THE

VOYAGE OF H.M.S. CHALLENGER.

ZOOLOGY.

REPORT on the ACTINIARIA dredged by H.M.S. Challenger during the years 1873–1876. By Prof. RICHARD HERTWIG.

INTRODUCTION.

IN investigating the Anthozoa the majority of earlier naturalists were content to give the most exhaustive description possible of the parts which are externally visible in the living animal, and of the skeleton where such a structure existed; on the other hand, they only went slightly into more exact anatomical details, as the observation of these presented great difficulties. The majority of the Anthozoa are not sufficiently transparent to allow of the recognition of the form and arrangement of the organs in the living animal, whilst after death they are so contracted that all the parts become misplaced in many ways and pressed one against the other, and can only be demonstrated, with great care, by means of knives and scissors. Up to the present time the systematic survey and characters of the orders, families, and genera are founded upon external characteristics which are of less morphological importance.

In this way many errors arose, which have only become intelligible from the work of the last decades. Following the steps of Agassiz (Contrib. to the Nat. Hist. of the United States, vol. iii.), Moseley (Phil. Trans., vol. clxvi. pt. 1, p. 91, 1876; vol. clxviii. pt. 2, p. 425, 1878) has shown in the most convincing fashion that many hydroid polyps which form skeletons have been long placed among the reef-forming corals, and that, moreover, in consequence of the skeletal formation alone having been taken into consideration, many Octocorallia have been disconnected from their natural systematic place, and united to forms entirely remote. It cannot by any means be asserted that

as for example *Halcampa clavus*. We may gather from this how closely the Edwardsiæ are connected by transition forms with the other Actiniæ, and how advisable it is to discuss them along with the latter, and to separate them from the Alcyonaria. From this point of view the constitution of the tentacles is of great importance, as they in no way resemble the tentacles of the Alcyonaria.

Tribe V. Zoantheæ.

Actiniaria with numerous septa of two different kinds, smaller, imperfect, sterile microsepta, and larger perfect macrosepta furnished with reproductive organs and mesenteric filaments; the two kinds usually placed alternately, so that each pair is composed of a larger and a smaller septum; two pairs of directive septa at the ends of the sagittal axis, one pair containing only macrosepta, the other only microsepta; only one œsophageal groove, corresponding to the larger directive septa; animals usually forming colonies; wall usually traversed by ectodermal canals, and having the outside encrusted with foreign bodies.

Zoologists differ very much in their opinions as to the limits and the definition of the Zoantheæ. Milne-Edwards (Hist. des. Corall., tom. i. p. 298) includes in this division only colonial, sessile forms which increase by basal gemmation and have a leather-like sheath hardened by encrustation with sand granules (faux polypiéroïde); Gosse agrees with him (Actinologia Britannica, p. 295), but considers the encrustation with sand granules as a secondary character. Most zoologists keep to the definition given by Milne-Edwards and Gosse.

In 1856, Steenstrup described an Actinia under the name *Sphenopus marsupialis*, which closely resembles the Zoantheæ, but is distinguished from them by not forming colonies and not being sessile. (Overs. Kongelige danske Videnskab. Selskabs Forhand., p. 37, 1856). As Gray (Proc. Zool. Soc., p. 235, 1867) included this Actinia among the Zoantheæ, he set aside the characters used by Milne-Edwards, viz., the formation of colonies and the sessile mode of life, but without replacing them in the diagnosis by new characters, which would be at once common to all Zoantheæ, and distinctive from other Actiniaria. To what degree the sharp limitation of the Zoantheæ suffered from this may be seen from the fact that Gray included in this tribe the genera *Edwardsia*, *Halcampa*, &c.

The discovery of *Sphenopus* led to difficulties as to the limitation of the Zoantheæ which were also not obviated by the fact that Verrill considered *Sphenopus* to be related to the Edwardsiæ, to which it has certainly a strong external resemblance. But anatomically *Sphenopus* agrees so thoroughly with the Zoantheæ that it cannot be separated from them. A study of the arrangement of the septa is the only possible means of discovering distinctive characters for the division.

