ON TWO NEW SPECIES OF THE HYDROID MYRIOTHELA

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MYRIOTHELA PENOLA sp. nov.

Origin of the Material

Two specimens of *Myriothela penola* were found by the British Graham Land Expedition 1934–37 floating alongside R.Y. *Penola* in a creek at the Argentine Islands. Ice was floating on the surface of the water, which was about 2 fathoms in depth. Both specimens were attached to the apex of a pennatulid, a species of *Virgularia*, which had been torn from its substratum. The soft tissue of the pennatulid was absent from the upper 10 cm. of the animal, and the hydroids were attached directly to the horny axis. One apparently mature female individual measures 850 mm. in length and bears actinula larvae ready for liberation. The smaller male specimen is about 55 mm. long and bears very young blastostyles and rudimentary gonophores. The specimens were preserved in formalin after narcotization with tobacco.

General Description of the Hydroid (pl. I, fig. 10)

Tentacles are restricted to the distal $\frac{5}{6}$ of the hydranth. This region is tapering in shape, about 75 cm. long with a diameter at the oral end of 7·5 mm. increasing to 30 mm. proximally. The aboral $\frac{1}{6}$ of the hydranth, about 10 cm. in length and 12 mm. in diameter, is devoid of body tentacles, and bears numerous lobed blastostyles carrying tentacles on the lobes. The hydrorhiza is in the form of adhesive tentacles which spring from the base of the hydranth and from some of the proximal blastostyles. There is no perisarc, but the adhesive tentacles, when attached, are capped by a chitinoid disk. The species is dicœcious, an immature male and a mature female are known. The colour of the living animal closely resembles that of *M. austro-georgiae* (Jäderholm, 1905, pl. 1), the tentacle bearing zone being bright orange, the gonophores white, and the blastostyles ranging from orange to light greenish-brown. A coloured sketch was made of the living animal which has enabled a direct comparison to be made with the coloured plate of *M. austro-georgiae*.

Nematocysts

No nematocysts have been seen in the discharged state, but four types can be seen in sections (fig. 1). Similar preparations have been made of *M. cocksi*, because the nematocysts of this species have been described by Weill (1934). In *M. penola* mature haplonemes have been found only on the younger and larger body tentacles, and on the tentacles of small young blastostyles, but the other three types occur on the body wall and on older tentacles of both hydranth and blastostyles. Details of the distribution of the nematocysts are given with the description of the various parts.

Desmonemes are of variable size. The capsule measures 9–18 μ, and contains a thick thread coiled into about $2\frac{1}{2}$ turns. The thread stains red and the capsule contents remain unstained with Mallory's triple stain. The lasso thread is conspicuous and the cnidopod is very stout and anchored by numerous rooting threads to the fibrils of mesogloea in the capitulum of the tentacle. These roots do not appear to penetrate into the mesogloea, but end as darkly staining thickenings on the ends of

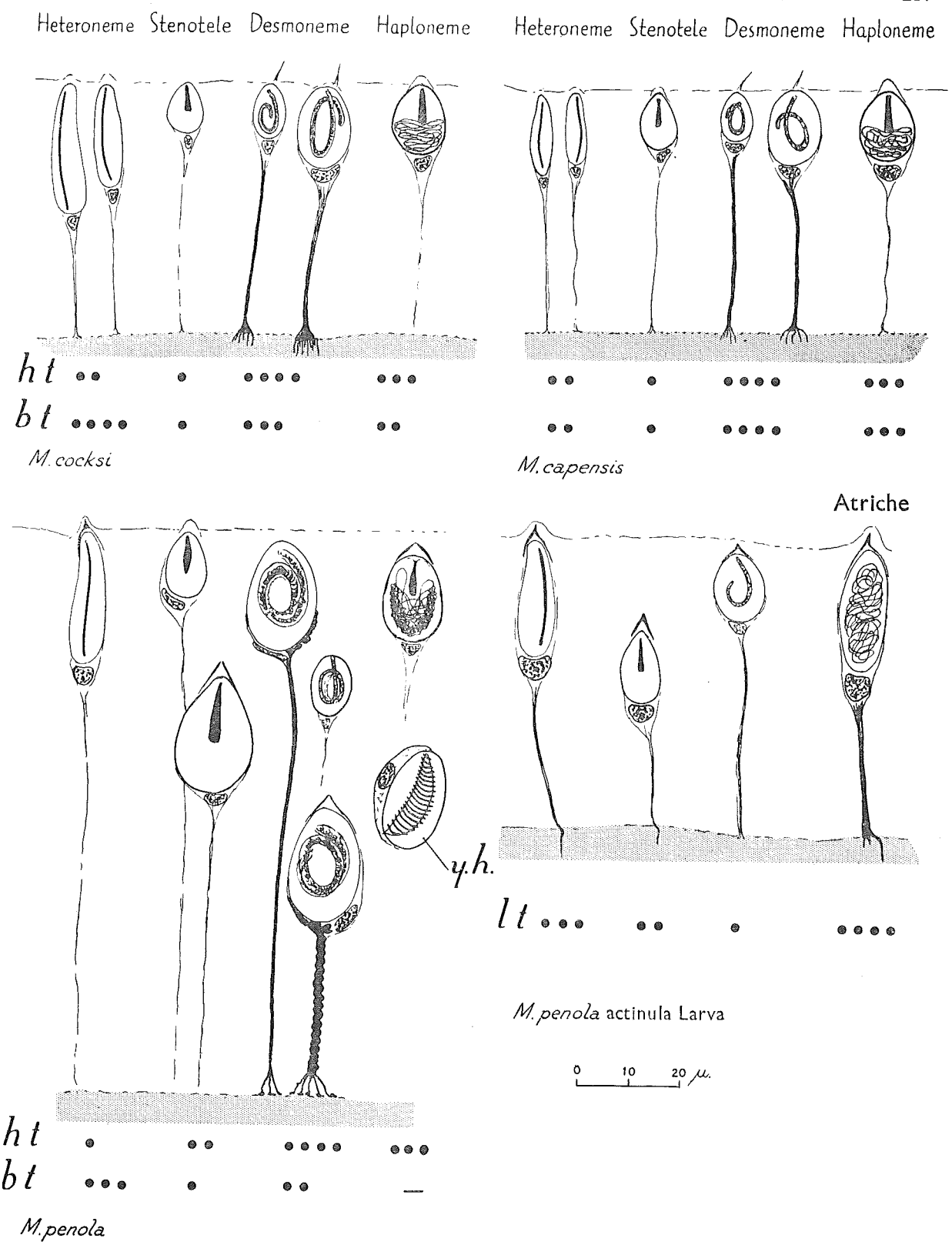

FIG. 1.—Diagrams illustrating the composition of the cnidome of *M. cocksi*, *M. capensis*, and *M. penola*. The relative abundance of the different types of nematocyst on the body tentacles "h.t.", on the blastostyle tentacles "b.t.", and on the long provisional tentacles of the actinula is shown by the number of black dots below each type. The mechanical tint represents the mesogloea.

the fibrils (pl. III, fig. 22). When a desmoneme is situated deeply in the ectoderm the cnidopod fibre appears to be tightly twisted in a spiral, but as the capsule approaches the surface of the epithelium the cnidopod elongates and its coils become straightened (pl. III, figs. 22 and 23). These cnidopods are much stouter than those of other types of nematocyst in *M. penola*.

Haplonemes are almost uniform in size, the ovoid capsule measuring 13 × 9 μ. The capsule contents stain little with Mallory's triple stain, and the thread forms a refringent yellowish basal mass of predominantly transverse coils. The developing haplonemes from the tentacle nurseries show the thread coiled in about 20 regular transverse turns (fig. 1, "y.h.").

Heteronemes are of two types, both showing blue-grey capsule contents and a red axial body after Mallory's triple stain. Those with an elongated pyriform capsule are fairly uniform in size, attaining 20 × 5–6 μ, and they show a slender axial body of almost even thickness. Ovoid *stenoteles* are variable in size, the capsule measuring 10 × 7 to 18 × 13 μ. The axial thread can only be seen in the upper half of the capsule and increases in thickness towards the middle of the capsule.

The capitula of the transitory larval tentacles of the actinula are mainly armed with a type of nematocyst unlike those of the adult. This presumably is comparable with the atriche of the actinula of *M. cocksi*. The capsule is ellipsoid (or possibly ovoid), 18 × 7 μ, and contains a fine thread staining purplish with Mallory's triple stain, the capsule contents remaining unstained. The cnidopod is well developed, appearing brilliantly red with the above stain, and shows one main rooting process sunk into the outer part of the mesogloea (pl. IV, fig. 29).

Body Wall

The body wall is about 200 μ in thickness at the oral end and increases to 400 μ in the proximal part of the tentacle bearing zone (it has not been sectioned in the blastostyle zone). The *ectodermal* epithelial cells are much elongated and are covered by a thin cuticle (pl. III, fig. 25, "cu."). The superficial cytoplasm of these cells contains a variable number of fine granules which may form a dense superficial layer; they stain black with iron haematoxylin and red with Mallory's triple stain. These granules are present everywhere, but are more numerous on the tentacles, blastostyles, and hydrorhiza (fig. 6 and pl. II, fig. 19) and most abundant on degenerating tentacles (see p. 261 and p. 264). Nematocysts lie at various depths in the ectoderm outside the muscle and mesogloea layer, desmonemes being the most frequent type. The mesogloea forms a solid cylindrical sheet, its thickness of 45–90 μ being greatest towards the aboral end. Longitudinal ridges of mesogloea project from this sheet into the ectoderm and bear the longitudinal muscle fibres over their surfaces. All other ectodermal elements are excluded from the furrows between the ridges. Towards the oral end where the musculature is more compact, the ridges project for 25–35 μ and are set at intervals of 10–15 μ or less (pl. III, fig. 28), while at the aboral end of the tentacle zone the ridges are 120 μ deep and set at intervals of about 30 μ.

The *endodermal* epithelium forms a regular peripheral layer of columnar cells with their circular muscle processes lying against the smooth inner surface of the cylinder of mesogloea. Most of these cells are binucleate with scanty, lightly staining

cytoplasm; many are probably ciliated. Gland cells are irregularly distributed. At intervals of about 0·3–0·5 mm. endodermal villi project into the enteron forming longitudinal ridges 1·5 mm. deep (fig. 2). They are mainly parallel, and 80–150 may be seen in one transverse section. The free edges of adjacent villi occasionally unite (this is probably caused by their manner of growth, see p. 262). A flange of mesogloea 7 μ or less in thickness projects into each villus separating the two layers of endoderm. The peripheral $\frac{1}{2}$–$\frac{3}{4}$ of each villus is composed mainly of cubical vacuolate cells, each possessing two similar nuclei, very little cytoplasm, and sometimes a few nutritive spheres. Gland cells lie among the vacuolate cells in the upper part of the hydranth. The free inner $\frac{1}{4}$ or $\frac{1}{3}$ of each villus is composed of darkly staining cells which are mostly binucleate and contain coarse granules of various sizes. These cells probably represent the apical cells restricted to the extreme edge of the villus in other species, and they probably carry out intracellular digestion. In some parts the darkly staining edges of the villi are in a disintegrating condition. This may be an artefact, or it may indicate that disintegration and casting off of parts of the villi occur in *M. penola* as in *M. cocksi* (Allman, 1875). I have not been able to find such a condition in the available specimens of *M. cocksi*; and the process described by Allman may thus be intermittent in occurrence. A more detailed description of the histology of the endoderm of the hydranth body is not possible owing to damage caused by the folding and bending of such a large animal since it was preserved. There is no reason to believe that cell elements described for other species and not mentioned above are in reality absent from *M. penola*. The enteron of the main body of the hydranth is continued into the blastostyles and into the hydrorhiza tentacles.

Body Tentacles

About 330,000 tentacles cover the distal 75 cm. of the hydranth. The tentacles are 0·5–2·5 mm. in length, becoming smaller towards the proximal part of the body. The tentacles on the oral few centimetres are largest and most elaborate in structure, and the smaller tentacles, except for those round the mouth (see p. 262), show progressive stages of degeneration. The fully formed tentacle bears a rounded capitulum 0·6 mm. in diameter, the stem being 0·4 mm. or less across and sharply demarcated from the capitulum. The structure of the tentacle is more elaborate than in any hitherto described species of *Myriothela*, and is shown diagrammatically in fig. 2. The mesogloea is represented by heavy black lines, and the external longitudinal and internal circular muscles have been omitted from the figure. In the capitulum the mesogloea is produced externally into a pad of radial fibres up to 180 μ in length. This is covered by an ectodermal layer of 60 μ with the cell nuclei lying at various levels. Nematocysts are close together through the whole ectodermal thickness, and they do not form mainly a peripheral layer as in some species. Desmonemes with very stout anchoring cnidopods (see p. 256) are most numerous. In large young tentacles haplonemes are next in abundance and occur all over the capitulum, but in ageing tentacles situated only a few centimetres behind the mouth and post-orally no mature haplonemes are found. Stenoteles are always present and various in size, and they become more numerous as the haplonemes disappear in older tentacles. Heteronemes of uniform dimensions are always present but are the least abundant

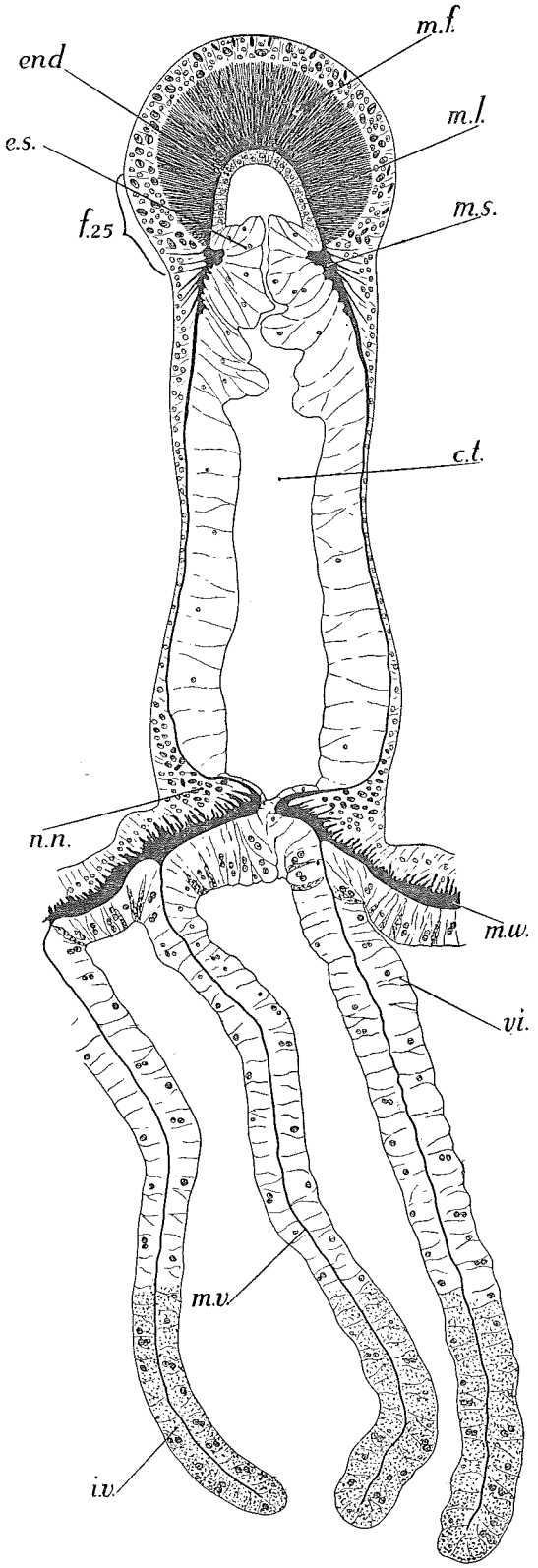

FIG. 2.—*M. penola*. Diagrammatic transverse section of hydranth body, from about 15 cm. behind the mouth, showing a tentacle in sagittal section and the endodermal villi. The mesogloea is shown by heavy black lines and the musculature is omitted. × 77.

type. The endoderm forms a regular layer of darkly staining small columnar cells lining the capitulum.

At the junction of the capitulum and stem a sphincter of elongated endodermal cells leaves a narrow channel connecting the cavity of the capitulum with that of the stem. These cells resemble those of the stem in staining reactions. This sphincter is supported by a thick ring of mesogloea bearing internal circular ridges which are covered by well-developed circular muscle fibrils (text-fig. 2 and pl. III, fig. 25 "c.m.") Externally this ring of mesogloea sends processes out into the ectoderm.

The stem of the tentacle is covered by a thin ectodermal epithelium of 6–15 μ which is almost devoid of nematocysts, and is lined by lightly staining cubical or columnar endodermal cells which are extensively vacuolated and which surround a wide cavity. The endoderm is continuous with that of the body through a narrow basal perforation of the mesogloea (fig. 2). Whether a narrow channel putting the lumen of the tentacle into communication with the general enteron exists could not be determined with certainty; most sections do not show any clear channel through this endoderm although the mesogloea is perforated. Where the mesogloea of the tentacle converges towards the body wall mesogloea around the perforation, the ectoderm is thickened and is richly provided with developing nematocysts, appearing to form a nursery from which nematocysts migrate. The most abundant type in the nursery is a developing haploneme (fig. 1 "y.h."). I am indebted to Dr. Weill for its identification. Stenoteles are next in frequency followed by heteronemes. Young desmonemes are frequent, but fully formed ones are rare.

The smaller tentacles covering the middle and lower part of the tentacle zone are undoubtedly older and in process of dedifferentiation and absorption. The majority are 1–0·5 mm. in height, but those at the proximal edge of this zone are smaller still. The structure of the tentacles becomes simpler with decrease in size, the nematocysts become fewer, and the nursery may appear almost worked out. The endodermal valve below the capitulum and the supporting rim of mesogloea disappear. In longitudinal section such a tentacle resembles those of smaller species such as *M. capensis* (fig. 7, *b*). The capitulum then shrinks and merges into the stem and the pad of radial mesogloea fibres becomes shorter, the height of the pad being 18 μ in a tentacle 0·45 mm. in length. The stem shortens and its ectoderm thickens and becomes indistinguishable from that of the capitulum. The superficial granules in the ectodermal cells (see p. 258) become increasingly abundant as the tentacle shrinks.

