct evidence as to the reproductive function of the basal bulb: no young hydranths have been observed springing from the coenosarc of an old bulb, unless it be that where two basal bulbs occur on one hydranth, one represents the original bulb from which the hydranth grew while the other is a development of the hydranth itself.

But the evidence of the structures and development of the bulb seem to point clearly to reproductive function. Thus the disappearance of the ectoderm at the junction of bulb and hydranth seems to be analogous with the similar retrogression in the sporosacs of *Dicoryne* and to indicate a regular preparation for the breaking away of the hydranth. An example of a recently released hydranth has been observed. Again basal bulbs are frequently found alone,- and in these the coenosarc is in good preservation. Here we seem to have a parallel to the conserving power of the stolon as exhibited in the hydrorhiza of *Dicoryne conybearei* (Allman) in which, by the development of partitions of chitin within the lumen of the stolon the coenosarc is preserved unharmed in various sections during unfavourable conditions (see Ashworth and Ritchie, 1915). In *D. conybearei* the conservation of the coenosarc in this way is succeeded so soon as favourable conditions return, by a new development of hydranths produced by the coenosarc; and it seems highly probable that a similar recrudescence of hydranth life arises from the coenosarc of the basal bulb.

THE RELATIONSHPS OF *ANNULELLA GEMMATA.*

I have already drawn attention to the curious combination in *Annulella gemmata* of peculiar characters some of which have been found rarely, and generally one at a time, in other species. The most accurate conception of the significance of these resemblances will be attained by a short comparison of each with its analogues.

UNATTACHED HYDROIDS.

Several genera of Hydroids share with the Pennatulid and a few other types of Alcyonarians, the character of gaining a more or less insecure anchorage by simply embedding their proximal end in the mud of the sea-floor. They are generally characterized by solitary habit and by the weak development or absence of perisarc. Amongst such are to be reckoned the Corynids—*Myriothela* and *Blastothela* ; the Pennarid, *Heterostephanus* ; and the Tubularids— *Corymorpha, Lampra, Gymnogonos, Monocaulus* and *Branchio-cerianthus.* It is probable that with these should also be grouped the lake forms—*Moerisia* and *Caspionema.* Many of these gain firmer anchorage by the development of "rootlets," but the

majority or all of them have the power of slight movement, and it is possible that they may be able even to withdraw from the mud and creep along the bottom. In any case, as Hartlaub has pointed out [1] these forms, both in their systematic affinities and the in their habit, present a well-defined half-way house between permanently fixed species and those which are able to leave their attachment and move freely on the substratum or in the sea.

Amongst such temporarily creeping or floating forms we have the freshwater *Hydra*, and its relatives *Protohydra* and *Polypodium*; the Tubularid, *Hypolytus*; and *Haleremita* of uncertain relationship, but closely resembling the larval stage of *Gonionemus*. Here also I am inclined to include the Pennarid, *Trichorhiza*, which, found by Russell (1906) on the tentacles of *Corymorpha nutans*, was apparently caught in the act of moving. General but not universally present characters which link these forms (with the exception of *Trichorhiza*) are the almost total absence of perisarc and the presence of a basal thickening of coenosarc—the pedal disc. I have not included definitely recognized larval forms, but perhaps the floating stage of *Acaulis* ought to be mentioned here, since floating individuals bear well developed medusae buds and may be considered adult.

In a slightly more advanced category of unattached hydroids are to be placed the pelagic forms *Margelopsis* or *Nemopsis*, which represent the detached buds of such forms as *Tiarella* (see Bedot, 1911, p. 211); the unique *Microhydra* and the metagenic form of the Trachymedusan, *Liriope* which " is a true hydra, although its free-swimming mode of life and its superficial aspect caused it to be mistaken formerly for a gonosome " (Perkins, 1903, p. 752).

In none of these groups of unattached Hydroids is to be found an exact parallel to our Indian brackish-water species, the adults of which are at one stage firmly attached, and at another are released from their attached portions in order to lead a temporary free (? pelagic) existence. But, as we shall see in discussing the basal bulb, that structure links *Annulella* with the creeping type, especially common in the family Hydridae.

Tentacles and Cnidoblasts.