Angelo Andres (Quart. Jour. Micros. Sci., new ser., vol. xvii. p. 221, 1877) and my brother and myself (Actinien, p. 127) had already pointed out that the position of the septa in the Zoantheæ was regulated on an entirely different principle from that in other Actiniaria, though G. v. Koch was the first to find out the true nature of it. He discovered what I fully corroborate, that the septa present are of two different sizes (Morphol. Jahrb., Bd. vi. p. 359, 1880). The larger or macrosepta only reach the œsophagus and bear reproductive organs and mesenteric filaments, whilst the smaller or microsepta are sterile and end on the oral disk; the latter are not, as I formerly supposed, young septa destined to be developed into larger, but are really rudimentary formations.

Both the larger and the smaller septa bear muscles on both sides: one side bears longitudinal fibres, the layer of which is, however, only slightly pleated, the other side bears fibres which rise obliquely, and are homologous with the transverse muscular fibres of the other Actiniæ, though they can easily be mistaken for longitudinal fibres in transverse sections. There is here, therefore, a predisposition to the paired arrangement of the septa, the existence of which was first recognised by G. v. Koch. Each pair consists of a small and a large septum, having longitudinal muscles on the faces turned towards one another (Pl. XIV. fig. 2). The two pairs of directive septa form an exception, however, as one pair of them, the ventral, contains large septa only,—the other pair, the dorsal, only small septa; in some Zoantheæ, we must also except two pairs of ordinary septa which lie right and left at a little distance from the small directive septa, and contain macrosepta only (Pl. XIV. fig. 3).

The manner in which the larger and smaller septa are distributed can be more accurately determined if we start from the directive septa, and disregard provisionally the grouping in pairs. In the Zoantheæ, as in all Actiniæ, two kinds of septa alternate; in the septa of the one system the muscles are disposed in the same way as they are in the ventral pair of directive septa, whilst in the other system the case is reversed, and they have the same disposition as they have in the dorsal pair of directive septa. The septa which have the same arrangement of the muscles as the small dorsal directive septa, viz., the dorsal septa, are likewise small, whilst the others, the ventral septa, are strong; it is only in the neighbourhood of the small directive septa that the conditions are reversed as the dorsal septa are strong, and the ventral septa are weak. We can therefore divide the ordinary pairs of septa into two different regions; in the one (the larger, or ventral region), the ventral septa of the single pairs are macrosepta, and the dorsal septa are microsepta, whilst in the other (the dorsal region), the reverse is the case, and the dorsal septa are macrosepta. When all the pairs of septa are equally developed, the two regions are bounded on either side by microsepta, but those two microsepta are often wanting left and right, and in this way the pairs formed of macrosepta alone, which have been already mentioned, are produced: these contain two large dorsal septa of the dorsal region and two large ventral septa of the ventral region.

The correlation, which exists in all Actiniaria between the œsophageal grooves and the directive septa, is also shown in the Zoantheæ, for there is only one œsophageal groove, whilst the other is wanting, in correspondence with the rudimentary nature of the directive septa to which it should belong. The tentacles, on the other hand, are equally developed and placed in two circles, the inner of which belongs to the intraseptal spaces, the outer to the interseptal spaces.

All the characters taken into account by former naturalists in the diagnosis of the Zoantheæ are of subordinate value when compared with the peculiar conditions just mentioned. The animals are united into colonies either by means of branched stolons or by means of a broad basal plate, but there are also solitary forms which are embedded with their rounded aboral ends in the sand like the Edwardsiæ. The entire surface of the wall is often permeated with foreign bodies, though in many specimens such encrustations are wanting completely. Finally, the canals, which make their way from the ectoderm into the wall, where they become branched and connected into plexuses, are confined to certain forms only.