In the fully formed tentacles near the mouth, which are those most essential for feeding, the presence of the supported muscular sphincter at the base of the capitulum must make possible the closure of the endodermal canal. This will enable the turgidity of the capitulum to be maintained during movements of the tentacle. Serpentine body movements of a feeding *Myriothela* have been described by Billiard (1921), and if there is an opening at the base of the tentacle, pressure changes of the enteric fluid may be transmitted to the tentacle, but need not pass the capitular sphincter.

Growth of the Body

That growth in length of the hydranth body takes place most actively at the extreme oral end is indicated by the structure of the body wall, and by the position

of the young tentacles. The endodermal villi become less deep and disappear just within the edge of the mouth. Immediately behind the oral union of ectoderm with endoderm a thin layer of material can be seen between the two epithelia, but it stains in the same manner as does the cytoplasm of the cells. Post-orally this layer thickens and gradually takes on the blue colour with Mallory's triple stain which is typical of mesogloea, and when considerable thickness is attained the external lamellae begin to appear and become larger with increasing distance from the mouth. Such a series of developmental stages of the massive mesogloea layer would be expected to be found in this position if linear growth takes place actively at the oral end. On the ectodermal side of the mouth rim can be found a few small tentacles which are undoubtedly young. They are rich in nematocysts and their capitula are quite distinct from the stem, although both may be half the size of these parts in a fully formed tentacle, and their apical mesogloea fibrils are well developed. Tentacles reduced in size by degeneration do not show these features (see p. 259), and the small tentacles below the oral 6 cm. show progressive stages of degeneration. Thus new tentacles arise at the oral end, but others must also grow between existing tentacles as the body increases in diameter.

If the tentacle bearing zone increases in length mainly by a circumoral growth zone, its growth in diameter must take place gradually throughout much of its length as the greatest diameter is found in the older lower part of the tentacle bearing zone. The union of the free ends of some of the endodermal villi is indicative of increase in diameter after the original villi have been formed. This can be seen in the developing spadices of the gonophores where increase in size leads to sub-division of some of the original villi, a peripheral division of the villus taking place progressively from without inwards as the diameter of the spadix increases.

At the proximal end of the tentacle bearing zone the dedifferentiating tentacles become completely absorbed. The body wall contracts in diameter and young blastostyles make their appearance (pl. I, fig. 10, "z. y. b."). The blastostyles increase in size post-orally. Full sized blastostyles are absent from the oral 2 cm. of the blastostyle bearing zone (fig. 10) although they are present elsewhere. In both specimens some of the small blastostyles are appearing before the tentacles are completely absorbed at the junction of the tentacle and blastostyle bearing zones. Thus it may be concluded that the blastostyle bearing zone increases in length at its oral end at the expense of the tentacle bearing zone.

Blastostyles

The proximal $\frac{1}{6}$ of the larger hydranth bears about 300 mature blastostyles 20–25 mm. in length, and a smaller number of shorter immature blastostyles situated at the distal end of this region and in between the larger blastostyles (pl. I, figs. 10 and 11, text-fig. 5, *a* and *d*, and pl. II, fig. 15). Mature blastostyles are irregularly lobed or branched in their middle and distal parts; this branching is absent from young blastostyles and from those of the smaller specimen (fig. 5, *d*). Short tentacles are borne on the blastostyle lobes, and where these are absent the tentacles occur on the main axis. A description of the structure of a mature blastostyle and of the structure, development, and degeneration of the blastostyle tentacles from the larger specimen follows.

The small blastostyles of the smaller specimen are simpler both externally and internally.

The *wall* of the blastostyle (pl. III, fig. 26) is a little thinner than that of the main hydranth, and resembles the latter with certain modifications.

The wall is about 180 μ thick. The ectoderm forms a regular epithelium with nuclei situated midway between the surface and the mesogloea. The superficial granules (see p. 258) below the cuticle are few at the base of the blastostyle and become progressively more numerous towards the apex. Nematocysts are absent except on the lobes bearing developing tentacles; here a nematocyst nursery may be found close to the growing tentacles.

The mesogloea is much less robust, the solid lamella being only 8–10 μ thick and the outer longitudinal ridges 9–18 μ in depth. These ridges are absent from the tentacle-bearing lobes and from tracts on the main blastostyle leading to the lobes. In the zones where the ridges are disappearing they become fewer, but often deeper, projecting farther into the ectoderm.

The endodermal cavity is continuous with that of the main hydranth. The endodermal villi, about 1 mm. or less in depth, are more frequent than in the hydranth body and their supporting mesogloea is less thick. The villi are separated peripherally by acute grooves lined with ciliated cells which also spread over the faces of the villi to a distance of 40–80 μ (pl. III, fig. 26, "f."). Gland cells are numerous at the base of the grooves lying between the ciliated cells. Many of these grooves pass directly into the lumen of the spadix of the gonophores. The free parts of the villi are composed almost entirely of vacuolate cells, gland cells are few, and the apical cell zone is almost or entirely absent (pl. III, fig. 26). A few nematocysts are sometimes present near the apical cells where these occur. The vacuolate cells each possess two similar spherical nuclei; they may contain no nutritive spheres, as in fig. 26, "vc.", but near developing gonophores or tentacles nutritive spheres are frequent.

The villi show various physiological and morphological states in different parts of the blastostyle. In the growing lobes carrying developing tentacles the vacuolate cells are young. Their nuclei are the same as elsewhere, but the cells are smaller with dense cytoplasm and a turgid appearance, the free margin being often strongly convex. Nutritive spheres may or may not be present, and stages in the formation of the vacuolate condition can be seen (pl. II, fig. 16 "e.y."). The tongue-like villi of the growing spadices also show a juvenile condition (see p. 267 and fig. 4, "vi."), and the vacuolate cells here carry more nutritive spheres than in any other region. Mature villi from the middle region of the blastostyle have been described above, but distal to the gonophores the villi are senile. No food reserves are present here and the vacuolate cells have lost almost all their cytoplasm. The gland cells are shrunken or absent, and the ciliated cells in the grooves between the villi have almost or entirely disappeared.

The *tentacles* of the blastostyle, unlike those of the hydranth body, are not clearly divisible into capitulum and stem (pl. II, fig. 17, "j."), and their bases are demarcated from the blastostyle by a constriction (pl. II, fig. 15. "t.2" and fig. 17). Fully formed tentacles are present only in the middle part of the blastostyle (fig. 5, *a*, "m.b.t."; pl. II, fig. 15, "t.2"). The apex of such a tentacle is rounded and composed of regular columnar ectodermal cells covering a pad of mesogloea fibrils about 25 μ in length

(pl. II, fig. 17). Nematocysts occur only at the apex of the tentacle where they form a peripheral layer of radially arranged and closely packed heteronemes and occasional stenoteles. In the deeper parts of the ectoderm a few heteronemes and stenoteles can be found, but they are orientated in no particular manner. Larger desmonemes, strongly anchored to the mesogloea (see p. 256), are most numerous in the deeper parts of the ectoderm. The convolutions of their cnidopods become drawn out as the capsules approach the surface (pl. III, figs. 22 and 23). Haplonemes have only been found in tentacles on small young blastostyles. Proximally the tentacle increases in diameter, and the stem mesogloea forms a simple lamella. The endodermal lumen does not communicate with that of the blastostyle, a layer of mesogloea, covered on both sides by endoderm, spanning the tentacle base. The tentacular endoderm lacks gland cells, ciliated cells, and nutritive spheres. Basally and distally this epithelium is cubical and laterally it is thicker and columnar. The apical endoderm lacks inclusions, but elsewhere fine granules staining red with fuchsin lie in the distal parts of the cells.

The *development of a tentacle* starts in the endoderm of the blastostyle. A diverticulum grows into the overlying ectoderm and becomes nipped off by the mesogloea. A hollow endodermal vesicle thus lies in the ectoderm with its covering mesogloea continuous with that of the blastostyle wall. The endodermal vesicle increases in size and elevates the overlying ectoderm. At the same time the blastostyle wall here bulges outwards so that the developing tentacle becomes borne on a lobe from the main axis of the blastostyle. The endodermal vesicle continues to increase in size, and the apical mesogloea fibrils start to develop; the overlying ectoderm thickens and the peripheral layer of nematocysts make their appearance (pl. II, fig. 16). Growth continues; the superficial ectodermal granules (see p. 258) become more abundant, and the endodermal epithelium becomes differentiated into apical, basal, and lateral parts. The full development of the mesogloea fibrils and of the nematocysts results in the mature tentacle already described (pl. II, fig. 17).

Degeneration of the tentacle follows. The lateral endoderm thickens and the elongated cells become charged with fuchsin-staining granules. The mesogloea fibrils gradually shorten (pl. II, fig. 18) till they vanish (fig. 19), the nematocysts disappear, and the apical endoderm becomes indistinguishable from that of the lateral region, the cells of both becoming distended with granules. The base of the tentacle spreads out, and the basal endoderm, also filled with granules, becomes stretched (fig. 19). Finally the shape of the tentacle becomes irregular and the apex invaginates or breaks down (fig. 5, *a*, and pl. I, fig. 14, "s.b.t." and pl. II, fig. 15, "t.3"). The ectodermal granules become increasingly abundant, but unlike those of the endoderm, they remain in a surface layer (fig. 19).

Mature *gonophores* of the female only have been seen, the gonophores of the small male specimen being immature. Not more than about 10 gonophores lie on each mature female blastostyle, and a smaller number, sometimes as many as 7, lie on some of the male blastostyles, many of which lack gonophores. The gonophores of each blastostyle form a graded series of developmental stages, all of which are different. The older gonophores are situated distal to the younger ones which may be scarcely visible externally (fig. 5, *d* and pl. II, fig. 15 "g.2"–"g.10"). Usually one gonophore only approaches maturity at a time on each blastostyle; one blastostyle of the larger specimen appears to be exceptional in bearing two advanced gonophores.

The female specimen carries 19 mature gonophores, they are about 7·2 mm. in diameter and contain an actinula larva almost ready for liberation (pl. I, figs. 10 and 11, pl. II, fig. 15 "g.10"). In two of these gonophores the wall has split and the actinula is almost free (pl. I, fig. 11 "a.e." and fig. 5, *a*). Many other blastostyles lacking an old gonophore show a shrunken knob or scar which represents the remains of a gonophore which has recently liberated its larva. The largest gonophores, apart from the above, are uniform in size and do not exceed 2·6 mm. in diameter. They are numerous, but not more than one is present on each blastostyle (pl. I, fig. 11, and pl. II, fig. 15, "g.9." In these gonophores the definitive ovum is very small, about 110 × 80 × 80 μ. The specimen must have been collected during the period of distribution of its larvae and the gonophores of 2·6 mm. diameter would have become mature in the following breeding season.

The older gonophores of the immature male specimen are of about the same size and do not exceed 0·6 mm. in diameter. These gonophores are clearly young. Their spermatocytes are equal in size and lie about 12 cells deep over the spadix, and these gonophores correspond to a stage of development intermediate between those of gonophores "g.5" and "g.6" of the female specimen (pl. II, fig. 15).

The mature female gonophore is cryptomedusoid in structure with no trace of canal system. A velar opening must be formed at a stage intermediate between the two larger types of gonophore mentioned above (pl. II, fig. 15 "g.9" and "g.10"), but such a stage is absent from the specimens. The gonophores are sessile and attached by a base 0·9 and 1·9 mm. in diameter respectively in gonophores of these two sizes. The structure of the gonophore is shown in fig. 4 and in pl. II, figs. 20 and 21, and will be described more fully with the account of the development of the gonophores given below.

Development of the Gonophores

A single blastostyle from the large female specimen is shown in pl. II, fig. 15. This blastostyle has been sectioned and the development of its gonophores followed. The 10 gonophores are numbered in order of age. The youngest, "g.1" lies near the junction of the blastostyle with the hydranth, and gonophores "g.1", "g.3", and "g.6" are situated on the side of the blastostyle not visible in fig. 15. A gonophore-bearing blastostyle from the immature male specimen has also been sectioned.

In the *female* the earliest stage sectioned, "g.1" fig. 3, *a*, shows the rudiments of the spadix and bell endoderm ("r.") and of the subumbrella and spadix ectoderm ("r.e."). The former is a closed vesicle with a small lumen completely cut off from the enteric cavity. It lies mainly in the ectoderm, the mesogloea being elevated by it. The cells composing this rudiment are much smaller than those of the main blastostyle endoderm and their cytoplasm is dense and darkly staining. The rudiment is raised peripherally into a rim. The subumbrella ectodermal rudiment or "nodule médusaire" of Benoit (1925), is a rounded mass of cells which lies above the endodermal rudiment and sinks down into the hollow within the rim of the latter. The overlying ectoderm is thickened, and projects slightly above the general level. A younger stage showing the origin of these two rudiments is not present on this blastostyle, but it is probable that the ectodermal rudiment may arise from the endodermal rudiment in *M. penola*

just as Benoit (1925) described for *M. cocksi*. In three of the younger gonophores the central part of the mesogloea separating the two rudiments is very thin and appears to be interrupted in the middle. Here the cells of the two rudiments seem to be confluent, and the cytology of the cells in the two rudiments is identical at this point, thus suggesting that the mesogloea has not yet completely united after the "nodule médusaire" has passed through it from the endoderm.

With increase in size of both rudiments the endodermal rim, which will give rise to the bell endoderm, grows up and gradually encloses the subumbrella ectoderm (figs. 3, *b* and *c*). This is completed by the fusion of the mesogloea-tipped edges of

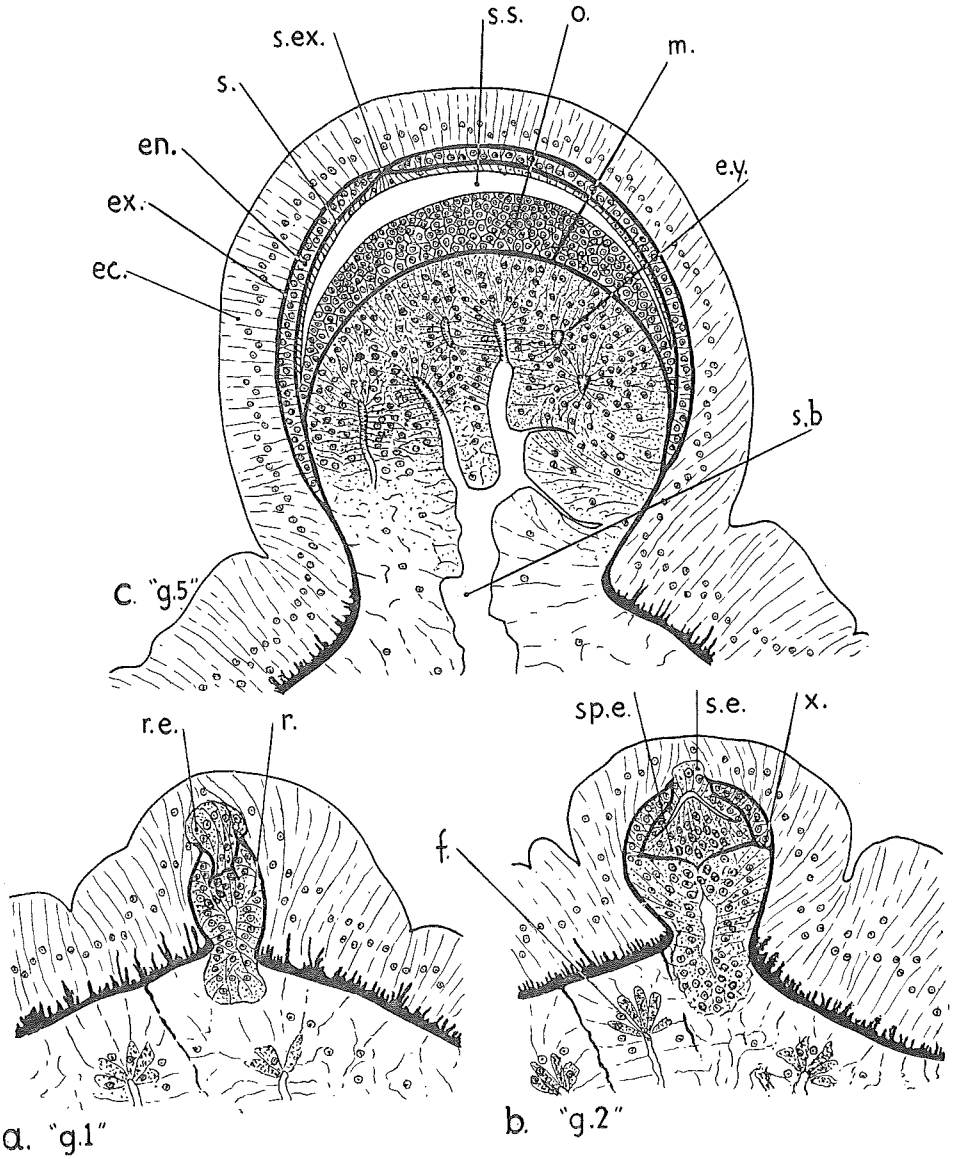

FIG. 3.—Diagrams representing sagittal sections of three stages in the development of the female gonophore of *M. penola*, from gonophores shown on the blastostyle in pl. II, fig. 15. Fig. 3, *a*, represents "g.1" which is situated on the invisible side of the blastostyle in fig. 15, fig. 3, *b*, represents gonophore "g.2", and fig. 3, *c*, represents gonophore "g.5". The mesogloea is shown by heavy black lines and the musculature is omitted. × 145.

the rim. This point of fusion (fig. 3, *c*, "s.ex."), where solid mesogloea excludes the endodermal layer, persists in later stages. The mesogloea lining the rim of endoderm grows outwards at the basal angle of the rim and fuses with the outer layer of mesogloea, so cutting off the endoderm of the bell from the main endodermal vesicle. This fusion is complete on the right side only in fig. 3, *b*, "x.").