The arrangement of the cnidoblast batteries of the tentacles in well-defined projecting rings is characteristic of very few hydroid stages. It is, however, moderately common in the medusoid generations, being exhibited in such well-known forms as *Thamnostylus dinema*, or in the medusoids of *Corymorpha nutans, Stauridium* and *Syncoryne eximia.* [2] In the hydroid stage, so far as I know, it is confined to *Trichorhiza brunnei*, Russell 1906, *Heterostephanus annulicornis* (M. Sars 1859), *Hypolytus peregrinus*, Murbach 1899, *Asyncoryne ryniensis*, Warren 1908, and occurs to a limited extent

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[1] Hartlaub, 1902, p. 29.

[2] Compare particularly the representations of the last species as drawn by Allman, 1871, pl. v, figs. 3-4.

in *Tiarella singularis*, Schulze 1876, with its three distal rings of cnidoblast batteries and in *Margelopsis stylostoma*, Hartlaub 1903, which has been shown by Bedot (1911, p. 211) to be the free bud of the preceding species.

It is a striking fact that annulated tentacles should be common in the free-swimming medusoid generation, and should occur in the hydroid generation only in a few species, which, with the exception of *Asyncoryne*, are outstanding on account of their free or partially free habit. The connection of habit and structure appears to be no coincidence, and, on the evidence before me, I would suggest that the arrangement of large cushion-shaped cells in prominent rings is an adaptation to a creeping or free-swimming life. Not only would the greatly enlarged surface area, due to the rings, add to the resistance offered by the organism to the surrounding water, and so check the rate of sinking, even were the organism immobile, but the very large vacuolar spaces, which the nodal cells of *Annulella gemmata* contain (and which in absence of direct evidence I assume to occur in the similar cells of other species), may act directly as buoying agencies. It is possible also that these vacuoles in the tentacular rings may by their enlargement and contraction supply in some degree the means of the daily vertical migrations so characteristic of most hydroid medusae.

In none of the cases mentioned above has the detailed structure of the cnidoblast rings been investigated. But the cushion-shaped cells of which the rings or nodes are made up in *Annulella* closely resemble in general appearance and detailed structure the isolated battery-cells which stud the tentacles of *Hydra*. A comparison of the description and figures of these batteries in *Hydra fusca*, as given by Schneider (1890, p. 332, Tab. xvii, fig. 20), with the description and figures of *Annulella* in this paper throws particular emphasis on this resemblance.

The resemblance to *Hydra* is further emphasized by comparison of the structures of the cnidoblasts themselves (see Schneider, 1890, p. 332 and pl. xvii). In *Annulella* I have recognized only two types of nematocyst, but both occur in almost identical form in *Hydra*. It is true that there are differences in detail; that Schneider describes no connection between the basal prolongation of the cytoplasm of the cnidoblast and a " ganglion mass," that he mentions neither the gubernacula within the macrocnides nor the spiral arrangement of barbules on the ejected filament. But these are negative evidences and in the examination of structures so notoriously difficult as cnidoblasts negative evidences are of even less moment than usual.

The conjunction of capitate and scattered tentacles suggests relationship with the family Corynidae, but the capitation is very slight and might be regarded as a terminal development of the tentacle nodes. Some cases of scattered tentacles (without capitation) occur in the family Hydridae.

The solid multiserial endoderm of the tentacles appears to be paralleled in only one other genus, *Tubularia*. Solid endoderm is,

indeed, characteristic of almost all Hydroids, but it consists of a single row of central thick-walled cells. Chun (1897, p. 316) says regarding the occurrence of such uniserial solid endoderm "Was zunächst ihr Vorkommen unter den Hydroiden anbelangt, so fehlen sie lediglich der durch hohle Tentakel ausgezeichneten Gattung *Hydra.* Alle übrigen Hydroidpolypen besitzen solide Tentakel, welche von einer einzigen Reihe derbwandiger centraler zellen gestützt werden." With the exceptional case of *Hydra* must be included that of the since described *Moerisia lyonsi,* Boulenger (1908), and possibly that also of *Caspionema pallasi,* Derzhavin (1912), regarding the endoderm of which the author makes no remark. In *Hydra* and *Moerisia* the endoderm consists of several longitudinal rows of thin-walled cells, penetrated by a fine central lumen. But in species of *Tubularia* which I have examined in detail, the lower or aboral whorl of tentacles contains a solid endoderm composed of many small thin-walled cells. These are not arranged in series but fill in irregularly the centre of the tentacles (see also Warren's account of *Tubularia betheris,* 1908, p. 282). The oral tentacles of *Tubularia* contain the ordinary type of uniserial endoderm.