In the division of the Zoantheæ I agree chiefly with Verrill, who divided the species forming colonies into four genera; *Mammilifera*, *Zoanthus*, *Palythoa*, and *Epizoanthus*. The former two are distinguished from the latter by the absence of sand encrustations. *Zoanthus* and *Epizoanthus* are distinguished from *Mammilifera* and *Palythoa* by the fact that in the former two the polyps project plainly above the common basis, whilst in the latter two they are united up to the free end by the basal cœnenchyma. I have restricted the family Zoanthidæ to those genera which form colonies, and have associated all those which are solitary under the name Sphenopidæ.

Family Zoanthidæ.

Zoantheæ forming colonies; the individuals of a colony connected with one another by endodermal canals, which run out from the gastric space at the lower end of each polyp.

Zoanthus, Cuvier, *pro parte*.

Zoanthus, Verrill.

Zoanthidæ without sand encrustations and with a slightly developed cœnenchyma consisting either of a plexus of stolons or of a thin plate; the single polyps projec to a considerable height above the cœnenchyma.

Zoanthus, sp. (?) (Pl. XIV. figs. 1–4 and 6).

Habitat.—Bermuda Islands.

Dimensions.—(Of the individual polyps): height, 0·1–1·3 cm.; breadth, 0·1–0·4 cm.

Numerous species of the genus *Zoanthus* have been described which resemble one another closely, and probably only differ slightly in their anatomy, so that the species can only be determined by the colour, the number and arrangement of the tentacles, &c. This is the reason why I have not given any specific name to the single specimen of the genus *Zoanthus* found among the Challenger material, in which the colour of the body and the nature of the tentacles could not be made out, and why I have refrained from giving any diagnosis of species, as from insufficient knowledge of the closely allied species it is impossible to determine which characteristics belong to the whole genus and which to the individual species.

The colony, which was about 4 cm. long and 2 cm. broad, was firmly attached to a stone, and consisted of some thirty individuals varying greatly in size. The smallest of these are little knobs which hardly project 1 to 2 mm. above the cœnenchyma, the largest are long cylindrical tubes, more than 1 cm. in length. They lie so thickly compacted that the cœnenchyma is almost entirely covered, and only shows here and there as a thin plate. The cœnenchyma is abundantly developed on the margin into stolons, which are alternately broad and narrow.

I made a thorough anatomical examination of three individual polyps of different sizes, which were highly contracted like all the animals of the colony. The upper end of the wall is not only contracted but inverted a little; the only indication of the point at which we can reach the interior of the body is a small navel-like depression. Apart from the folds caused by contraction, the surface of the body is perfectly smooth.

The wall (Pl. XIV. fig. 4) is of considerable thickness, and consists histologically of a homogeneous fundamental substance, with fine fibres embedded in it. The fibres are hardly double contoured, are slightly waved, and run sometimes directly, sometimes obliquely, from one epithelial surface to the other. They begin at the endoderm with a granular enlargement which seems to pass directly into the epithelium; towards the ectoderm they branch repeatedly behind one another. They are furnished with nuclei, and therefore bear a strong resemblance to the muscular fibres of the Ctenophora, but their state of preservation did not admit of determining the histological value of the fibres.

The cells of the connective substance are strongly granulated bodies, either rounded or branched.

Finally, we find canals in the wall, such as do not exist in any other Actiniaria, though they are found in the Alcyonaria. These canals vary greatly in diameter; the smaller are simple cords of cells, and only the larger ones show a lumen surrounded by a layer of epithelium. As the canals repeatedly ramify and anastomose, they form a thick net-work, which extends from the endoderm to the ectoderm, but is thickest near the latter. Kölliker's observations show that in the Alcyonaria the canals are produced from the ectoderm, which is also the case in *Zoanthus*; I have repeatedly found

that the epithelium of the body-surface sinks like a funnel into the mesoderm, where it is prolonged into a broad or narrow canal which soon begins to throw out branches (fig. 2).