The ectodermal rudiment becomes bilaminar as it increases in size. A thick layer covers the flat outer surface of the endodermal vesicle and gives rise to the germinal epithelium over the spadix; a thin outer layer becomes applied to the endodermal rim and will form the subumbrella ectoderm, the central space being the subumbrella cavity (figs. 3, *b* and *c*, "s.s."). The subumbrella ectoderm becomes very thin except below the point of fusion of the bell mesogloea (fig. 3, *c*, "s.ex."). The over-lying ectoderm forms the exumbrella covering, and thus all layers of the bell wall are laid down.

The main endodermal vesicle remains closed until the gonophore rudiment is larger than in fig. 3, *b*. As the vesicle grows its cavity elongates towards the axis of the blastostyle, and a hollow outgrowth in this direction finally puts this cavity into communication with the enteric space of the blastostyle at a stage intermediate between those shown in figs. 3, *b* and *c*. With further increase in size the endodermal vesicle bulges outwards to form the spadix (fig. 3, *c*), and its epithelium becomes furrowed so that tongue-like villi project into the central space. With further growth in diameter new villi are formed and fresh peripheral furrows are made, so that villi originally single sometimes becomes subdivided at their bases. The endodermal cells in young stages (figs. 3, *b* and *c*), and in the peripheral region against the mesogloea in older stages are small, uninucleate, and densely staining, and early become ciliated. Where the epithelium becomes continuous with that of the blastostyle the cells enlarge and lose their cilia and much of their cytoplasm (fig. 3, *c*, and pl. II, fig. 20). The villi are rounded in cross-section and lack muscles. They are entirely composed of vacuolate cells loosely attached to a core of mesogloea (fig. 4 and pl. II, fig. 20). These cells become larger, nutritive spheres appear in their cytoplasm, and some of them develop large vacuoles as they increase in age and become further removed from the growing peripheral epithelium (figs. 4 and 20). In young gonophores the vacuolate cells possess one nucleus (fig. 3, *c*), but in older stages almost all these cells are binucleate, so that the villi, except for the tips of a few of the larger ones, are composed of binucleate cells. No mitoses have been seen, and the origin of the binucleate condition is not known. The cytoplasm of the mature vacuolate cells of the spadix is more dense and granular than elsewhere.

Hardy (1891) first pointed out for *M. cocksi* that "the whole spadix is a specialized structure for the absorption of nutriment from the somatic fluid of the blastostyle, which nutriment is doubtless largely derived from the stored material of the vacuolate cells through the help of the somatic fluid." This must also be true for *M. penola*. Here ciliated grooves between the blastostyle villi lead into the ciliated grooves between the villi of the spadix (pls. II and III, figs. 20 and 26 "f"), and the surface of the latter appears to be ciliated in many places. Thus a route is indicated for the transport of food material to the spadix. In both *M. cocksi* (Hardy, 1891) and in *M. penola* the peripheral spadix endoderm, which lacks nutritive spheres, shows many fine radial spaces in the cytoplasm (fig. 4). These may be concerned with

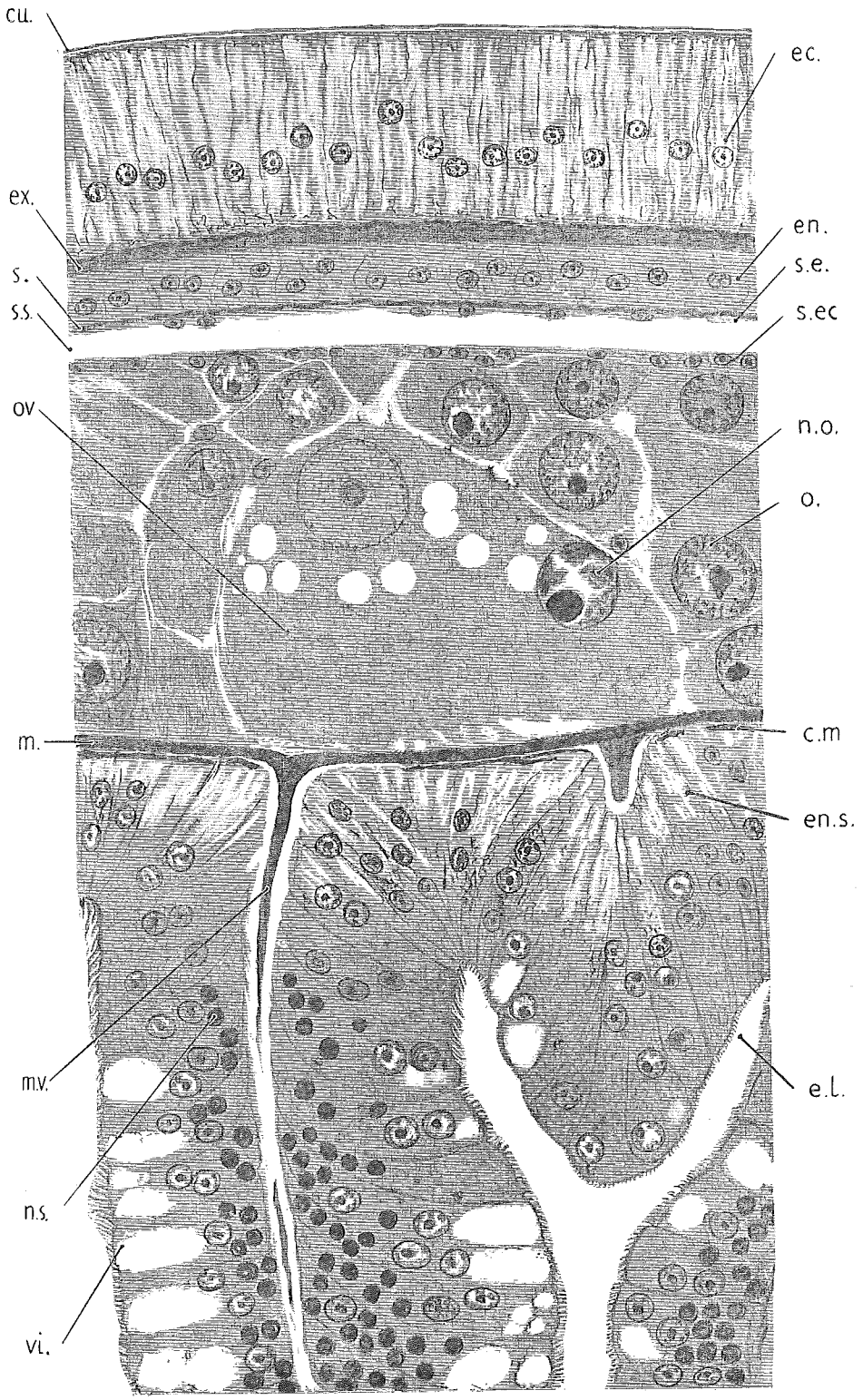

FIG. 4.—*M. penola*. Part of a section of gonophore "g.9" parasagittal to that shown in pl. II, fig. 20, and situated opposite the bracket marked "t.f.4". The gonophore wall is cut just to one side of the future velar perforation where the bell endoderm is excluded (see fig. 3, *c*, "s.ex."). The section passes through the definitive ovum which is in the process of uniting with the neighbouring oocytes; it shows one oocyte nucleus in its cytoplasm, which has not yet degenerated. The outer part of the endoderm with its villi is shown, see also pl. II, fig. 20. × 600.

the transport of nutriment from the lumen of the spadix to the germinal epithelium.

The cells of the multilaminar ectoderm covering the spadix are at first equal in size. The oocytes below the surface layer of cells start to grow (fig. 3, *c*) and enlarge most rapidly near the endoderm and towards the apex of the spadix; they lie about six cells deep. In the gonophores of 0·5 mm. diameter and over (fig. 4) a single large ovum is present at the apex of the spadix, almost underneath the point of fusion of the bell mesogloea (fig. 3, *c* "s.ex."), where the velar opening will be formed (see below). The youngest ovum observed was in gonophore "g.6" (a little younger than "g.7" in pl. II, fig. 15) and measured 24 × 15 × 24 μ, the largest oocytes being not more than 12 μ in diameter. Adjacent oocytes in the lower layers are incorporated into the ovum and their nuclei degenerate. In gonophore "g.9" (pl. II, figs. 15 and 20) the ovum measures 119 × 75 × 80 μ and lies just to one side of the future velar opening (fig. 4). No older ova have been seen.

A velar perforation of the bell is formed in mature gonophores of *M. australis* and *M. harrisoni* (Briggs, 1928, 1929, 1931), and a perforation is almost completed (fig. 9) in one gonophore of *M. capensis* described on p. 280. This gonophore is not quite mature, but it is much older than those at the "g.9" stage in *M. penola*. The younger gonophores of *M. capensis* exactly resemble those of *M. penola*, and it is probable that a velar perforation is formed in *M. penola* when the gonophore reaches an age intermediate between "g.9" and "g.10" (pl. II, fig. 15), and that the perforation is situated where the bell endoderm is interrupted by the fusion of the two layers of mesogloea (fig. 3, *c*, "s.ex."). It is unlikely that fertilization in *M. penola* occurs by way of the enteric spaces of the hydroid as it does in the hermaphrodite *M. cocksi* (see p. 286).

Gonophores of the age of "g.10" (pls. I and II, figs. 11 and 15) contain one actinula larva, and are stretched and degenerate in structure. The larvae are all orientated with the aboral end against the spadix and the oral end towards the position of the velar perforation. The long provisional tentacles of the actinula are coiled about the sides of the larva leaving the oral disk of the larva uncovered. These tentacles are visible through the stretched bell wall (fig. 11). The latter is entire, and its component layers can be recognized. Sections show a thickened zone in the distal part of the bell in which the two layers of mesogloea unite. The stretching of the tissue has obliterated further details. It is probable that this zone represents the closed velar perforation, the lips of which fused after entry of spermatozoa to the subumbrella space. The spadix is degenerate and flattened (pl. II, fig. 21) and no longer projects (as in fig. 20) into the subumbrella space, which is entirely occupied by the larva. Most of the endodermal villi of the spadix have been absorbed, and the remains are shrunken, devoid of food reserves, and deficient in cytoplasm (pl. II, fig. 21, "sp."). The mesogloea layer, which originally separated the germ cells from the endoderm, is exposed and adheres to the stretched egg membrane (fig. 21 "e.me.") which is now about 14 μ thick and encloses the larva. The external layer of this membrane stains red and the major part of the membrane stains blue with Mallory's triple stain (pl. IV, fig, 34, "e").

Two of the older gonophores show the beginning of the process of liberation of the actinula (pl. I, fig. 11, "a.e."). One of these shown in the photograph is traced in fig. 5, *a*, so that the details can more easily be identified. The gonophore bell has

split and shrunk back, forming a rim of tissue "g.s." round the flat spadix. The tentacles of the actinula have become less tightly packed, and the larva is retained only by the egg membrane which is attached to the spadix mesogloea (pl. II, fig. 21, "e.me.") Finally this membrane breaks down and the actinula becomes free. The gonophore is then represented by a shrunken rim of tissue on the blastostyle, often with a central perforation leading to the enteric space through the disintegrated spadix.

The development of *male* gonophores on the young specimen is not quite the same as that of the gonophores on the large female specimen. The rudiment of the endodermal part of the gonophore (fig. 3, *a*, "r.") appears at the earliest stage as a simple diverticulum of the blastostyle endoderm, the lumen of the two being continuous. It is probable that this difference between the male and female gonophores is not a sexual or a permanent one, but that it is connected with the great size difference of the two specimens and of their blastostyles (figs. 5, *a* and pl. I, fig. 10). The thin blastostylar endoderm of the small immature male allows the gonophore rudiment to be formed as in small species such as *M. cocksi* (Benoit, 1925), but in the large female specimen of *M. penola* the blastostylar endoderm is much thicker, and the endodermal gonophore rudiment is separated as a solid or almost solid vesicle which only later opens to the enteron of the blastostyle by growing through the thick endodermal epithelium. The further development of the male gonophores, as far as they are known, resembles that of the female.

Growth of the Blastostyle

The method of growth of the blastostyle is clearly indicated by the structure of its parts. On the blastostyle shown in pl. II, fig. 15, for example, the older gonophores are situated in progressively more distal positions. Fully developed tentacles are only found in the middle region of the blastostyle "t.2" where they are borne on small lobes; distal to these the blastostyle is almost bare of tentacles, and here lies the oldest actinula-bearing gonophore. The terminal bunch of lobes carries only degenerate tentacles "t.3" (see p. 264). Below the zone of fully formed tentacles, tentacle-bearing lobes are little developed. A younger gonophore "g.9" occupies a relatively bare zone, and near this gonophore and below it lies a zone of young tentacles, some projecting, as "t.1", and others, younger still, are represented by endodermal vesicles which cause no external elevation. The endoderm in the upper $\frac{1}{3}$ or more of the blastostyle is degenerate and devoid of food reserves (see p. 264) and the ectodermal cells near the apex of the blastostyle are laden with granules (see p. 258). It is probable that after the liberation of the actinula from gonophore "g.10" the distal part of the blastostyle, with its degenerate tentacles and gonophore remains, would be either absorbed or thrown off, and that the proximal part would then elongate and develop. The mature tentacles "t.2" would become terminal, gonophore "g.9" would take the place of gonophore "g.10", and the young tentacles "t.1" would grow and replace tentacles "t.2", and another gonophore proximal to "g.1" would be initiated. Other blastostyles indicate that considerably more than their distal $\frac{1}{3}$ may be lost. With the increase in diameter of the blastostyle, and with the formation of baggy tentacle lobes, the mesogloea layer must become stretched, and the external ridges, characteristic of the lower half of the blastostyle, become farther apart and

obliterated and absorbed. Growth of the blastostyle thus appears to take place from the proximal end, a condition unlike the main hydranth where growth in length occurs mainly from the oral end.

Hydrorhiza

The hydrorhiza in the young individual is represented by adhesive tentacles arising from the base of the hydranth below the blastostyles. These tentacles are

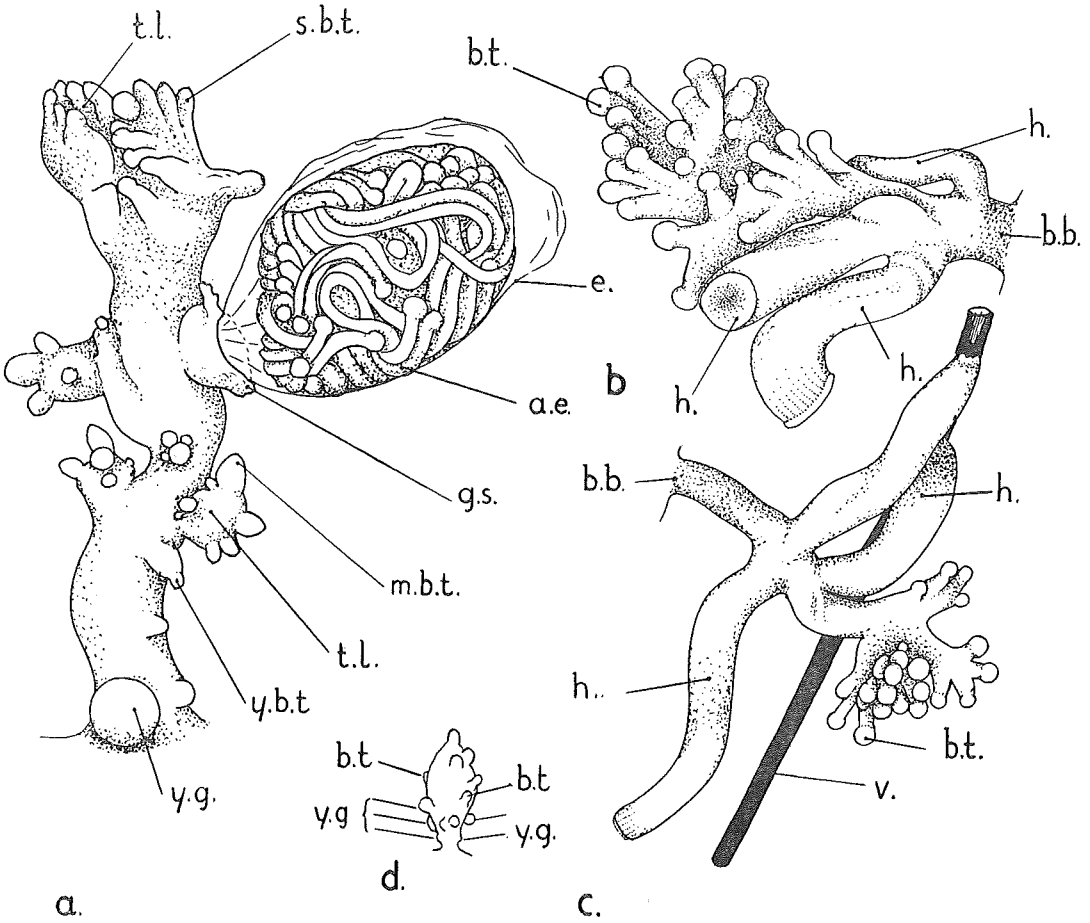

Fig. 5.—Figs. 5, *a–c*. Tracings of parts of *M. penola* shown in the photographs on pl. I, figs. 11 and 14, and orientated as in the photographs. Fig. 5, *a*, single blastostyle bearing an actinula larva retained only by the adhesion of the egg membrane to the spadix mesogloea, the gonophore wall having shrunk back "g.s." × 4. Fig. 5, *b*, blastostyle bearing three unattached adhesive hydrorhiza tentacles. × 4. Fig. 5, *c*, blastostyle bearing one unattached hydrorhiza tentacle and two which are attached to the substratum (the rachis of a *Vigularia*). × 4. Fig. 5, *d*, blastostyle from the immature male specimen. Similar blastostyles occur on the mature female specimen on the distal part of the blastostyle zone. ×4.

from 1–8 mm. in length and 1 mm. or less in thickness, and they end in a flat disk. About 30 are attached to the substratum and all appear stretched, the longer tentacles being attached farthest from the animal and appearing to pull out the base of the hydranth. A few more adhesive tentacles spring from the hydranth near the more basal blastostyles and are unattached. In the adult specimen the adhesive tentacles

are larger and more numerous, reaching a length of 12 mm. and width of 2 mm., but the dimensions are variable. The tentacles arise from the base of the hydranth below the blastostyles, as in the younger specimen, but also from the spaces between the lower blastostyles and from these blastostyles themselves. Up to three adhesive