The solid delicate-walled multiserial endoderm of *Annulella* bears no resemblance to the solid uniserial endoderm of the majority of Hydroids, but closely resembles in structure and arrangement (except that there is no central cavity) the multiserial endoderm in the tentacles of *Hydra* and *Moerisia,* and resembles in a general way the solid endoderm of the aboral tentacles of species of *Tubularia.*

BUDDING.

The phenomena of budding in the Hydroid Zoophytes may be divided into three types: (1) where the bud develops on the parent into a miniature adult and remains attached, thus giving rise to colonial formation; (2) where the bud develops on the parent into a miniature adult which is then set free; (3) where the bud is set free at a simple planula-like stage and develops into a miniature adult away from the parent.

(1) The colonial type of budding is exhibited by the majority of cnidoblastic and gymnoblastic hydroids. (2) The setting free of a miniature adult is much less common but is familiar through the example of *Hydra,* and occurs in a few forms such as *Moerisia* (Boulenger 1908, p. 363) and *Tiarella* (Schulze 1876, p. 411). (3) The escape of a planula-like bud is an exceedingly rare mode of propagation, and since it is the type exhibited by *Annulella* calls for some remark. In its ultimate results it closely resembles the phenomena of those peculiar propagating branches of many Hydroids, the separation of which—"Scissiparité"—has been most recently and ably investigated by Dr. A. Billard (1904). "Scissi-parité," however, connotes the adaptation of an old structure, stolon or branch, to a new purpose, and can be reduced to a simple form of transverse fission in a portion of the hydroid

already existing. On the other hand, buds which ultimately become free seem to have evolved to this end alone: they are new structures the one purpose of which is the multiplication and distribution of forms like the parent. They are probably the most primitive of the budding types and the forerunners of the other types mentioned above.

Amongst the rare cases of escaping buds that of *Myriothela cocksii*, Vigurs [British specimens of which have been frequently misnamed *Myriothela phrygia* (Fabricius)] stands somewhat apart. In this species the buds are spherical masses attached to the parent by a thick stalk, and appear to reach a miniature adult stage before they are set free. Hardy, however, assures us that "all connection with the body of the parent is lost at a very early period, almost before the bud has reformed its ectoderm and endoderm and enteric cavity. It remains attached to the perisarc, however, by a sucker-like arrangement at the aboral pole until it is fully formed" (Hardy, 1891, p. 513 and pl. xxxvi, fig. 13). This might almost be regarded as a transitional stage, which although in fact a free bud, retains the aspect of an attached miniature adult.

Moerisia furnishes a more definite example of exparental development. The buds of this peculiar form are oval and are attached by short peduncles to the parent body, usually in the proximal region of the hydranth. As indicated above they "occasionally develop one or two tentacles" before they are set free, and some may therefore be regarded as attached miniature adults, but the majority of the buds "become completely detached from the parent body" before they begin to assume polyp structure (Boulenger, 1908, p. 363). Rare as such cases are, *Moerisia* is by no means a unique example.

Haleremita cumulans, Schaudinn, seems to depend entirely upon liberated planula-like buds for its dissemination and multiplication, for no trace of sex-cells has been discovered (Schaudinn, 1894, p. 227). The buds, which at the time of liberation are much elongated and planula-like, arise sometimes just beneath the tentacle zone and sometimes near the base of the hydranth and up to six may be found on a polyp at one time. After being set free they develop a mouth and creep upon the bottom, simple two-layered sacculae, which retain their simplicity for some 1½ months before the tentacles of the adult make their appearance. Some have been observed to develop buds of their own while yet in the saccula stage.