The ectodermal epithelium is covered by a fibrous cuticle, which recalls the "epidermis" of *Phellia pectinata* and *Cereus spinosus*. The endodermal epithelium has produced a thin, circular muscular layer, and is traversed by small, roundish, sharply-contoured bodies. I consider these bodies as parasitic, unicellular organisms of the same kind as those which my brother and I have already observed in various species of Actiniæ. There was no visible trace of the usual yellowish and greenish colour, but this was probably owing to the preservation in spirit.

In the inverted part of the wall I found a sphincter of a very peculiar nature (Pl. XIV. fig. 1). It consists of two perfectly separate portions, a larger, which begins at the outer part of the wall, bends round at the inverted edge, and extends a little way into the invaginated part, and a smaller, which lies at the boundary between the wall and the oral disk. When the animal is expanded, this second portion of the sphincter will lie above the larger portion of the muscle; when the animal is contracted it occupies the lowest part of the invaginated wall. A space without muscles, which does not contract, and, therefore, becomes pleated, lies between the two portions.

Both parts of the sphincter are mesodermal and placed at an equal distance from the endoderm and the ectoderm; their bundles of fibrillæ are arranged irregularly and repeatedly crossed and interwoven in their course, so that the same transverse section passes obliquely through some, transversely through others. The bulk of them lies in the inverted part of the wall, whilst the muscles merely form a thin layer in the outer part of the wall.

The oral disk bears a double corona of small tentacles, corresponding in number to the septa, in that part of its periphery which is contiguous to the wall. The inner tentacles communicate with the intraseptal spaces, the outer tentacles with the interseptal spaces, the two are therefore placed alternately. The muscular system of the oral disk and of the tentacles is ectodermal and extended in a smooth layer.

The distribution of the muscles can be very well recognised in the septa of the strongly contracted polyps. The longitudinal muscular lamella is pleated both in the small rudimentary septa and in the large septa so as to form a small muscular pennon, whilst the fibrillæ which rise obliquely are less strongly developed (Pl. XIV. fig. 2). The paired grouping of the septa is consequently very distinct, and we can also easily distinguish the two pairs of directive septa from the ordinary pairs. The number of the latter varies according to the size of the animal. In the largest polyp examined, there were in all twenty-nine pairs of septa (Pl. XIV. fig. 3). Of the two pairs of opposite directive septa, one pair is rudimentary, does not bear mesenteric filaments, and does not reach the œsophagus, whilst the other pair is perfect, bears mesenteric filaments,

and does reach the œsophagus. The remaining twenty-seven pairs are distributed in the space to the right and left of the œsophagus, so that thirteen pairs lie on the one side and fourteen pairs on the other. Each pair consists of a larger perfect macroseptum, and a smaller imperfect microseptum.

If we term the side marked by the larger pair of directive septa, the ventral side, we see that almost all the pairs of septa are placed in such a way that the larger, perfect septa are directed ventrad, the smaller imperfect septa dorsad; the two pairs of septa next to the small dorsal pair of directive septa form the only exception to this rule as their dorsal septa are the larger, their ventral septa the smaller. We can therefore distinguish two systems of pairs of septa, a dorsal and a ventral. The result is the following perfectly regular arrangement of the septa: as a rule the larger and smaller septa alternate, but at three points two small septa lie between two large septa, viz., at the dorsal end where the small pair of directive septa lie, and a little way further right and left from the directive septa, where the dorsal and the ventral systems of septa are mutually bounded by small septa.

At the ventral end, on the other hand, we find three spaces between large septa, in which the small septa are wanting, viz., the intraseptal space of the large directive septa, and the two adjacent interseptal spaces. To explain this more clearly I give formulæ for the dorsal (1), and for the ventral side (2), showing the distribution of the septa.