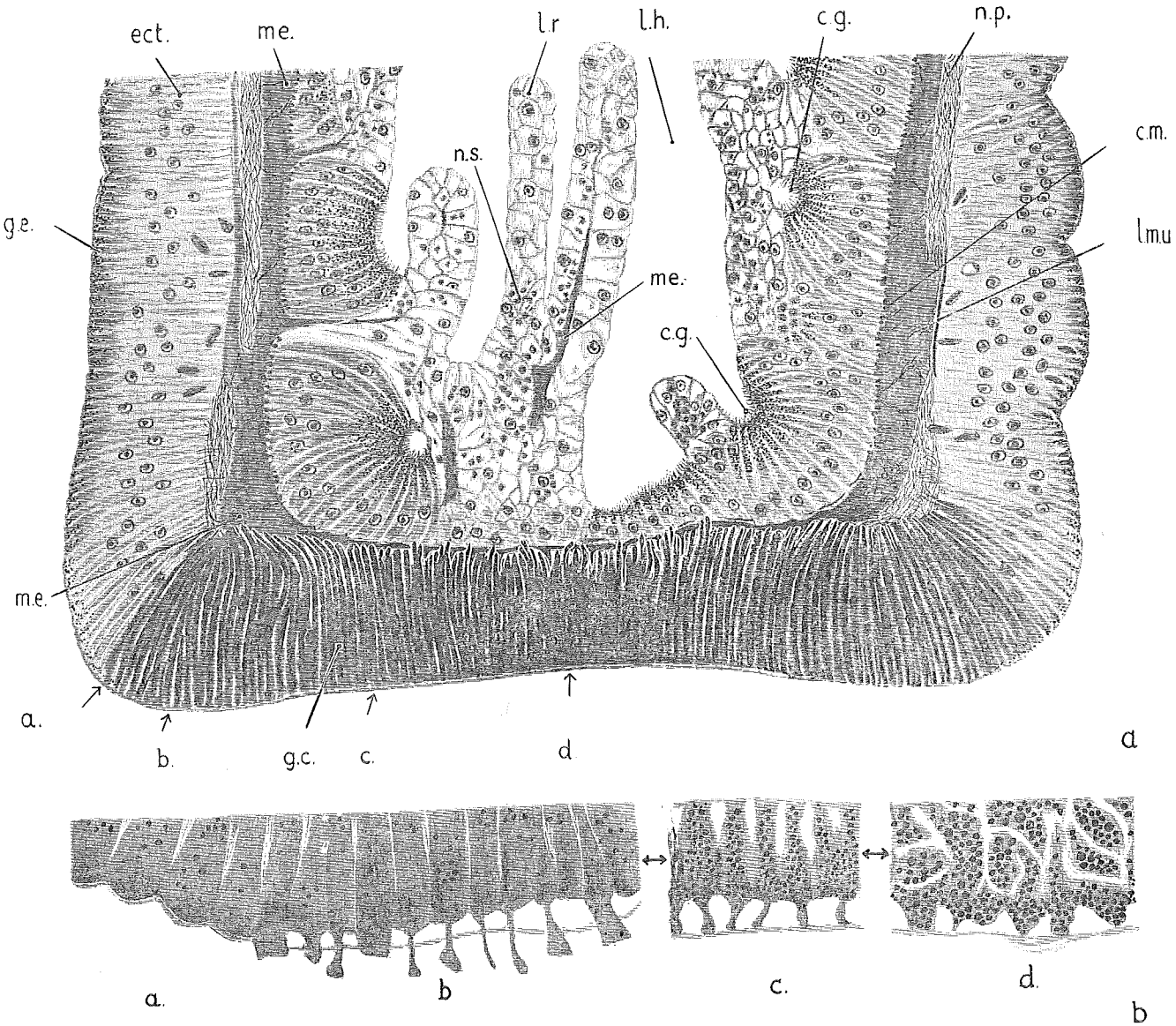

FIG. 6.—Fig. 6, *a*, shows a slightly oblique longitudinal section of a large adhesive hydrorhiza tentacle of *M. penola*. The grooves "c.g." and the ridges "l.r" are longitudinally orientated in the tentacle. × 140. Fig. 6, *b*, shows the outer part of the ectodermal epithelium in the regions *a*, *b*, *c*, and *d*, in fig. 6, *a*. × 426.

tentacles may be borne on the middle and basal part of one blastostyle. About 50 of these tentacles are attached to the horny axis of the *Virgularia* (pl. I, fig. 14), and a smaller number are free. In order to facilitate the identification of the structures shown in the photograph two of the blastostyles with their adhesive tentacles are traced in fig. 5, *b* and *c*. No perisarc is present on the unattached tentacle, but the

fixed tentacles adhere by means of a brown chitinoid layer situated between the flat end of the tentacle and the substratum. In section the young tentacles resemble those of the smaller species *M. capensis* (fig. 7, *c*). A simple layer of columnar endodermal cells surrounds a central cavity communicating by a wide opening into the general enteron. The mesogloea layer is thick laterally, and compressed and denser across the flat terminal disk. The ectoderm over the flat end of the tentacle is formed of very long and narrow cells. Their bases are either sunk into, or project through, the mesogloea, and they are laden throughout with granules of various sizes which stain crimson with Mallory's triple stain and almost black with iron haematoxylin. Nematocysts are present in the ectoderm of the stem but not in the terminal disk.

The adult unattached tentacle differs from the above in its greater size and complexity of structure (fig. 6). The mesogloea of the stem is longitudinally furrowed on the ectodermal side. The ectodermal nerve plexus is very thick in the stem and forms a layer over the mesogloea which fills the valleys between the ridges of mesogloea. Ectodermal muscles are feebly developed, but the circular endodermal muscles form a substantial layer. This may be correlated with the need for an unattached tentacle to stretch out in search of its substratum. Strands of nerve fibrils pass through the mesogloea to reach the endodermal muscles.

The endodermal layer is grooved longitudinally. The angles of the furrows are formed by ciliated columnar epithelium, the distal parts of the cells being laden with granules staining scarlet with Mallory's triple stain, but remaining undifferentiated from the cytoplasm with haematoxylin, eosin, light green, etc. The ridges are bilaminar, being supported by a flange of mesogloea. They are composed almost entirely of vacuolate cells containing large vacuoles, nutritive spheres, and other inclusions, and usually showing two nuclei. These ridges and grooves are continued on to the inner side of the terminal disk (fig. 6).

The ectodermal epithelium of the stem resembles that of other regions of the body, and the sub-cuticular layer of granules is well developed. Over the terminal disk the darkly staining granular ectodermal cells are inserted into the mesogloea as in the young tentacle (fig. 6 and pl. IV, fig. 31, "e.i."). Their granules are most numerous near the mesogloea, but occur throughout the cells of the middle part of the disk. Certain differences can be seen among these cells which may be interpreted as changes associated with adhesion to the substratum. At the margin of the disk, where the granule-bearing cells merge into the stem ectoderm, the granules are fewer; here the surface cuticle is raised into a cone over each cell, the cytoplasm remaining in contact with the cuticle (position "a.", fig. 6) ; in most regions of the body the surface cuticle is flat (pl. III, figs. 22, 25 and 26). Towards the middle of the disk the surface cuticle becomes raised off the cells, each of which puts out one irregular cytoplasmic lobe. These lobes are largest in position "b." (fig. 6), and most of them here project right through the raised cuticle. Farther towards the middle the cytoplasmic lobes are smaller and lie below the raised cuticle (fig. 6, "c."), and the granules previously abundant in the middle and basal parts of the cells, now occur in the peripheral zone as well. In the central part of the disk, where the granules are largest and most abundant, the cytoplasm appears to be breaking up into irregular zones, and the peripheral parts of the cells appear to have fused forming a continuous sub-cuticular layer (fig. 6, "d."), bearing broad lobes which also contain granules.

It was not possible to section an attached tentacle or to remove one undamaged from its substratum. It is probable that the structure of an attached tentacle does not differ materially from those of *M. capensis* which have been sectioned in this condition. Here the terminal ectoderm is replaced by a chitinoid disk which is anchored to the mesogloea and adheres to the substratum (see p. 281 and fig. 7, *d*). The chitinoid disk shows the same staining properties as do the terminal ectodermal granules of the unattached adhesive tentacle. It is probable that in *M. penola* the substratum is first held by the lobes of cytoplasm which penetrate through the cuticle, and that a subsequent breakdown of the terminal epithelium and a fusion of the granules results in the replacement of the epithelium by the chitinoid disk. This is dove-tailed into the mesogloea where the bases of the epithelial cells penetrated this layer.

Actinula Larva

The orientation of the actinula larva within the gonophore has been described (p. 269). Just before liberation the larva is pear-shaped and about 9 mm. long and 6 mm. wide (pl. IV, fig. 32). The mouth at the narrower end is not yet formed, and the oral pole is thickly beset with small tentacles 0·2 mm. long covering an area 1–2 mm. in diameter (pl. I, fig. 11 "t.o.", and pl. IV, fig. 32). These small tentacles also clothe the upper $\frac{4}{5}$ of the larva, and among them arise about 40 long larval tentacles bearing rounded capitula. The more distal of these tentacles are about 30 mm. long and the proximal ones are shorter. The basal $\frac{1}{6}$ of the actinula is covered with about 30 short hydrorhiza tentacles (pl. II, fig. 21 and pl. IV, fig. 32).

The *oral and the short body tentacles* (pl. IV, figs. 30, 33 and 34, "s.t.") have an ill-defined capitulum supported by a pad of short mesogloea fibrils. Nematocysts are most abundant distally. Heteronemes and stenoteles, slightly smaller than those of the adult, are abundant, desmonemes are few and small, and haplonemes are almost if not entirely absent. The endoderm surrounds a narrow central cavity, but this does not communicate with the main enteron, although the endodermal epithelia are continuous through a gap in the body wall mesogloea. The endoderm in the tentacle shows no regional differentiation as it does in those of the adult.

The capitulum of the *long larval tentacles* is well defined, and no pad of mesogloea fibrils is present. The capitulum is provided with a dense peripheral layer of atriches (pl. IV, fig. 29 "a.t." and pl. III, fig. 24). These nematocysts do not occur elsewhere in either larva or adult. The insertions of their large cnidopods into the outer part of the mesogloea give the latter a striated appearance (fig. 24, "m.o."). Among the atriches can be found a few heteronemes and fewer desmonemes and stenoteles. The endoderm surrounds a spacious cavity. Over the stem of the tentacle the ectoderm is produced into curious fluffy or dendritic processes (pl. IV, fig. 33, "ect.l."), in which heteronemes and stenoteles are present but orientated in many directions. The stem endoderm is very thick leaving a narrow central lumen which is continuous with that of the main enteron. The inner parts of the endodermal cells contain many fine fuchsin-staining granules. An endodermal valve is situated at the base of the tentacle, where the columnar cells are supported by a flange of mesogloea (this mesogloea does not show clearly in the photograph, pl. IV, fig. 30, "v.l.").

The *adhesive hydrorhiza tentacles* (pls. II and IV, figs. 21 and 32, "h."), about 0·6 mm. in length, are miniatures of those of the smaller of the two adults. Their cavities communicate with the enteron, and their flat ends are covered by columnar ectodermal cells, full of fuchsin staining granules, which are anchored into the mesogloea. The bases of some of these ectodermal cells can be seen to be projecting right through the mesogloea in the section shown in fig. 31, "e.i.". The endoderm is a simple and regular epithelium (compare adult, p. 273, fig. 6), a condition doubtless associated with the small size of the tentacle. The inner parts of the endodermal cells are laden with fuchsin staining granules, as in the larval tentacles (pl. IV, fig. 31).

The enteric cavity of the actinula is traversed by numerous tongue- and ribbon-shaped villi about 0·5 mm. long (pl. II, fig. 21, "vi."). They are mainly composed of large vacuolate cells containing nutritive spheres, and their cytoplasm is scanty. The peripheral endoderm between the villi is composed of numerous small uninucleate cells with darkly staining cytoplasm (figs. 21 and 33, "p.e."). These cells doubtless give rise to the binucleate vacuolate cells, gland cells, etc., as the animal grows.

Age and Rate of Growth

The methods of growth of the hydranth body and of the blastostyles and their appended organs have been described (p. 261 and p. 270), but the rate at which these processes take place is unknown. The condition of the two specimens of *M. penola*, however, enables various tentative suggestions to be made concerning the rate of growth and the age of the specimens.

There is probably a limited breeding season for the following reasons. The mature female shows a uniformity of condition among the larger gonophore bearing blastostyles. These each carry a series of gonophores, the largest of which are about 7·2 mm. in diameter and bear an actinula ready for liberation; on many of the blastostyles this actinula has already been liberated. The second largest gonophores are about 2·6 mm. in diameter, and contain a minute ovum and many oocytes. These would be expected to give rise to actinulae during the following breeding season.

It is also probable that there is only one breeding season in the year. The antarctic climate is unlikely to allow of more, but this cannot be proved. If this is so, then a year would elapse between the ripening of the gonophores of these two size groups ("g.10" and "g.9", pl. II, fig. 15), and for the distal part of the blastostyle to be replaced. Similarly the difference between gonophores "g.8" and "g.9" (fig. 15) would represent another year's growth. Since one gonophore only ripens annually on one blastostyle (only one exception to this generalization has been found, p. 264), it would take 9 years for the youngest gonophore on the blastostyle shown in fig. 15 to reach maturity; the gonophore "g.10" may be as much as 9 years old, and the female hydroid can be not less than 10 years of age.

Comparison of the gonophores of the two specimens (see p. 264) suggests that the older gonophores of the young male would take another 3 or 4 years to become mature. Relatively few of the male blastostyles bear gonophores, and when present they do not exceed 7 in number. Unless the gonophores arise more rapidly in the young hydroid than in the older animal, the young male (5·5 cm.) will be as much as 7 years old. Its growth would thus be slow, and it would be unlikely to attain the size of the

larger female specimen (85 cm.) by the time it was sexually mature. Thus the animal would start to breed at a smaller size than that of the female specimen. If this is true, then the species must continue to grow after sexual maturity.

Both specimens of *M. penola* appear to have been increasing in size at the time when they were collected. The female specimen already enormously exceeds the size of the hydranth of any other known hydroid. The size of the hydranth body of most hydrozoa, under favourable environmental conditions, appears to be constant for each species, and in actinozoa, such as sea anemones, there is a maximum size for each species, although the hydranth may reproduce sexually before it has attained this size. In *M. penola* there is reason to believe that sexual maturity is first attained at a size intermediate between those of the two known specimens (that is at a size exceeding those of temperate species), and that growth continues throughout many subsequent breeding seasons. There may be a maximum size for the hydranth of *M. penola*, but if there is, it does not appear to have been reached by the larger specimen in spite of the enormous dimensions; alternatively it is possible that under polar conditions of cold undisturbed waters there is no maximum size characteristic of the species, and that growth, without a compensating dedifferentiation (but with increasing complexity of structure, see p. 282), continues indefinitely, and results in a giant such as the larger specimen of *M. penola* with a hydranth body of 85 cm. The latter suggestion receives some support from the records of a large arctic species. Bonnevie (1899) describes fragments of Myriothelas which are probably referable to *M. phrygia*; they were sexually mature but ranged in size from 4 to 40 cm. in length. If prolonged growth over many breeding seasons has led to an increase of size from 4 to 40 cm. it is unlikely that there is a fixed specific size in *M. phrygia*, such as is found in shallow water temperate and tropical hydroids. It is probable that growth in an extremely large hydranth may become slower and ultimately cease for mechanical or physical reasons.

MYRIOTHELA CAPENSIS sp. nov.

Origin of the Material

Six specimens of *M. capensis*, obtained from the "Aquarium Rocks," East London, South Africa, on the 17th and 19th of July 1937, are present in the ecological collections of Professor Stephenson and Miss Eyre. All were attached to the alga *Ecklonia radiata*. One expanded specimen, measuring 17 mm., and one contracted specimen, are probably full sized, and bear female gonophores approaching maturity. Two expanded specimens 8 and 12 mm. long and one contracted individual are juvenile with small gonophores of undeterminable sex. The sixth specimen is much contracted and also young. The internal preservation of the material is not very good, and a detailed histological examination such as that carried out on *M. penola* was not possible on *M. capensis*.

General Description of the Hydroid (pl. I, figs. 12 and 13)

Tentacles cover the distal $\frac{9}{10}$ of the tubular hydranth, a zone about 15 mm. long and 1·5 mm. wide in the largest specimen. The proximal $\frac{1}{10}$ or less of the hydranth

bears a ring of about 20 cylindrical tentacle bearing blastostyles; they arise close together leaving no visible body surface between them. The hydrorhiza is in the form of about 20 adhesive tentacles which arise from the base of the hydranth. No perisarc is present, and the tentacles, when attached, are capped by a brown chitinoid disk which adheres to the substratum. The species is dioecious, but only the mature female is known. Several specimens had recently swallowed copepods and small amphipods which were filling the enteron.

Nematocysts

The types of nematocyst found in *M. capensis* (fig. 1) correspond exactly with those of *M. cocksi* which have been described by Weill (1934). Stenoteles, desmonemes, and haplonemes of exactly the same size occur in the two species, and their staining reactions are those already described for *M. penola* (p. 256). Heteronemes are a little smaller than in *M. cocksi* and do not exceed 13·5 μ in length. The distribution of the nematocysts is recorded with the descriptions of the various parts. Those of the actinula have not been seen.