Much resemblance exists between the general structure and bud-formation of *Haleremita* and that of the larva of *Gonionemus murbachii* Mayer, described by Perkins (1903). The unusual stumpy conical shape of *Haleremita* is duplicated in the *Gonionemus* hydroid, and in both there are four tentacles set crosswise in a single whorl. Both lack sex-cells and both reproduce by planula-like buds. *Haleremita* is unusual amongst hydroids is possessing' only one type of nematocyst, but Perkins' description (p. 786)

indicates that only one form, long and bean-shaped, is present in *Gonionemus.* It is possible that these resemblances points to the true relationship of the problematical *Haleremita*: that it is the metagenetic hydroid phase of a hydrozoon medusa, a larva which in due course will assume medusa form. It is interesting to find some confirmation of this view in the simplicity of structure (to be expected in a larval form) which has led to the relegation of *Haleremita* to the primitive family Hydridae; yet the bud-formation in the two is by no means identical.

Perkins describes some interesting features in the development of the *Gonionemus* hydroid buds. The buds, which occurred singly on the hydroids, arise about halfway between the base of the polyp and the ring of tentacles. During their early growth the endoderm is solid, and in this condition becomes isolated from the endoderm of the polyp by the gradual constriction of the ectoderm at the junction of the two. Finally the bud comes to be attached simply by a long thin neck of transparent ectodermal protoplasm. The release of the bud, in the only case followed throughout its complete development, was accomplished by the gradual stretching and final rupture of the ectodermal neck. The released bud settled down upon its former *free* or *distal* end, and at the other pole, formerly attached, a mouth and tentacles developed. This bud became attached near the parent polyp, but in most cases an escaped bud was discovered after a few days some distance from the parental form. During the interval " it seems probable that it is a creeping unciliated form, although my first conjecture that it was a ciliated planula has not been proved erroneous " (Perkins, 1903, p. 771). A general idea of the developmental period of such planula-like buds can be gathered from Perkins' observations. The development of a bud from its first appearance as a simple knob to the completion of the formation of the coelenteron and the appearance of tentacles, lasted from ten to fourteen days, distributed as follows:—" (*a*) the first period including as far as the detachment of the bud, 5 days; (*b*) motile form, 2 to 5 days; (*c*) from attachment to appearance of tentacles, 3 to 5 days (Perkins *loc. cit.*). Schaudinn found that the development of *Haleremita* buds, up to the point of escape from the parent, varied from 5 hours to 6 days (Schaudinn 1894, p. 230).

In all the cases above mentioned, as well as in that of our Indian form, the buds arose equally from ectodermal and endo- dermal elements, confirming the observations of Braem (1894) and contrasting with Lang's (1892) description of the purely ectodermal origin of Hydroid buds.

So far as can be determined from my examination of the comparatively few buds available in the Indian species, they agree most closely with those of *Haleremita cumulans.* In both species, in contradistinction to *Gonionemus*, the bud possesses a hollow structure from the beginning, and the internal cavity remains in connection with the coelenteron till the time of escape.

The special resemblances to *Gonionemus* buds are slight and of little account. In both the buds seldom occur more than one at a time on a polyp; and in both it seems that the usual polarity of hydroid buds is reversed, and that the free end becomes the area of attachment, and the attached end the oral and tentacle-bearing area. It may possibly be that this remarkable inversion of the general mode of hydroid development is not a regular habit, but simply emphasises that in hydroid buds there exists an indeterminate polarity ready to be determined by external physical conditions. Such has been shown experimentally to characterise the adult stems of forms like *Tubularia* and *Corymorpha*, or in closer analogy exists in the larva of *Corymorpha*. It is likely that here as in these larvae " external factors such as contact and possibly gravity determine the kind of structure (*e.g.* hydranth or holdfast) which will ultimately appear in connection with the area of differentiation. That is they determine the polarity of the adult." (Torrey, 1907, p. 292).

Analogues of the Basal Bulb.

The normal organs of attachment of the vegetative stocks of the Hydrozoa fall into two broad classes: (1) those in which the base of the hydranth is simply modified into a fleshy disc or cylinder, occasionally naked, more often covered by a mucous secretion in which foreign debris becomes embedded, or rarely enclosed in a membranous film of chitin; (2) those in which a more specialized structure is apparent, the attachment being due to well-defined root-like strands of coenosarc, enclosed in a distinct coat of perisarc (the stolon or hydrorhiza) and forming simple threads, or branched " roots," or anastomosed networks, or even thick skeletal layers (as in *Hydractinia*).