1. Dorsal side, &c. *gk gk* ⋮ *kg kg* <u>*k*</u> | <u>*k*</u> *gk gk* ⋮ *kg kg* &c.
2. Ventral side, &c. *kg kg* *kg kg* <u>*g*</u> | <u>*g*</u> *gk gk* *gk gk* &c.

In these formulæ the letter *g* indicates the large septa, *k* the small septa, the dotted lines the boundaries between the dorsal and ventral systems, the black lines the position of the sagittal axis, the underlining the directive septa.

Three of the twenty-seven pairs of septa are still imperfectly developed, and much smaller than the others; the two pairs lying to the right and left of the ventral directive septa, and the extra pair of septa which is only present on the one side. As I discovered from other polyps of the same *Zoanthus* colony, the two pairs named at first are the youngest in age. Their macrosepta resemble on the whole the small septa of the other pairs; they have no mesenteric filaments, and the uppermost section only reaches to the œsophagus.

I got an explanation of the manner and sequence in which the septa are developed from examination of a small polyp, only a few millimetres high. It had forty-eight septa in all; exclusive of the directive septa, there were twenty-one on one side and twenty-three on the other (Pl. XIV. fig. 6). In the region of the smaller directive septa, the conditions were the same as in the developed polyps, but towards the ventral side the

septa all became smaller as they approached the larger directive septa; on one side only the first seven, on the other side only the first six, macrosepta reached the œsophagus, then followed five other macrosepta which still decreased in size, so that the smallest, which came next the ventral directive septa, hardly projected at all into the gastric space. The microsepta left off still earlier, for they became smaller in exact proportion to the macrosepta, and as they were in general less they disappeared sooner. On the ventral side the directive septa only were perfect, and were separated by a wide interspace from the septa which were next in development.

Two facts may be deduced from the above observations: (1) The macrosepta and microsepta can be distinguished from the first by the difference in size; they develop independently and at different periods, whilst in the Hexactiniæ and Paractiniæ the septa of a pair start simultaneously and are of the same size from the first. (2) The septa are not produced regularly in the periphery of the body of the Actinia, but within a limited, ventral productive zone. The dorsal septa are therefore the oldest, the ventral septa the youngest, with the exception of the directive septa, which are developed very early.

The third polyp was intermediate between the two specimens described, both in the size and the number of its septa, which amounted to fifty-two. A more minute description of it is therefore unnecessary, and I shall conclude my remarks on the Zoantheæ with some details as to the structure of the septa.

A cellular cord, or a canal filled with cells, runs in the supporting lamella of the septa in immediate proximity to the wall (Pl. XIV. fig. 2). It is usually divided into several cords by commissures of the supporting lamella and is of such strength that the whole septum becomes visibly and locally thickened. I never could make out any connection between this septal canal and the ectodermal cords of the wall in any of the numerous sections which I prepared, and I am inclined to believe that it is produced from the endoderm. My reason is that I have observed that the same roundish bodies which are to be found in the endoderm, which I regard as parasitic, unicellular organisms, force their way into the septal canal, but never into the canals of the wall. I attach less importance to the origin of the canals, as they seem to be connected with the endoderm here and there where the septa spring from the wall. However, the figures, which led me to consider such a mode of connection as probable, did not furnish sufficient proof of its actual existence.

The structure of the mesenteric filaments is essentially the same as in the Actiniæ; during the greater part of their course they consist entirely of the median glandular streak, and it is only a little way below the œsophagus that they are widened by the addition of paired ciliated streaks, the surface of which is indented at regular intervals by transverse furrows. This upper section of the mesenteric filaments appears to me identical with the "flattened organs" described by Verrill as "having a curved or crescent form and a transversely striated surface,—attached to the principal radiating lamellæ, near the base of the stomach" (Trans. Connect. Acad., vol. i. p. 494). Verrill, Andres, and others

erroneously consider these organs as peculiar to the Zoantheæ, and explain them to be gills, a view which is, however, quite unwarranted.