Body Wall

The body wall is about 160 μ in thickness. The ectoderm calls for no particular comment; nematocysts are irregularly distributed, and desmonemes are the most frequent type. The cylinder of solid mesogloea is about 10 μ thick, and externally at intervals of about 16 μ longitudinal lamellae project from it into the ectoderm. These lamellae are about 80 μ deep, and many of them branch into two or three processes. Strap-shaped longitudinal muscle fibres are attached by their narrow edges to these lamellae, and nematocysts and other ectodermal elements lie in the grooves between the muscles. The endoderm provides circular muscle fibres over the inner side of the mesogloea. The endodermal epithelium is thrown into longitudinal villi. Near the mouth the villi are formed by elongation of the cells (fig. 7, *b*), but in the middle and lower part of the hydranth the villi are deeper and the epithelium is reflected forming a double-layered structure, but no flange of mesogloea passes into these villi. Gland cells are present, and in the middle and lower parts of the hydranth the cells composing the inner parts of the fold are laden with nutritive spheres. The poor preservation does not permit of more detailed description.

Body Tentacles

About 400 tentacles, 0·4 mm. in length cover the hydranth above the blastostyles. The capitulum is sharply demarcated from the stem, and an apical pad of mesogloea fibrils reaches a thickness of 87 μ (fig. 7, *b*). The nuclei of the capitular ectoderm lie at various levels, but the majority are half-way between the mesogloea and the surface. Almost all the nematocysts are situated in a dense peripheral layer. Desmonemes of various sizes with stout straight cnidopods are most numerous, haplonemes are frequent, and heteronemes and occasional stenoteles are present. The endoderm of the capitulum forms a darkly staining regular columnar epithelium. The lumen of the capitulum passes into that of the stem without constriction, and

no endodermal valve or mesogloea elaboration lies at this junction. The stem is almost devoid of nematocysts, the ectoderm is thin, and the endoderm forms an irregular epithelium of large lightly staining cells. Neither the lumen of the tentacle nor the endodermal epithelium passes through the mesogloea of the body wall which is continuous across the tentacle base (fig. 7, *b*). Proximally the endodermal lumen of the

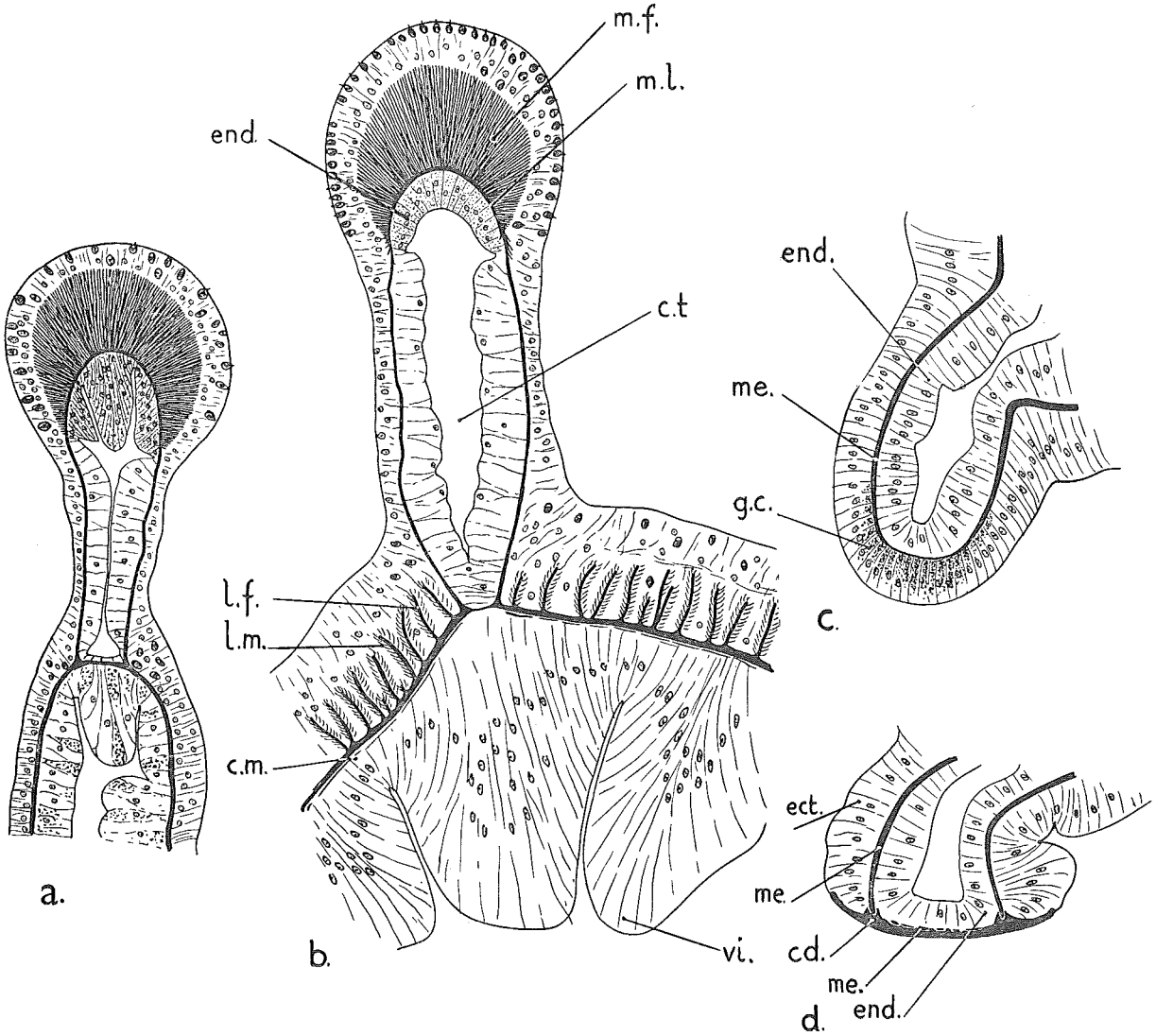

FIG. 7.—Fig. 7, *a*, shows a diagrammatic longitudinal section of a blastostyle tentacle and the tip of the blastostyle in *M. capensis*. × 150. Fig. 7, *b*, shows a diagrammatic transverse section of the body wall and body tentacle near the oral end in *M. capensis*. × 160. Fig. 7, *c*, shows a longitudinal section of an unattached hydrorhiza tentacle, and fig. 7, *d*, shows an attached hydrorhiza tentacle of *M. capensis*. × 140.

tentacle is obliterated. No nematocyst nursery lies near the base of the tentacle as in *M. penola*, and nematocysts here may not be more numerous than elsewhere on the body wall.

BLASTOSTYLES

The proximal end of the hydranth may be simple or lobed, and bears a ring of about 20 cylindrical unbranched blastostyles 1·5 mm. in length (figs. 8, *b*, and pl. I,

figs. 12 and 13). Distally each blastostyle of the female bears about 5 capitate tentacles, and from the middle and basal parts spring about 4 sessile gonophores. Each blastostyle carries but one advanced gonophore. The wall of the blastostyle is simpler in structure than that of the hydranth. The ectoderm lacks nematocysts, except in the vicinity of tentacle bases; the mesogloea cylinder bears no external projections; and the endoderm is irregularly lobed and furrowed but possesses no villi.

Tentacles superficially resemble those of the hydranth body, but the darkly staining capitular endoderm is thickened forming a few conical projections which divide the lumen of the capitulum into narrow channels (fig. 7, *a*); this feature does not occur in any other described species. The endodermal lumen of the stem is very

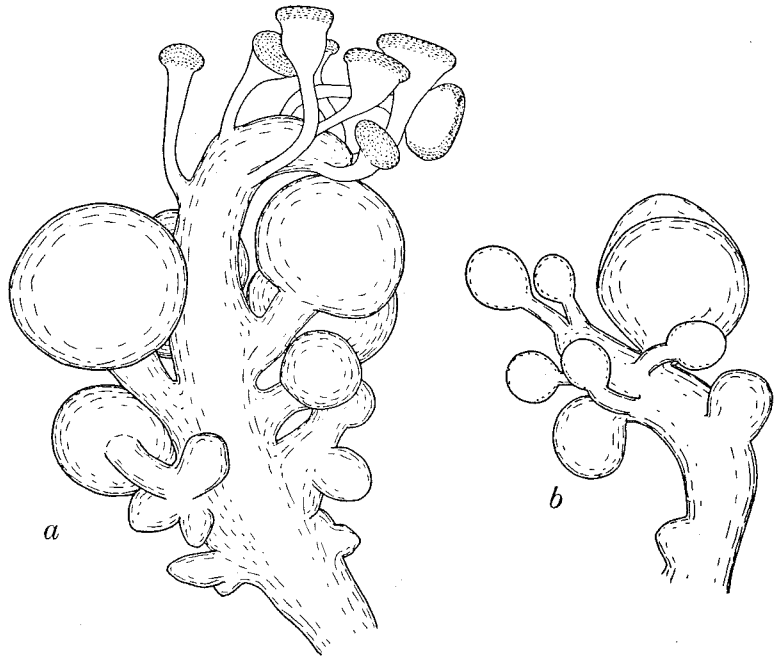

FIG. 8.—Outlines of female blastostyles of *M. australis* and of *M. capensis* to show the difference in the tentacles and in the insertions of the gonophores. × 28. Fig. 8, *a*, *M. australis*, distally bearing trumpet-shaped tentacles and proximally stalked gonophores of different ages. Fig. 8, *b*, *M. capensis*, distally bearing knobbed tentacles and proximally four sessile gonophores of different ages.

narrow; it does not communicate with that of the blastostyle, but it extends to the base of the tentacle where the endodermal epithelium becomes thin over the blastostyle mesogloea (fig. 7, *a*). The nematocysts of the capitulum are fewer than on the hydranth body tentacles, but the same types are present and in the same relative abundance (fig. 1).

Only female *gonophores* are known, male individuals, if present in the collection, being immature. Only the distal gonophore on each blastostyle matures at a time, the proximally situated gonophores being younger. The largest gonophore is probably not quite full-sized, it has a diameter of 0·8 mm. and its broad base of attachment is about 0·25 mm. across. The structure of the sessile female gonophore resembles that of *M. penola* (p. 265), except that the size is smaller, fewer endodermal villi project into the spadix lumen, and the ectodermal musculature is almost if not entirely absent.

The development of the gonophores takes place as in *M. penola* (p. 265 and fig. 3). In gonophores up to 0·6 mm. in diameter there is no trace of a velar opening, the bell wall appearing as in fig. 3, *c*. In the largest gonophore present, of 0·8 mm. diameter, a velar opening is starting to develop. At the point where the two layers of mesogloea in the bell are confluent (see fig. 3, *c*, "s.ex."), the ex- and subumbrella ectoderm has become transformed as shown in fig. 9. Both epithelia are here thickened and an exumbrella invagination is formed over the solid disk of mesogloea. The subumbrella ectoderm below forms a disk of compact darkly staining cells surrounded by a rim of elongated cells. No later stage has been seen, but if the invagination "v.in" broke through the bell wall, a condition would result which would resemble the velar perforation described and figured by Briggs for *M. harrisoni* and *M. australis*

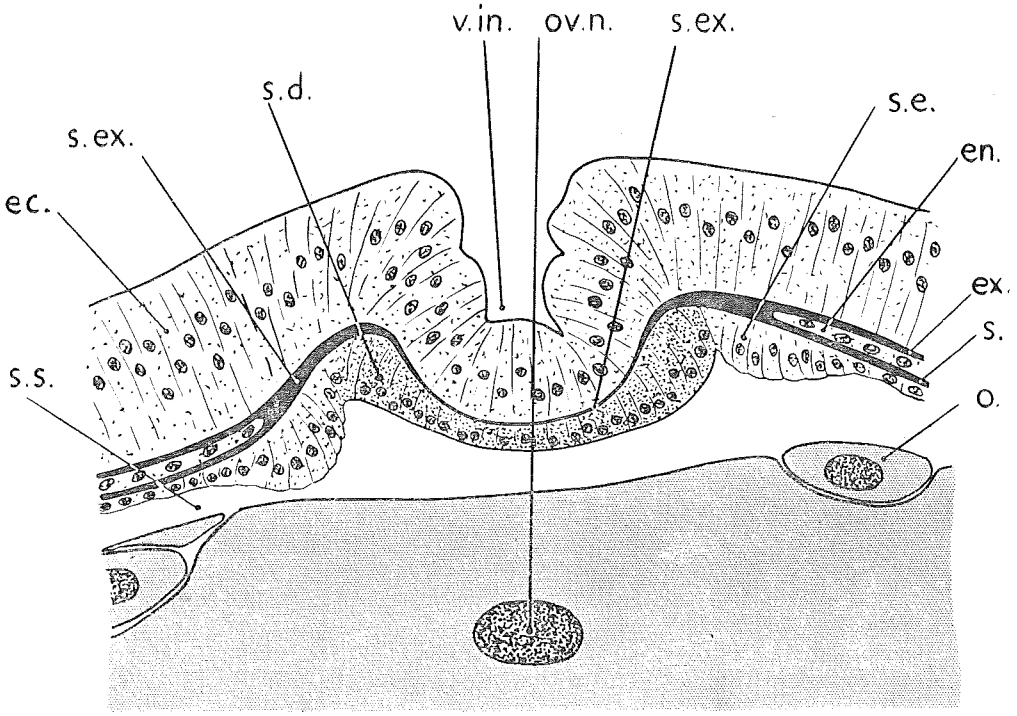

FIG. 9.—Sagittal section through the distal part of the female gonophore of *M. capensis* just before the velar perforation is made. × 105. Compare with the region near "s.ex." in fig. 3, *c*, a younger stage of *M. penola*, and with pl. 34, fig. 5, Briggs, 1928, an older stage of *M. harrisoni*.

(1928, pl. 34, fig. 5, and 1929, pl. 43, fig. 2). It is probable that an open velar perforation occurs in both male and female gonophores of *M. capensis*, and that fertilization takes place through this pore. This opening in the female gonophore may then close, as it must do in *M. penola*, during the period of development of the actinula larva.

The development of ova in *M. capensis* takes place by the second method described by Benoit (1925) for *M. cocksi*. When the gonophore reaches a diameter of 0·4 mm. and the oocytes, 24 μ in diameter, lie about three cells deep, three or four ova of larger size become differentiated and grow at the expense of the neighbouring oocytes. One gonophore of 0·68 mm. contained four ova 0·27–0·3 mm. in diameter, and the largest gonophore (referred to above) contained three ova of 0·5 mm. diameter, the

remaining oocytes being 0·04 mm. across. Older stages have not been seen, but the mature gonophore probably contains one ripe ovum, as in *M. cocksi* and other species.

Hydrorhiza

The hydrorhiza is in the form of 20–30 short adhesive tentacles springing from the basal surface of the hydranth below the blastostyles (pl. I, fig. 12). The tentacles arise close together and rarely exceed 0·4 mm. in length, many being much shorter. When attached to the substratum each tentacle is capped by a weakly convex chitinoid disk, 0·25 mm. in diameter, which adheres to the substratum. The tentacles radiate outwards from the hydranth and appear to pull out its base over as wide an area as possible. Longitudinal sections through unattached and attached tentacles are shown in figs. 7, *c* and *d*. Columnar ectodermal and endodermal epithelia are separated by a simple layer of mesogloea bearing no external projections. Muscles are not strongly developed; and the internal cavity communicates directly with the main enteron without any basal constriction. In the unattached tentacle (fig. 7, *c*), the apical mesogloea is thinner than elsewhere, and the apical ectodermal cells contain many granules which stain red with fuchsin. In the attached tentacle (fig. 7, *d*), which was pulled off its substratum before sectioning, the apical ectoderm has disappeared, and a chitinoid disk with the same staining properties as the ectodermal granules, has taken its place, and has presumably been formed from the granules previously in this position. Just within the rim of the chitinoid disk its substance is thickened and closely attached to the stem mesogloea, which is sunk into a groove in the disk. The terminal sheet of mesogloea within the middle of the chitinoid disk also adheres closely to the latter, and the disk appears to be dove-tailed into the mesogloea in many places.

DISCUSSION

Different species of *Myriothela* occupy parallel *types of environment* in both southern and northern hemispheres. There are small shallow water forms attached to rocks or seaweed, *M. cocksi* (50 mm.) in the northern, and *M. capensis* (17 mm.) and *M. harrisoni* (15 mm.) in the southern hemispheres. Larger forms occur in deeper and colder water, *M. gigantea* (300 mm.) and *M. phrygia* (400 mm.) have been dredged from over 2000 m. by the Norwegian North Atlantic Expedition 1876–88, and *M. austro-georgiae* (300 mm.) has been collected from various depths below 20 mm. by four antarctic expeditions. Both *M. austro-georgiae* and *M. penola* (850 mm.) have been found torn from their substrata and floating on the surface of the sea, the former in a hole cut in the ice over 20–30 fathoms (Scottish National Antarctic Expedition), and the latter among ice-floes in a shallow creek. The hydrorhiza of *Myriothela* if pulled from its substratum, cannot affect a new attachment, but any unattached adhesive tentacles might adhere to a new substratum, and in any case actinula larvae may be liberated from the floating hydroid which may possibly live in this position for a long time.

The only other hydroid known to attain great size is *Branchiocerianthus*, and this genus is also found only in cold water. Stechow (1909) has suggested that *Branchiocerianthus* needs absolute quiet water in which to attain large size, and this may be

true also for the larger species of *Myriothela*. *Branchiocerianthus* has only been collected from the cold abysmal regions of the warmer seas (Broch, 1918, p. 176), while giant Myriothelas have been found in the cold seas of the north Atlantic and Antarctic regions, either at great depths or in sheltered water.

The *preservation* of such a large animal as *M. penola* whole in formalin has been remarkably good, and has made possible a thorough examination of much of its structure. The good fixation may be due to the low temperature at which it was fixed and to the care with which Dr. Bertram narcotized and preserved the animal. *M. capensis*, only $\frac{1}{50}$ the size of *M. penola*, and also preserved in formalin, but in a warmer climate, is very poorly preserved for histological purposes.

M. penola, 850 mm. long, is a giant among hydroids, and is more than double the length of the largest known species of the genus. This great *size* has led to many *elaborations of structure* not found in smaller species, and these features are doubtless due to the impossibility for an organism to increase in size beyond certain limits without alteration of both the structure and the proportions of its parts. Features which may be so interpreted occur throughout the organism and its large actinula, and some of these will be mentioned below.