It seems to me that these two types of hydroid attachment are homologous, that the simple fleshy attachment was the direct forerunner of the hydrorhiza, and may be regarded as a primitive. characteristic in those forms in which it occurs. In known species of Hydroids it is possible to trace the steps by which the simple basal disc became branched and split to form a root-like organ, and by which the final complexity of the hydrorhiza was built up. A process parallel to that suggested by a survey of the attachment organs of adult hydroids seems to be followed in summary during the development of certain individuals. One need only point to the early life-history of the colonial form *Eudendrium ramosum*, after the planula has relinquished its free state and settled down, to illustrate the development of a facsimile of the basal disc into a complex hydrorhiza (see Allman, 1871-72, pl. xiii, figs. 12-16 and 2).

It would be out of place, however, to develop a thesis of the evolution of the hydrorhiza in this paper, and I shall merely indicate the forms which seem to stand most closely related to our Indian species as regards their mode of attachment.

The simplest definite attachment is that of the larval hydroid of *Gonionemus.* Here there simply occurs at that surface of the planula-like bud which comes in contact with the substratum an increase in the thickness of the cells, so that the ectoderm of the base becomes a columnar epithelium. There seems to be no secretion of masses of mucus, but at any rate " it has now secured a firm hold upon the bottom, being so closely applied that it is quite hard to dislodge it " (Perkins, 1903, p. 771). In the above sentence Perkins would seem to hint that the adhesion is physical. In *Haleremita* the attaching area has differentiated a stage further : for while it still consists of a simple layer of special elongated epithelium, there are associated with it many gland-cells which exude the secretion by means of which the polyp is attached to the substratum (Schaudinn, 1894, p. 228).

A clear advance is marked by the condition of *Hydra* and *Protohydra,* for here a first organ of attachment, as distinct from a mere differentiation of ectodermal cells, is apparent. Nevertheless this organ (the foot, pedal disc, disque pedieux, Fusscheibe, Fussplatte) retains the condition of elongate epithelium, with associated secretory cells the mucus of which acts as an accessory holdfast, but it is capable of grasping a firm surface and relinquishing its hold at will.

I regard as closely akin to the foot of *Hydra* in differentiation the "sucker-like" adhesive organs of the miniature adults of *Myriothela cocksii* ("*phrygia*"), mentioned by Hardy (1891, p. 513) as remaining attached to the surface of the parent during development.

Greater structural complexity is shown by the problematical "Basalscheibe" of the miniature-adult buds of *Tiarella singularis* minutely described by Schulze (1876, p. 412 and Taf. xxx, fig. 2). In shape and minute structure this curious organ bears a striking resemblance to the naked basal disc observed in one young individual of *Annulella* with five tentacles, to the basal bulb of young specimens (see plate xxx, fig. 1) or to a section of an adult bulb (pl. xxxa, fig. 9). On account of these resemblances I have no hesitation in discarding Hartlaub's suggestion that it may be " ein fur die pelagische Lebensweise wichtiges Organ " (Hartlaub, 1903, p. 34), and regarding it is an attachment organ developed in preparation for the settling down of the pelagic phase. In exactly the same category may be placed the basal discs of *Margelopsis stylostoma,*[1] *Margelopsis gibbesi,* and *Margelopsis haeckelii* discussed by Hartlaub (1903, p. 34).

Subsequent to fixation the flattened disc-like " Fussplatte " of the adult *Tiarella,* with its coats of both dark and amorphous perisarc, continuous with those of the hydrocaulus, seems to have degenerated from the larval state as regards cellular distinctiveness.

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[1] A designation which since it indicates simply a young phase of *Tiarella singularis,* must lapse (see Bedot 1911, p. 211).