I did not find reproductive organs either in the three polyps minutely examined or in several others which I only opened longitudinally.

The cœnenchyma consists of the same tissue as the wall of the polyps, but the proportions of the component parts are altered. The branched fibres are more scanty and crossed irregularly in every direction, whilst the cells of connective substance are remarkably abundant, and many of them have assimilated black granules, and so become branched pigment cells. The ectodermal canals are more numerous than usual, and form a thick net-work; it is often difficult to distinguish them from the endodermal connective tubes, which run from one polyp to another, and which also may become branched into small vessels.

Epizoanthus, Gray.

Zoanthidæ, in which the outer layer of the body is encrusted with sand granules; cœnenchyma a thin lamella usually stretched over Gasteropod shells which have been abandoned by their owners and are inhabited by *Paguri*; polyps projecting considerably above the surface of the cœnenchyma.

Epizoanthus parasiticus (Pl. III. figs. 2, 9, 12; Pl. XIV. fig. 5).

Zoanthus parasiticus, Verrill, Memoirs Boston Soc., vol. i. p. 34.

The upper part of the wall of the polyps, which is a few millimetres broad, separated from the lower by a circular furrow, forming a shallow disk when contracted, and covered with forty radial ridges; tentacles seventy to eighty, filament-shaped, arranged in two rows. Colony parasitic upon a Gasteropod shell, the calcareous components of which have been absorbed and replaced by the cœnenchyma.

Habitat.—Station 235. June 4, 1875. Lat. 34° 7′ N., long. 138° 0′ E. Depth, 565 fathoms. Two specimens.

Dimensions.—Height of the individual polyps, 1·5–2·5 cm.; breadth, 1·4–1·7 cm.

Epizoanthus parasiticus, of which there were two specimens among the Challenger material, belongs to those Actiniaria which settle as parasites on shells inhabited by hermit crabs. As Verrill, who was the first to give a detailed account of *Epizoanthus*, observed, the Gasteropod shell is almost entirely dissolved, even the columella being completely replaced by the cœnenchyma of the parasite. The form of the shell, however, is still retained, and the hermit crab continues to live comfortably inside, undisturbed by the changes which his home has undergone. The snail shell can only be recognised externally by the wide opening and the point which projects as a stumpy knob.

The number of the individual polyps and their arrangement on the surface of the body is almost the same in both the colonies investigated. Eight polyps are uniformly distributed along that circumference which divides the upper half of the shell from the lower when the *Pagurus* is crawling about on the bottom; the polyps just mentioned are the largest and most powerful of the colony, and are plainly most favourably placed for acquiring nutriment, as they are always at a little distance from the bottom (Pl. III. fig. 2). A medium-sized polyp rises nearly in the middle of the convex upper side of the colony, and in one colony a second smaller polyp lay close beside it. On the lower side an obviously rudimentary polyp grows on the posterior margin of the opening of the shell (fig. 9); it has the best position on the lower side, which is on the whole disadvantageous to development, as it is raised from the bottom as long as the *Pagurus* is crawling about, and only lies upon it when the *Pagurus* has retreated into the shell. In the colony consisting of eleven individuals there was the indication of a twelfth between the eight marginal polyps. It may be taken as a general rule that the distribution of the polyps on the surface of the colony is not accidental, but that those spots are preferred in which the animal has room for free development, and also a convenient position for acquiring nutriment.

The whole surface of the colony is covered by a dirty yellow substance permeated by sand granules, which can be easily scraped off; underneath this the fundamental substance of the wall becomes visible, which resembles cartilage in consistency and colour, and is also hardened superficially by sand granules. This hardened layer is so thin that it can be removed by sections parallel to the surface, and yet leave sufficient fundamental substance both in the cœnenchyma and the wall for transverse sections. These conditions were extremely favourable to examination, so that I regretted the more that the colonies were not better preserved.