The height of *M. penola* is 50 times that of *M. capensis*, but the tentacles of *M. penola* are not enlarged proportionately; they are only 5 times the length of those of smaller species, and the capitulum is only about $2\frac{1}{2}$ times as wide as in *M. capensis*. This larger tentacle has a more complex and mechanically stronger structure (see p. 259), but its nematocysts are only slightly larger than those of smaller species.

Some dimensions of full-sized specimens of four species of *Myriothela* are given in Table 1. The body wall mesogloea of *M. capensis* and *M. penola* is shown in pl. III,

TABLE 1

	Small Species		Large Species		
	M. cocksi	*M. capensis*	*M. austro-georgiae*	*M. penola*	
Length of body	50 mm.	17 mm.	300 mm.	850 mm.	
Width of body	1·5 mm.	1·5 mm.	12 mm.	middle tentacular region 12 mm.	lower tentacular region 30 mm.
Thickness of body wall.. ..	140 μ	160 μ	300 μ	180 μ	360 μ
Thickness of basal sheet of mesogloea	15 μ	10 μ	20 μ	45 μ	90 μ
Depth of external processes of mesogloea	30 μ	80 μ	70 μ	30 μ	120 μ
Distance apart of external processes of mesogloea	6 μ	18 μ	12 μ	9 μ	40 μ

figs. 27 and 28, and that of *M. austro-georgiae* in pl. 2, figs. 3 and 4, Jäderholm, 1905. The thickness of the body wall is greater in the larger species, but the thickness does not increase proportionately with the external dimensions of the body; thus in *M. penola* the body wall is only a little thicker than in *M. austro-georgiae*, an animal less than half the length. The body wall, is, however, more strongly constructed in the two larger species, where the amount of mesogloea is greater. The proportion of mesogloea in the form of a solid sheet may be greater (see figs. 27 and 28), and where the external mesogloea lamellae are shallow, they are set closer together, so providing plenty of surface for muscle attachment. In parts of *M. penola* where these lamellae are shallow they are much thicker than in smaller species, and must thus be stronger. The variations in the mesogloea layer in different parts of the body of *M. penola* are also seen to be correlated with the size of these parts and their requisite support. In the lower and middle regions of the blastostyles, for example, the basal sheet of mesogloea is only 10–20 μ in thickness and the external lamellae project about 20–30 μ, whereas in the body the basal sheet is 45–90 μ thick and the external lamellae project 30–120 μ. These proportions of mesogloea in the blastostyle of *M. penola*, moreover, closely resemble those in the body wall of *M. australis*, an animal in which the whole hydranth is of about the same size as a single blastostyle of *M. penola* (compare pl. III, fig. 26, with Briggs, 1928, pl. 34, fig. 4).

The depth of the endodermal villi of large and small species appears to be proportional to the diameter of the body, but the thickness of the villi in larger forms is only about double that in the smaller forms, and the villi are correspondingly more numerous in the larger species. The apical cells, which may be concerned with the absorption of food, only form the extreme edge of each villus in small species such as *M. cocksi* (Hardy, 1891) and *M. australis* (Briggs, 1928), but in *M. penola*, where a relatively larger absorptive area would be expected, a larger part of each villus is formed by these cells (see p. 259).

The evidence for the view that the "metabolic activities of different parts of the endoderm are brought into relation with one another through the agency of the somatic fluid" which fills the enteric space was first put forward by W. B. Hardy (1891) working on *M. cocksi*.[1] He showed that this fluid must convey stored nutriment from one part of the body to another, and he followed the breakdown and utilization of the nutritive spheres. He suggested that the fluid was "circulated by the active movements of the animal, which include the extension and retraction of the blastostyles, and possibly by cilia, which appear to be borne here and there by the endodermal cells." These suggestions are undoubtedly true also for *M. penola*. The blastostyles of this species are the largest known in the genus, and their more elaborate structure is doubtless associated with the need for more efficient circulation of the enteric fluid. The close set villi separated by ciliated grooves do not occur in the blastostyles of smaller species, where the endoderm is only slightly lobed and furrowed, and these ciliated grooves must provide direct and rapid channels for the transport of fluid from the general enteron to the cavities of the spadices of the gonophores.

Two other features correlated with size have already been mentioned. The internal structure of the hydrorhiza tentacles becomes more complex with increase

[1] The name *M. phrygia* has been used by Hardy and others for the British species of *Myriothela*.

of size (p. 271); and the unusual details of the development of the gonophore rudiment in the larger specimen is probably due to the size of the blastostyle (pp. 265 and 270).

The large size of the *actinula* of *M. penola* probably accounts for the structural differences between this larva and those of smaller species. Tentacles of all kinds are relatively more numerous and much more closely set, and the oral zone of crowded short tentacles is not seen in the small actinulae of *M. cocksi* and *M. phrygia* (Allman, 1875, pl. 38, fig. 6; Sars, 1877, pl. 2, figs. 35 and 36), or in the newly fixed young of *M. australis* and *M. harrisoni* (Briggs 1928, pl. 32, fig. 2 and pl. 33, fig. 3). The long larval tentacles which are later absorbed are locomotory in function, "the terminal capitula being used as suckers of attachment" (Allman, 1875). In *M. penola* these provisional tentacles have the remarkably wide spread of 65 mm., and their abundant nematocysts, well anchored to the mesogloea and probably adhesive in nature, are fitted to hold the large body of the actinula to any suitable substratum that is encountered. In small actinulae, such as those mentioned above, the aboral end of the body forms a single adhesive or suctorial disk. In *M. penola*, the precociously developed hydrorhiza tentacles covering the base of the larva provide a large number of potential points of adhesion; these will enable a much stronger attachment to be made than would be possible with a single suctorial disk. Endodermal villi are also precociously developed, they are absent from the small actinula of *M. cocksi*, where they only appear later in the growing hydranth.

It has been suggested (p. 275) that *continuous growth from growth zones* recognizable on the blastostyles and on the body of *M. penola* has led to the absence of specific size and to the large dimensions of the mature specimen of this species. A continuance of growth without compensating dedifferentiation may take place over very many years. Bidder (1932) has pointed out that "indefinite growth is natural", but indefinite increase in size, such as shown by the female plaice, is rarely seen. In the great majority of organisms, for a variety of reasons, growth is regulated and not indefinite, and specific size results.

Stechow (1909) has shown that in the giant solitary hydroid *Branchiocerianthus* growth is persistent, and so there is no specific size as in smaller colonial hydroids, where budding follows the attainment of the specific size. The growth of *Branchiocerianthus* is carried out by a unilateral growth zone on the hydranth body which continually adds new tentacles, blastostyles, radial canals, etc., to either side, and the hydranth body thus becomes bilaterally symmetrical. This remarkable method of growth is correlated with the enormous size of *Branchiocerianthus* (Stechow, 1909). Thus in both the known genera of giant solitary hydroids specific size appears to be absent, and continual growth occurs from definite growth zones, the details of which are quite different in the two genera. The largest *Branchiocerianthus imperator* known measures 7 ft. $5\frac{1}{2}$ in. (2235 mm.), but the hydrocaulus contributes 7 ft. 4 in., the hydranth body being only $1\frac{1}{2}$ in. long. In *M. penola* however, the hydrocaulus is absent and the hydranth body has attained the great length of 2 ft. $8\frac{1}{2}$ in. (850 mm.) in the largest known specimen.

The occurrence of *binucleate endodermal cells* is remarkable, such a condition being so unusual in any animal tissue. Binucleate nephrocytes and oenocytes occur

in some insects, and the ovarian tube in *Pediculus humanus* shows a binucleate epithelium (Keilin, 1917, 1930). Hardy (1891) recorded binucleate vacuolate cells in *M. cocksi*, a feature which can readily be confirmed. Briggs (1928, 1930) noted that some of the vacuolate cells of *M. harrisoni* but not those of *M. australis* are binucleate. In *M. penola* the greater part of the endoderm is composed of binucleate vacuolate cells, but the actively growing parts of the endoderm are uninucleate (see endoderm of body wall, but not villi, of the actinula, p. 275, and of the wall of the spadix, p. 267). These uninucleate undifferentiated cells presumably give rise to the binucleate cells. This binucleate condition may be characteristic of most species of the genus, irrespective of the size of either the whole animal or of its component cells.

The type of *hydrorhiza* which is composed of adhesive tentacles growing from the base of the hydranth occurs in *M. phrygia* and *M. verrucosa* in the northern hemisphere and in *M. australis*, *M. capensis*, *M. penola*, and *M. austro-georgiae*, in the southern hemisphere. Of the northern species, the hydrorhiza of *M. phrygia* is described and figured by M. Sars (1877), and in a mature specimen, $1\frac{1}{2}$ in. long, consisted of 10 fixed and 9 free tentacles, the former adhering by flat horny extremities. In a larger specimen 7 cm. long which I have examined[1] the adhesive tentacles are more numerous. They resemble those of the southern hemisphere species except that many of them appear to have shrunk in diameter, so leaving the terminal disk of attachment appearing much wider than the stem. The overlapping of the hydrorhiza and blastostyle bearing zones in *M. penola* is a feature which has not been described in other species. It also occurs to a minor degree in a specimen of *M. phrygia* in the Bergen Museum, where three of the proximal blastostyles bear adhesive tentacles arising from their lower parts.

The method of formation of the chitinoid disk on the hydrorhiza tentacles is a most unusual one. In invertebrates the integuments, apodemes, peritrophic membranes, etc., are usually formed by a secretion which lies outside the epithelium or gland cell (Yonge, 1932, Wigglesworth 1930, 1933, Manton 1928, 1938, etc.). The formation of a chitinoid layer in *Myriothela* by the destruction of an epithelium, which is replaced by material originally intracellular, in such a way that the disk is linked with the mesogloea, is doubtless associated with the necessity for the permanent adhesion by the tentacle to be strong. In the Alcyonaria a strong and permanent adhesion to the substratum is obtained either directly by the mesogloea or by a horny axis; in the former case the ectodermal epithelium disappears at this junction, and in the latter case the axial epithelium, if it is present, lies on the surface of the axis away from the substratum.

The development of the *gonophores* of *Myriothela* has been studied most extensively on *M. cocksi*, a complete and beautifully illustrated account being given by Benoit (1925) who has correlated the previous partial descriptions by Allman (1875), Korotneff (1879, 1888), and Hardy (1891). The very early stages described by Benoit have not been seen in *M. penola*, but the development recorded above differs in no essential manner from the corresponding stages of *M. cocksi*, a minor difference being correlated with size (see p. 270).

[1] By courtesy of Dr. Brinkmann.

The presence or absence of a velar perforation on the gonophore in different species of *Myriothela* probably depends on the method of fertilization of the eggs. In the hermaphrodite *M. cocksi* the gonophore wall remains entire. Benoit (1925) has shown that fertilization takes place at night, the sperm passing from the male gonophore by way of the endodermal spaces to the spadix of the female gonophore, and then through the endodermal epithelium to reach the ripe ovum. Development begins within the closed gonophore, and the embryo later escapes by a rupture of the wall which starts at the point where the endodermal layer is interrupted, that is, at a point corresponding with the velar opening. In *M. australis*, *M harrisoni*, *M. meridiana* (Briggs, 1928, 1929, 1938), *M. capensis*, and almost certainly in *M. penola* a velar perforation is formed when the sperm and ova reach maturity. Sperm are probably liberated through this opening and gain access to the female gonophore thereby. That such an opening has not been described in other dicœcious species may be due to suitable stages not having been available for examination; of the six specimens of *M. capensis* which have been inspected, only one gonophore on one specimen is old enough to show the formation of this opening, and on the two specimens of *M. penola* all the gonophores are either too old or too young to exhibit this feature. A closure of the velar opening of the female gonophore after fertilization has not been recorded in species other than *M. penola*, but this again may be due to the absence of available material of a suitable age. In *Tubularia* the velar perforation remains open during the development of the actinula, but the gonophore here contains several embryos of different ages, and the velar opening must remain open both for liberation of actinula and for intake of sperm.

Benoit (1925) described the mature *ovum* of *M. cocksi* developing by two alternative methods. Either one oocyte situated on the axis of the gonophore grows by progressive fusion with its neighbours, those oocytes close to the spadix being absorbed first; or several plasmodial areas (up to ten) are formed by fusion of oocytes near the spadix. These all grow for a time, but the one situated on the axis of the gonophore alone persists and unites with the others to form the mature ovum. All the gonophores bearing definitive ova which have been sectioned show the former type of development in *M. penola* and the latter type in *M. capensis*. *M. australis* and *M. harrisoni* resemble *M. capensis* in this respect.

In *M. penola* the development of the single ovum starts relatively earlier than the several ova of *M. capensis*. The ovum of *M. penola* becomes differentiated when the gonophore is less developed and the surrounding oocytes only half the diameter of those at a similar stage in *M. capensis*. This may be associated with the volume of the mature egg of *M. penola* being about 1000 times greater than that of *M. capensis*.

The genus *Myriothela* in the northern hemisphere comprises six species, and the desirability of retaining all these forms within a single genus was advocated by Bonnevie (1899). Since this date six southern hemisphere species have been found, *M. austro-georgiae*, *M. penola*, and *M. meridiana* from antarctic waters, *M. australis* and *M. harrisoni* from Australian, and *M. capensis* from South African coasts. The desirability of including the southern forms within the original genus has been questioned. I have examined four southern and two northern hemisphere species, and

from the available information there appears to be no character common to the southern hemisphere species which would justify their separation from the northern forms.

The nematocyst armature, where known, is similar in southern and northern species. (Of the previous descriptions of nematocysts of species of *Myriothela*, only that given by Weill (1934) for *M. cocksi* can be considered complete.) It has been emphasized by Weill that the cnidomes of the various genera of Gymnoblastea are distinctive. The similarity between the northern and southern species of *Myriothela* in this respect is even greater than it is within the genus *Tubularia*.

The structure of the body tentacles varies little among the species of *Myriothela*, beyond modifications correlated with size (see p. 282). The blastostyle tentacles, if present, vary greatly, but in no significant manner, except that the development of flat-topped, trumpet-shaped capitula appears to be a feature characteristic of the known Australian species.

The endodermal villi show some variations correlated with size (see p. 283), but the absence of a flange of mesogloea in the villi of *M. cocksi*, *M. capensis*, *M. phrygia*, and *M. minuta*, and its presence in those of *M. australis*, *M. harrisoni*, *M. austro-georgiae*, and *M. penola* is connected neither with size nor with geographical distribution.

The hydrorhiza shows three forms among the northern species (see Bonnevie, 1899), and two of these are also shown by the southern species (see Table 2). The claspers of the northern *M. cocksi*, previously considered to be unique, are probably comparable to part of the hydrorhiza of forms such as *M. penola* in the southern hemisphere (Manton, 1941).

Finally the cryptomedusoid gonophores are of much the same structure in southern and northern hemisphere species. The presence or absence of a velar perforation is associated with the method of fertilization (see p. 286). The southern hemisphere species are dicœcious, as are the northern *M. phrygia*, *M. venucosa* and *M. gigantea* (Bonnevie, 1899), but *M. cocksi*, and possibly others are hermaphrodite.

A table is given below summarizing the main characters of the southern species of *Myriothela*. This table may be compared with that given by Bonnevie (1899) for the northern hemisphere species. In structure and habits *M. capensis* superficially resembles *M. australis*, but their blastostyle tentacles and the insertions of their gonophores are unlike. The blastostyles of these two species are shown in fig. 8, and a section of a blastostyle tentacle of *M. capensis* in fig. 7, *a*, may be compared with that of *M. australis* (Briggs, 1928, pl. 39, fig. 2).

Bonnevie (1899) has summarized the views previously expressed concerning the relationships of the Myriothelidae, some authors suggesting that the family is closely related to the Corynidae and others to the Tubularidae. Weill (1934) has discussed the taxonomic value of the cnidome in the coelenterates; he has reviewed the classification of the gymnoblastic genera, and on the basis of the cnidome he has proposed a more rational grouping. A cnidome consisting of four types of nematocyst and including desmonemes and stenoteles, occurs only in the Myriothelidae, Tubularidae and Pennaridae (see Weill, 1934, and Russell, 1938), while in the hydroids once grouped in the family Corynidae the cnidomes are different, and consist of only two or three types of nematocyst. Thus the suggested affinity between *Tubularia*, *Ectopleura*, etc., and *Myriothela* is supported.

TABLE 2

SOUTHERN HEMISPHERE SPECIES OF MYRIOTHELA

Species.	*Size.*	*Hydrorhiza.*	*Body Tentacles.*	*Blastostyles.*	*Blastostyle Tentacles.*	*Gonophores.*	*Locality.*
M. austro-georgiae Jäderholm, 1905	300 mm.	Adhesive tentacles on base of hydranth, perisarc absent.	Covering whole hydranth.	Unbranched, 3 mm. long.	One long terminal tentacle, sometimes smaller ones also.	Sessile. ♀ 22 mm., < 6 per blastostyle. ♂ 1·5 mm., < 10 blastostyle.	South Georgia, Kerguelen Isl., Graham Land.
M. penola, n.sp.	850 mm.	*Ditto*	Covering hydranth above blastostyle bearing zone only.	Lobed, 22 mm. long.	Many knobbed tentacles on the blastostyle lobes.	Sessile. ♀ 8 mm., < 10 per blastostyle. ♂ ?	Graham Land.
M. australis Briggs, 1928	30 mm.	*Ditto*	*Ditto*	Unbranched, 3 mm. long.	About 8 trumpet-shaped tentacles.	Stalked. ♀ 1 mm., < 12 per blastostyle. ♂ less than 1 mm. < 15 per blastostyle.	Marouba Bay, New South Wales.
M. capensis n.sp.	17 mm.	*Ditto*	*Ditto*	Unbranched, 2·5 mm. long.	About 5 knobbed tentacles.	Sessile. ♀ 0·8 mm., < 5 per blastostyle. ♂ ?	Port Elizabeth, South Africa.
M. meridiana Briggs, 1938.	30 mm.	?	*Ditto*	Branched, 7 mm. long.	Absent.	Stalked. < 50 per blastostyle.	Macquarie Isl.
M. harrisoni Briggs, 1928, 1930	15 mm.	Expanded processes from basal cylinder, whole covered by perisarc.	*Ditto*	Unbranched, 1 mm. long.	A single terminal trumpet-shaped tentacle.	Sessile or shortly pedunculate. ♀ 0·9 mm., < 2 per blastostyle. ♂ 0·45 mm., < 7 per blastostyle.	Bulli, New South Wales.