A much greater advance in the differentiation of the simple basal attachment is exhibited in *Myriothela cocksii* Vigurs, well described by Allman (1876) under the name of *Myriothela phrygia*. In the long-tentacled, free-swimming larval stage, a few days old, an increase in the thickness of the ectoderm at the aboral extremity is noticeable (Allman, 1876, p. 567). This appears to be due to the formation of columnar epithelium (see Allman's figure 15, pl. 56). In any case a sucker-like pad is formed by which the larva attaches itself to the substratum (p. 565). At this early stage of fixation the aboral "sucker" is similar in appearance, structure and function to the pedal discs which have been mentioned above, but new developments soon set in. "The proximal extremity of the animal becomes bent at right angles to the rest of the body so as to form a sort of horizontal, stolon-like foot from which small fleshy processes with sucker-like extremities, and having a considerable resemblance to claspers, are emitted. The function of these processes, however, is very different from that of claspers; they serve to attach the animal permanently to some solid support, to which they fix themselves by their extremities. Along with the stolon-like foot they become clothed with perisarc, and the actinula has thus acquired all the essential characters of the adult trophosome" (Allman, 1876, p. 565).

There is some general resemblance here to the final result in *Annulella*, for although the perisarc-covered "foot" of the adult in *Myriothela cocksii* is a direct development of the larval basal disc, it is almost certain that the original basal bulb of any individual of *Annulella* follows the same course; but the absence of a narrow neck between the stolon-like foot and the hydranth of *Myriothela*, as well as the presence of specialized sucker-like processes, mark it as very distinct from the basal bulb of *Annulella*.

Almost as distinct is the perisarc-covered basal attachment of the Tubularid, *Corymorpha*; for not only does it bear many anchoring processes, but the perisarc is really a portion of that which at one time enveloped the whole hydranth and which by a process of recession became later confined to the lower section of the stem (see Torrey, 1907, p. 279).

As regards the development of its basal bulb directly from the proximal portion of the adult hydranth, and of the special development upon the basal bulb of a highly differentiated perisarc, *Annulella* stands alone. It seems to me that its closest affinity in respect of this organ may be with *Tiarella*, beyond the stage of which, however, it has made considerable advance in specialization. It is well to remember, however, that in its phylogenetic origin the basal bulb is undoubtedly a development of the much simpler naked basal discs characteristic of a primitive group of unattached hydroids.

BASAL TRANSVERSE FISSION.

Transverse fission as a means of multiplication in adult hydroids is not unusual, and varies from the separating of a minute

terminal section of branch or stolon, as in several Campanularians and Plumularians (Billard, 1904, p. 41 *et seq.*) to vital processes such as the exaggerated "decapitation" of *Moerisia* or the median division of *Hydra* or *Protohydra*.

So far as I am aware, transverse fission in a determinate region of the base of an adult individual, is a normal mode of multiplication in only one hydroid species other than *Annulella gemmata*. Even that solitary case differs from *Annulella*: for in *Hypolytus murbachii* the fission takes place near the proximal end of a distinct hydrocaulus; it proceeds gradually by means of constriction, but without any disappearance of ectoderm (so far as one can judge) so that there are set free successive small naked planula-like segments which, after more or less limited wandering, settle down and develop directly into new hydranths (Murbach, 1899). In *Hypolytus* a wandering "blastolyte" escapes from a free adult; in *Annulella* a wandering adult escapes from an attached basal section.

In this respect *Annulella* comes very near to the hypothetical form postulated by Murbach as a precursor of *Hypolytus* (Murbach, 1899, p. 353); but to me there appears to be no close relationship between the two forms.

The phenomena of transverse fission in *Annulella* naturally bears a general resemblance to other well-marked cases such as the strobilisation of *Moerisia* (Boulenger, 1908, p. 364) or the division of *Protohydra* (Chun, 1894, p. 217). But the transverse fission of *Annulella* stands by itself as regards the structural changes involved (such as the disappearance of ectoderm at the neck, paralleled only in the sporosacs of *Dicoryne*), and as regards the final results, since here a segment specially modified with a view to fission remains attached, while the hydranth which gave it origin escapes.

SYSTEMATIC POSITION OF *ANNULELLA GEMMATA*.

The majority of the outstanding features of *Annulella gemmata* are primitive in character, a few seem to be adaptive. Among the latter may be reckoned the annular arrangement of large cells upon the tentacles (see p. 558), the great length of the tentacles themselves, and the adoption of basal transverse fission. All of these bear upon the free-living stage, the last as the means of attaining freedom, the former as adjuncts to a (supposed) pelagic existence.