I am indebted to Dr. A. F. W. Hughes, Dr. J. P. Harding, and Dr. I. Manton for taking the photographs reproduced in the plates, and to Dr. E. A. Briggs and Dr. A. Brinkmann for kindly lending specimens of *M. australis* and *M. phrygia* respectively.

SUMMARY

(1) Two new species of the hydroid *Myriothela* are described: *M. penola*, a giant antarctic form, and *M. capensis* a small species from the coast of South Africa. For a summary of characters, see Table 2, pp. 288.

(2) The great size of *M. penola* is correlated with many structural features not seen in smaller species. Examples of such features are noted from the body tentacles, the mesogloea of the body wall and of the blastostyle, the endodermal villi of the hydranth and of the blastostyle, the hydrorhiza tentacles, etc. Characters of the actinula larva also correlated with size are the large number of the oral and body tentacles, the great length and the number of the provisional larval tentacles, and the precocious development of the hydrorhiza tentacles and endodermal villi which are present in the larva before its liberation.

(3) Provision is made in *M. penola* for direct transport of enteric fluid (and thus of food material) by ciliated grooves, situated between close-set blastostyle villi, which lead from the general enteron to the spadices of the gonophores.

(4) The method of growth of *M. penola* is described. Increase in length of the body takes place most actively at the oral end. Body tentacles become dedifferentiated and absorbed progressively in the post-oral positions, and finally disappear at the aboral end of the tentacle bearing zone. The blastostyle bearing zone grows in length at its oral end at the expense of the tentacle zone, young blastostyles growing in place of the absorbed tentacles.

(5) The blastostyles of *M. penola* are relatively larger than those of any known species and they show a zoning associated with growth. Increase in length occurs at the basal end where young tentacles and young gonophores are formed. Mature tentacles and gonophores lie in the middle region, and the terminal tentacles and blastostyle wall are degenerate in structure. After the liberation of an actinula larva the remains of the gonophore and the distal degenerate parts of the blastostyle are either absorbed or cast off.

(6) Only one gonophore on each blastostyle of *M. penola* matures at a time. All the older gonophores are at one of several distinct stages of development, which are uniform on all blastostyles bearing gonophores. There is a limited breeding season, and if this is annual, the differences between these gonophores represent one year's growth.

(7) Both *M. penola* and *M. capensis* are bisexual. There is evidence that a velar perforation is formed in both species when the genital products are ripe. The perforation closes after fertilization in *M. penola* and possibly in other species also.

(8) The development of the gonophores of *M. penola* and of the ova of *M. penola* and *M. capensis* are described.

(9) The method of attachment of the hydrorhiza tentacles to the substratum is described in *M. penola* and *M. capensis*. Adhesion is first made by the surface of the terminal ectodermal cells. Then intracellular granules in these cells unite and the cells break down. The epithelium is thus replaced by a chitinoid disk, formed from the granules, which adheres to the substratum and is dove-tailed into the mesogloea of the tentacle.

(10) Some tentative suggestions are made concerning the age and rate of growth of *M. penola*. It is probable that growth is slow and that it continues over very many breeding seasons. It is also possible that giant size is attained under polar conditions owing to the absence of a constant specific size, and an indefinite continuance of growth from fixed growth zones without compensating dedifferentiation.

(11) A review is given of the southern hemisphere species of the genus *Myriothela*. It is considered that there is no justification for a separation of the southern from the northern species of the genus.

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KEY TO LETTERING

a.e. actinula exposed by rupture of gonophore wall.
a.l. actinula larva.
at. atriche.
b. blastostyle.
b.b. base of blastostyle.
b.f.5, *a* blastostyle traced in fig. 5, *a*.
b.f.5, *b* blastostyle traced in fig. 5, *b*.
b.f.5, *c* blastostyle traced in fig. 5, *c*.
b.l. base of long larval tentacle.
b.t. blastostyle tentacle.
b.y. blastostyles of the younger specimens lying close against those of the older specimen.
c. capitulum of long larval tentacle.
c.d. chitinoid disk.
c.g. longitudinal ciliated groove.
c.m. circular muscle process.
c.t. endodermal cavity of tentacle.
cn. cnidopods of atriches.
cu. cuticle.
d. desmoneme.
d.t. degenerate short tentacles.
e. egg membrane stretched round actinula larva.
e.i. bases of terminal ectodermal cells inserted through mesogloea.
e.l. endodermal lumen of spadix.
e.me. attachment of egg membrane to spadix mesogloea.
e.s. endodermal sphincter.
e.t. connection between endoderm of tentacle and that of main body.
e.v. vacuolate endodermal cell.
e.y. young darkly staining endodermal cells.
ec. exumbrella ectoderm.
ect. ectoderm.
ect.l. dendritic ectoderm of long larval tentacle.
en. endoderm of bell of gonophore.
en.s. endoderm of spadix.
end. endoderm.
end.l. endoderm of long larval tentacle.
ex. exumbrella mesogloea.
f. ciliated furrow between blastostyle villi which leads into spadix of gonophore.
f.25. position of section shown in fig. 25, pl. III.
g. stretched bell of gonophore.
g.c. granules which will form chitinoid disk.
g.e. sub-cuticular granules in ectoderm.
g.s. shrunken gonophore wall.
g.2–g.10 gonophores at successive stages of development situated on the blastostyle shown in fig. 15.
g.10.s. gonophore at similar stage to that of g.10 in fig. 15, pl. II.
gr. fuchsin staining granules.
h. hydrorhiza adhesive tentacle.
h.t. hydranth body tentacle.
he. heteroneme.
i.v. inner part of villus composed of darkly staining cells.
j. junction of capitulum and stem.
l. long larval tentacle.
l.f. longitudinal mesogloea flanges projecting into ectoderm.
l.h. endodermal lumen of adhesive tentacle.
l.m. longitudinal muscles inserted on to mesogloea flanges, here cut transversely.
l.mu. longitudinal muscle process.
l.r. longitudinal endodermal ridge.
l.t. capitulum and stem of long larval tentacle of actinula.

m. mesogloea of spadix.
m.b. mesogloea of blastostyle.
m.b.t. mature blastostyle tentacle.
m.f. apical pad of mesogloea fibrils.
m.l. basal layer of solid mesogloea.
m.o. outer part of mesogloea, insertions of cnidopods causing the striated appearance.
m.s thickening of mesogloea supporting sphincter muscles.
m.v. mesogloea of villus.
m.w. mesogloea of body wall.
me. mesogloea.
n. nematocysts.
n.n. nematocyst nursery.
n.o. nucleus of oocyte recently fused with ovum and which has not yet degenerated.
n.p. nerve plexus.
n.s. darkly staining nutritive spheres.
o. oocytes.
ov. single ovum.
ov.n. nucleus of single ovum.
p. developing mesogloea fibrils.
p.e. darkly staining peripheral layer of endoderm (embryonic cells).
r. rudiment of gonophore endoderm.
r.e. rudiment of ectodermal lining of gonophore.
s. subumbrella mesogloea.
s.b. connection between endodermal cavities of spadix and blastostyle.
s.b.t. senile blastostyle tentacle.
s.d. darkly staining disk of subumbrella ectoderm which will unite with exumbrella ectoderm to form a velar opening.
s.e. subumbrella ectoderm.
s.ec. spadix ectoderm lying outside oocytes.
s.ex. union of ex- and subumbrella mesogloea (position of future velum).
s.s. subumbrella space.
s.t. small body tentacle.
sp. spadix.
sp.e. spadix ectoderm.
st. stenotele.
t.b. edge of tentacle base.
t.f.4 position of parasagittal section shown in fig. 4.
t.l. tentacle-bearing lobe of blastostyle.
t.1. young developing tentacles.
t.2. mature tentacles.
t.3. degenerate tentacles.
t.o. short tentacles covering oral pole of actinula.
t.y. tentacle-bearing zone of young specimen lying close to the large specimen.
v. rachis of *Virgularia* (substratum of hydroid).
v.a. apex of rachis of *Virgularia*.
v.c. binucleate vacuolate cell showing both nuclei.
v.in. velar invagination.
v.l. endodermal valve at base of long larval tentacle.
vac. vacuole of endodermal vacuolate cell.
vi. endodermal villus.
x. point of union of spadix mesogloea "m." with the exumbrella "ex." and subumbrella "s." mesogloea lamellae.
y.b.t. young blastostyle tentacle.
y.g. young gonophore.
y.h. young haploneme from nematocyst nursery.
y.t. mature body tentacle at maximum size.
z.y.b. zone of young blastostyles.

PLATE I: *M. PENOLA* and *M. CAPENSIS*

(Photographs by Dr. J. P. Harding)

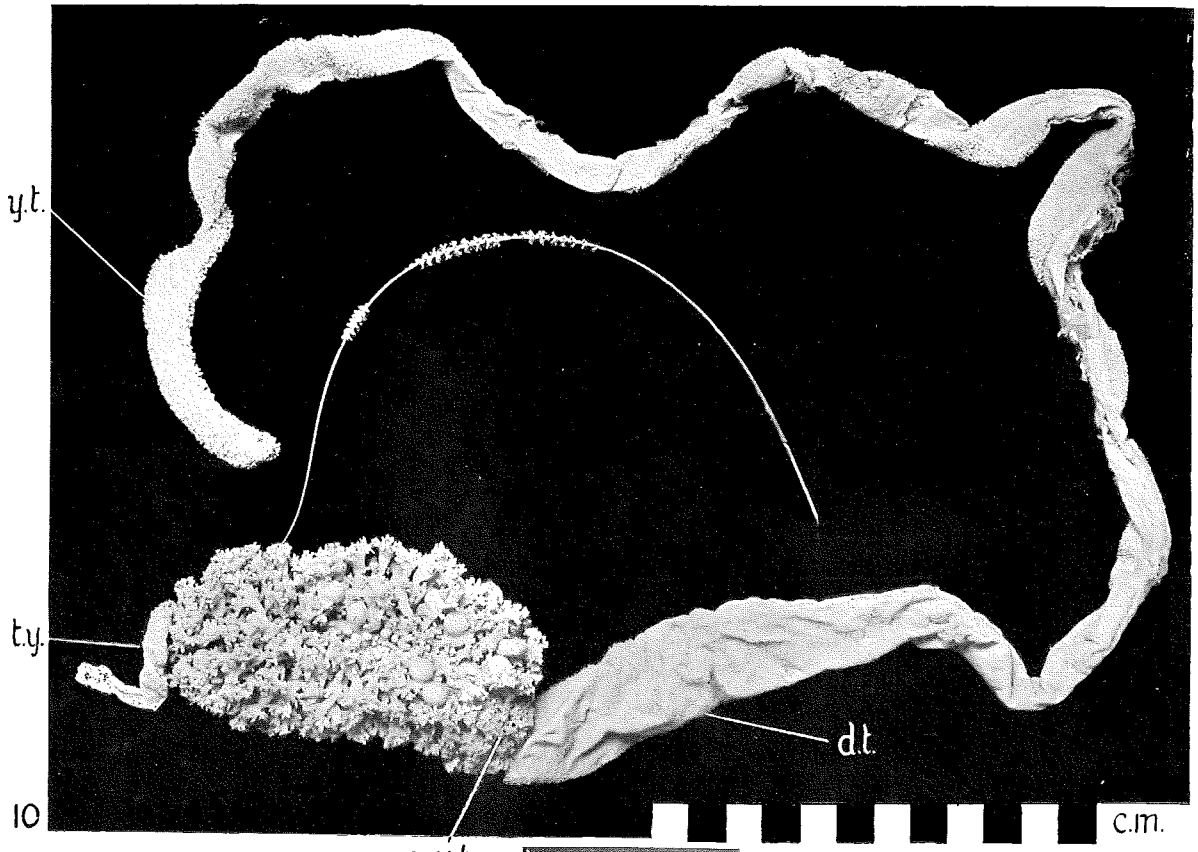
FIG. 10.—Photograph of two specimens of the hydroid *Myriothela penola* attached to the apex of the rachis of the penatulid *Virgularia*. The larger specimen is mature and measures 85 cm. Only the tentacle bearing zone of the smaller specimen (5·5 cm. long) can be seen, the blastostyles lie below those of the adult, and the hydrorhiza is attached to the same part of the *Virgularia*. × 0·48.

FIG. 11.—Photograph of part of the blastostyle bearing zone of the mature specimen of *M. penola*, with the blastostyles pushed apart to show the body of the hydranth which is devoid of tentacles in this region. The blastostyle "b.f.5, *a*" is traced in fig. 5, *a*, p. 271, where the parts are labelled. This blastostyle bears an actinula larva retained only by the egg membrane, the gonophore wall having shrunk back. Four other gonophores bear actinulae of the same age, the tentacles of which can be seen through the transparent bell wall. Other gonophores present are much younger and smaller in size. × 1·7.

FIG. 12.—*M. capensis*. Photograph is of an immature specimen which has been pulled off its substratum so as to expose the hydrorhiza. The chitinoid disks of the hydrorhiza tentacles can be seen at "h." × 4.

FIG. 13.—*M. capensis*. Photograph of an almost mature specimen attached to the brown alga *Echlonia radiata*. × 4·8.

FIG. 14.—Photograph of the basal end of the mature specimen of *M. penola* showing the adhesive hydrorhiza tentacles fixed to the rachis of the pennatulid. Many hydrorhiza tentacles are unattached. Two blastostyles bearing hydrorhiza tentacles "b.f.5, *b*" and "b.f.5, *c*" are traced in figs. 5, *b* and 5, *c*, p. 271, so that the identification of the parts may be facilitated. The majority of the adhesive tentacles shown in the photograph arise directly from the hydranth body and not from the blastostyles. The uppermost part of the rachis of the *Virgularia* is obscured by the blastostyles of both individuals, and lies towards the bottom of the figure, the apex is at "v.a." ×1·7.


y.t.
t.y.
d.t.
10
c.m.


z.y.b.
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a.e.
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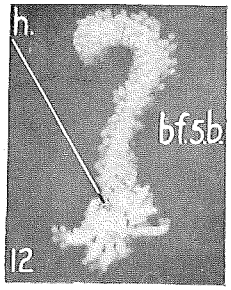
11
t.o.
l.
g.10.s.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bf.5b
12


mm
13

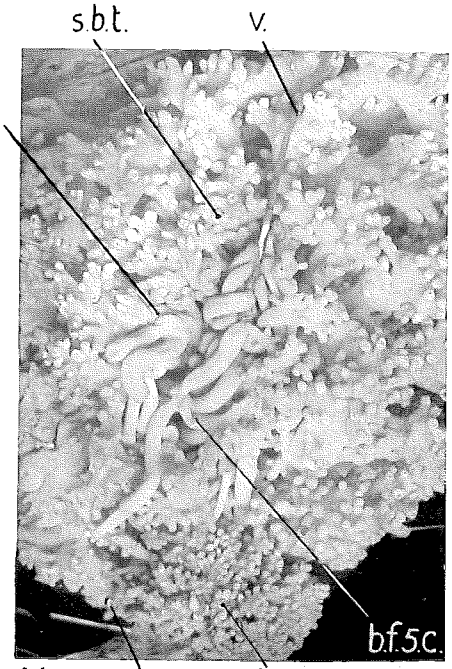

s.b.t.
v.
b.f.5.c.
14
v.a.
b.y.

PLATE II: *M. PENOLA*

(Photographs of figs. 16—21 by Dr. A. F. W. Hughes and photographs of fig. 15 by Dr. J. P. Harding)

FIG. 15.—Photograph of a blastostyle from the mature female. The series of gonophores "g.1" to "g.10" are numbered in order of age. "g.10" contains an actinula ready for liberation, and "g.1", "g.3", and "g.6" are on the opposite side of the blastostyle. Tentacles "t.1", "t.2" and "t.3" are at progressive stages of development and degeneration. × 1·8.

FIGS. 16–19 show blastostyle tentacles in sagittal section at progressive stages of development and degeneration. × 77.

FIG. 16. Young tentacle ("t.1" fig. 15) and tentacle bearing lobe of blastostyle. Mesogloea fibrils "p" are just appearing and nematocysts are few.

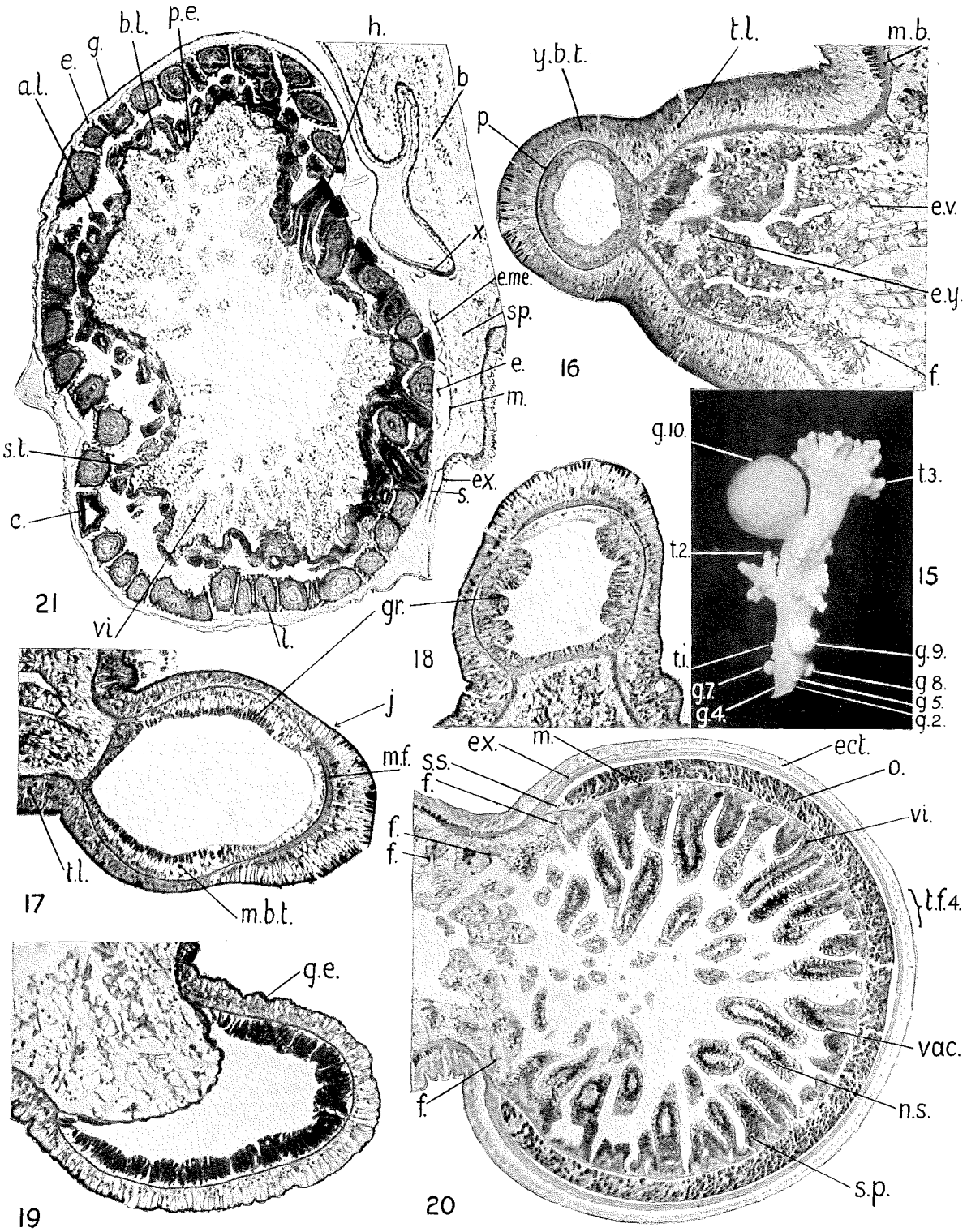
FIG. 17.—Mature tentacle ("t.2", fig. 15) with fully formed pad of mesogloea fibrils "m.f." and differentiated endoderm.

FIG. 18.—Older tentacle with shorter mesogloea fibrils, and many more granules in the lateral endoderm.

FIG. 19.—Degenerate tentacle ("t.3" fig. 15), the capitulum has merged into the stem, mesogloea fibrils and nematocysts are absent, and the undifferentiated endoderm is charged with granules.

FIG. 20.—Sagittal section of female gonophore "g.9", fig. 15. The exumbrella mesogloea is of considerable thickness "ex.", and within it can be seen the bell endoderm, but the subumbrella mesogloea and ectoderm are almost invisible at this magnification (see text-fig. 4). The dark inclusions in the endodermal villi are nutritive spheres "n.s.", and the clear dots in the villi are the vacuoles "vac." of the vacuolate cells. × 40.

FIG. 21.—Sagittal section of the female gonophore "g.10" fig. 15. The spadix has shrunk "sp.", and the actinula is now occupying the subumbrella space. The two layers of bell mesogloea "s." and "ex." and the spadix mesogloea "m." are clearly seen, and the latter adheres to the egg membrane "e." The aboral pole of the larva lies towards the spadix and is covered by adhesive hydrorhiza tentacles "h."; the rest of the larva is clothed with small tentacles "s.t.", and the long larval tentacles "l." which are folded round the body. The oral pole of the larva is not cut in this section. × 22.


a.l.
e.
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p.e.
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ex.
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vi.
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21
y.b.t.
t.l.
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e.v.
e.y.
f.
16
g.10.
t.3.
t.2
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t.1.
g.9.
g.8.
g.7.
g.5.
g.4.
g.2.
gr.
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j
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n.s.
s.p.
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g.e.
19

PLATE III: *M. CAPENSIS* and *M. PENOLA*

(Photographs of figs. 22—24 by Dr. I. Manton; photographs of figs. 25—28 by Dr. A. F. W. Hughes.)

FIG. 22.—Sagittal section through the apex of the capitulum of a blastostyle tentacle of *M. penola* showing the superficial layer of heteronemes and two desmonemes. The cnidopod of the desmoneme "d." near the surface is straight (the proximal part of the cnidopod is not in the same plane), compare fig. 23. × 385.

FIG. 23.—Similar section to fig. 22, showing a desmoneme in the deeper part of the ectoderm with its coiled cnidopod. × 770.

FIG. 24.—Sagittal section through the capitulum of a long larval tentacle from the actinula of *M. penola* showing details of the nematocysts, × 770; compare with the smaller magnification shown in fig. 29, pl. IV.

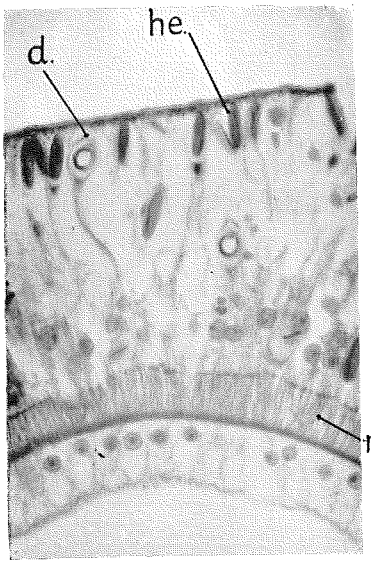
FIG. 25.—Part of sagittal section of a mature body tentacle of *M. penola*, the position of this region is shown in text-fig. 2 "f.25". The capitulum nematocysts are seen at the side of the apical pad of mesogloea fibrils. The endodermal circular muscle processes "c.m." lie against the right-hand side of the mesogloea; below lies the mesogloea support of the sphincter at the base of the capitulum. × 280.

FIG. 26.—Transverse section through the wall of the basal part of a mature blastostyle of *M. penola*. Close-set villi are separated by ciliated grooves, and the binucleate nature of the vacuolate cells is clearly seen. × 77.

FIGS. 27 and 28.— Transverse sections of the body wall of *M. capensis* and *M. penola* respectively to show the difference in the proportions of the parts of the mesogloea.

FIG. 27.—Body wall of *M. capensis* from the middle of the tentacular region. × 280.

FIG. 28.—Body wall of *M. penola* from the upper third of the tentacular region. × 264.



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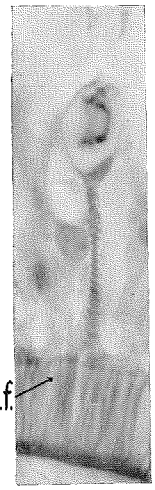

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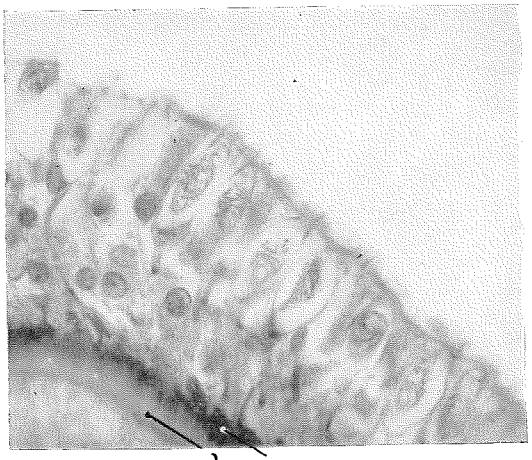

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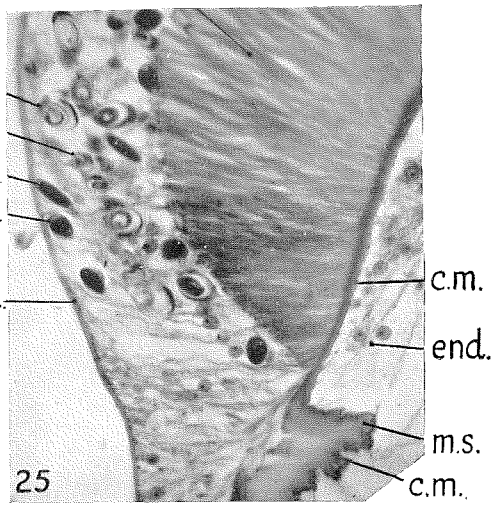

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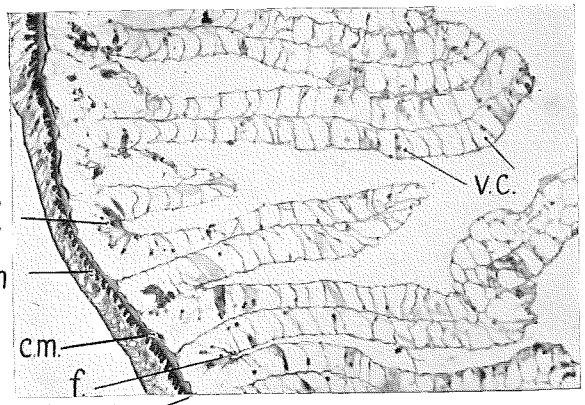

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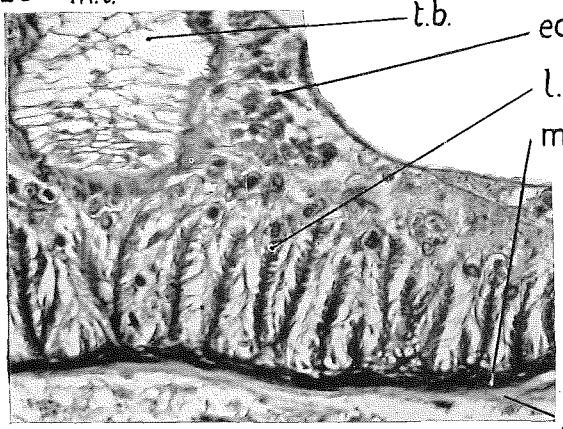

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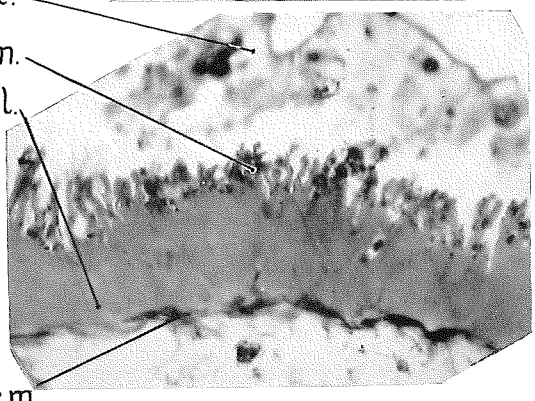

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PLATE IV: *M. PENOLA*

(Photographs by Dr. A. F. W. Hughes.)

FIG. 29.—Sagittal section through the capitulum of a long larval tentacle of the actinula. The cnidopods "c.n." of the atriches are inserted into the outer layer of mesogloea, for details of the capsules see fig. 24, pl. III, and for stem of the tentacle see fig. 33. × 300.

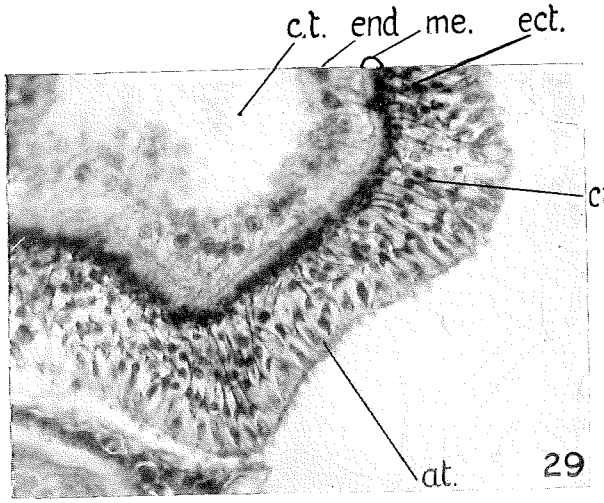
FIG. 30.—Section of the actinula body wall passing through the base of a long larval tentacle and showing the endodermal valve situated in this position. The limits of the mesogloea, so clear in a Mallory stained preparation, have been touched up on the photograph, as there is such a small difference in intensity between the reds and the blue colour. The dark spots in the villi are nutritive spheres and endodermal nuclei. × 80.

FIG. 31. Sagittal section through the tip of an adhesive hydrorhiza tentacle from the actinula. For the appearance of the whole tentacle at a smaller magnification, see fig. 21, pl. II, "h." The bases of the terminal ectoderm cells, which are laden with fuchsin-staining granules (black), are seen to be inserted into and through the mesogloea layer. These granules will later form the chitinoid disk. × 220.

FIG. 32.—Actinula larva removed from gonophore just before its liberation. The long larval tentacles have been uncoiled to expose the body. × 2·5.

FIG. 33.—Section through the middle region of the actinula showing the short body tentacles in sagittal section, and the stem of a long larval tentacle lying outside these and cut in longitudinal section (for capitulum, see fig. 29). × 80.

FIG. 34.—Section through the oral pole of the actinula showing the short body tentacles which are here not covered by the long larval tentacles. The villi are here so close together that there is no room for the peripheral endodermal layer of darkly staining cells; compare figs. 33 and 21. The gonophore wall and the stretched egg membrane are seen outside the tentacles. × 135.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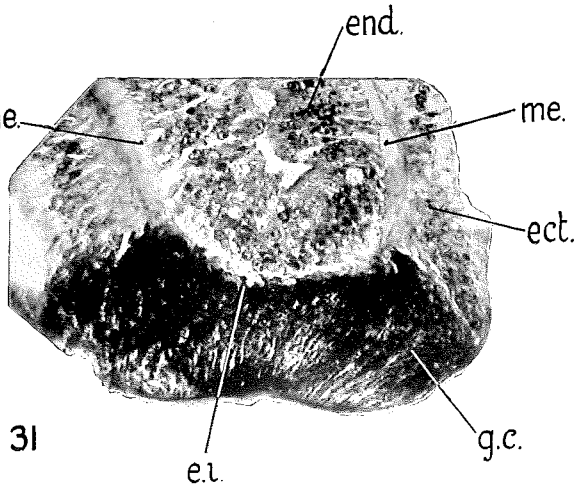
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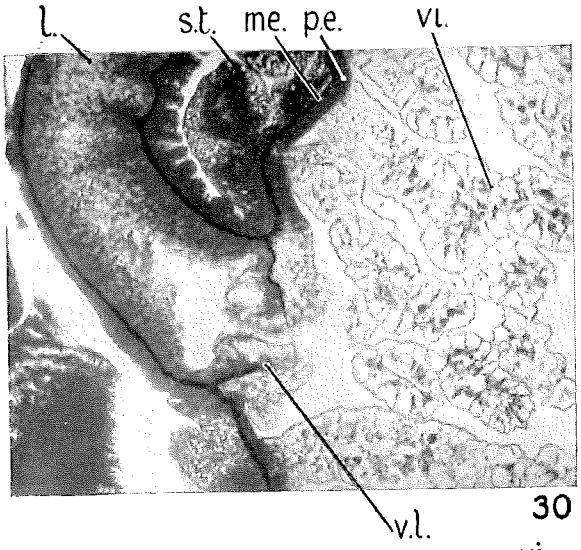
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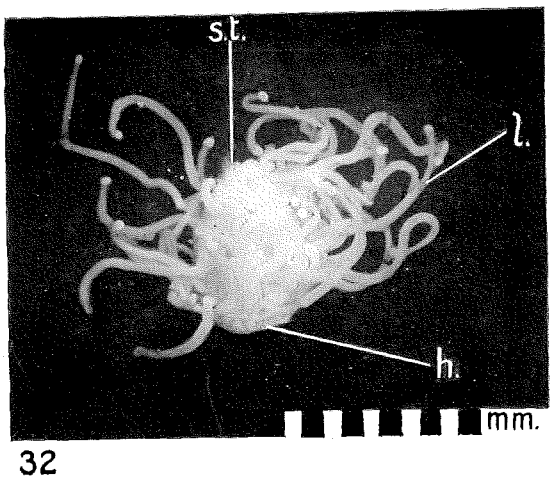
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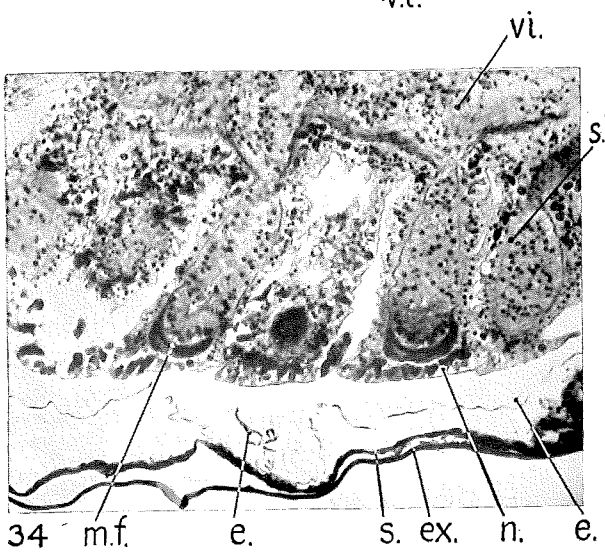
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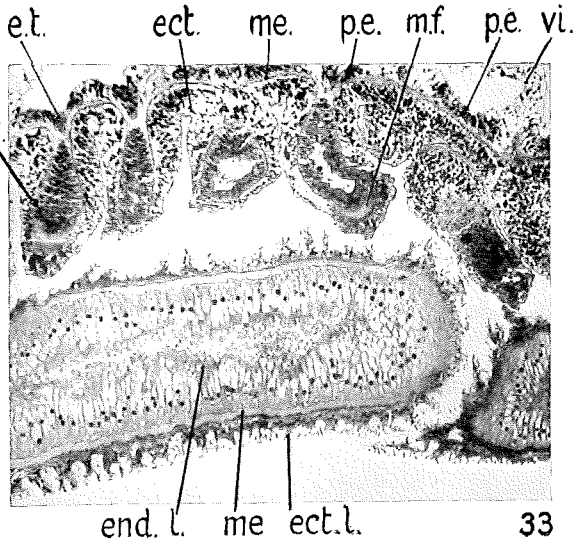
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