The primitive characters include the normal adoption of various types of vegetative budding; but even these are of simple nature. Thus the setting free of minute, non-tentacled, planula-like buds must probably have preceded in evolutionary development even the liberation of buds at a miniature adult-stage, as occurs in *Hydra* and occasionally in *Moerisia*, both of which are included in the family Hydridae. Further, the naked basal disc observed in one young specimen of *Annulella* appears to be homo-

logous with the similar structure common in adult members of the Hydridae and in young specimens of *Tiarella*, and the basal bulb in its first development phylogenetically and ontogenetically, may be taken as a highly specialized form of the basal disc or " Fuss-platte."

Finally, the multiserial endoderm of the tentacles finds a close analogy in the similar (but hollow) endoderm of the Hydridae (*Hydra* and *Moerisia*).

Perhaps one ought to add that if faith be placed in Haeckel's hypothesis of the origin of a capitate tentacle as the thrusting out on a stalk of a cluster of nematocysts, then the capitation of the tentacles may also be placed amongst the primitive characters.

A survey of the systematic distribution of the distinctive characters of *Annulella* shows that they are confined to four families of the Hydroidae—Hydridae, Corynidae, Pennaridae and Tubulariidae; but that they preponderate towards the more primitive end of the series—the Hydridae and Corynidae. Systematists have long regarded the tentacles as a primary basis of distinction, special stress being laid upon their capitate or filiform condition and their distribution upon the hydranth body. This basis being adopted, the capitate and scattered tentacles of *Annulella* place it definitely in the family Corynidae, but there are clear affinities in the multiserial endoderm of the tentacles, in the simple budding, and in the basal disc and bulb to members of the family Hydridae.

In the Corynidae, where, agreeing with Mme. Motz-Kossowska (1905, p. 45), I would place *Tiarella*, in preference to the position with the Pennaridae assigned to it by Schulze, there is no genus closely comparable to *Annulella*. But it bears some relationship to *Tiarella* from which it differs most markedly in possessing scattered tentacles, and beyond which it has advanced in the specialization of its basal bulb and of the nematocyst rings on its tentacles. In respect of the distribution of tentacles and of the general absence of perisarc except on the basal extremity, *Annulella* approaches *Myriothela*, and, since no more satisfactory alternative presents itself, I rank it with this genus in the sub-family Myriothelinae.

In these days of many tentative classifications misunderstanding may be avoided if I state that I consider the family Corynidae to contain those Gymnoblastic Hydroids in which the tentacles are all capitate and are either scattered or distributed in several whorls; and that in its sub-family Myriothelinae I would place such Corynids as possess scattered tentacles, are solitary, and lack a supporting skeleton of perisarc.

GENERIC AND SPECIFIC DIAGNOSES OF *ANNULELLA GEMMATA.*

Annulella,[1] nov. gen.

GENERIC CHARACTERS.

Trophosome.—Ployps solitary and naked, with conical proboscis, and long, scattered, capitate tentacles bearing nematocyst batteries arranged in many rings and furnished with solid multiserial endoderm. During their fixed stage the polyps are attached by an adherent base, connected to them by a narrow neck and enclosed in perisarc. Multiplication by vegetative reproduction is the rule.

Gonosome.—? Gonophores producing free medusae.

Annulella gemmatta,[2] nov. sp.

SPECIFIC CHARACTERS.

Minute solitary polyps, 0·15 mm. to 1·0 mm. in height, bearing from 4 to 12 scattered capitate tentacles with nematocyst rings (nodes) along their whole length, and delicate solid endoderm. Tentacles and polyp-body are furnished with two types of nematocysts (macrocnides and microcnides). The polyp is alternately fixed and free, escaping from its basal bulb by rupture of the connecting neck, and again developing a new basal bulb by a modification of its proximal end.

Reproduction is normally asexual, by means of buds set free in a planula-like stage, by means of the detached basal bulb, and possibly by means of longitudinal fission. The type of sexual phase is not known with certainty.

Locality.—A brackish pond, Port Canning, Lower Bengal, India.

Type Specimens.—In the collections of the Indian Museum.

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[1] Feminine diminutive from Lat. *annulus,* a ring, signifying the ringed tentacles.
[2] Lat. *gemmatus* – budded.

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