The large marginal polyps were 2–2·5 cm. high, 1·4–1·7 cm. broad, and slightly flattened from above downwards. The upper part of the wall is inverted, and forms a horizontal roof; this might be taken at first sight for the oral disk, as it is separated from the bulk of the wall by a circular furrow, and also differs in its structure, being furnished with numerous (about forty) radial ridges, already observed by Verrill, which are broad where they begin at the margin and become narrower as they run inwards. The radially striated part of the wall is distinguished from the oral disk by being encrusted with sand granules like the rest of the wall. In the middle of this horizontal roof is a fissure running parallel to the margin of the colony, through which, in many polyps, the points of the incompletely retracted tentacles peep out. Through this fissure we may reach the inside of the polyp, first passing through the space lying above the oral disk.

The fundamental substance of the wall is homogeneous, but in transverse and longitudinal sections it shows a striation parallel to the surface of the body, which looks as if it were deposited in layers (Pl. XIV. fig. 5). The striated layers are crossed by fine

fibres, which end in repeated branches under the ectoderm like those of *Zoanthus*, but are more numerous, more sharply contoured and waved repeatedly in their course. Besides the branched corpuscles of connective tissue, small and large islands of cells lie in the supporting substance; I presume that these islands of cells represent the system of cellular cords which are always found in *Zoanthus*, but are wanting in *Epizoanthus*. At certain points they are prolonged into longish sausage-shaped cords, several of which may also become united into a dendritic figure. In many parts of the cœnenchyma I still found the remains of a branched vascular system, which formed very small meshes, especially about the endodermal connective tubes. I therefore feel justified in my conjecture that the oval islands of cells are caused by the unsatisfactory state of preservation, and are produced by the disintegration of a system of anastomosing cords.

A powerful circular muscle lies in the horizontally inverted part of the wall; it is broad at the beginning of the oral disk and becomes narrower from within outwards. The imperfect state of preservation did not allow me to give any histological description of its bundles of fibrillæ which run in the mesoderm between the ectoderm and endoderm. I could not make out that it was divided into a larger and a smaller part as in *Zoanthus*.

The large size of the individual polyps of *Epizoanthus parasiticus* renders them admirably suited for dissection by means of knife and scissors. If we cut open the animal longitudinally and spread it out by turning back the upper end of the wall (Pl. III. fig. 12), we find adjacent to the latter, the double corona of long, filamentous tentacles, the aggregate number of which amounts to seventy or eighty. The tentacles of the inner row alternate with those of the outer. The oral disk extends far down, and is covered with shallow radial furrows corresponding to the tentacles. It is divided by a distinct thickening from the œsophagus, in which our attention is at once attracted to the single œsophageal groove. When spread out the œsophageal groove forms a scutiform plate, separated from the adjacent parts of the œsophagus by longitudinal furrows, and divided by a more distinct median furrow into a right and a left half; it is prolonged far below the lower margin of the œsophagus, so that it is almost twice its length. The triangular lappet formed in this way is likewise divided into two by the prolonged longitudinal furrow, and deeply indented at the end.

Below the lower margin of the œsophagus there are seen thirty-two to thirty-four septa, the zigzag margins of which are caused by the reproductive organs; these are macrosepta, the microsepta only becoming visible when the others are folded back. I examined the mutual relations of the two kinds of septa in transverse sections and with essentially the same result as G. v. Koch in *Epizoanthus axinellæ* (Morphol. Jahrb., Bd. vi. p. 359, 1880). Two pairs of directive septa lie at the ends of the sagittal axis, the dorsal pair consisting of microsepta, the ventral of macrosepta; the latter only reach the œsophagus and are

attached close to the œsophageal groove, which is also ventral. Besides these there are fifteen pairs of septa on either side (if the aggregate number of pairs of septa is increased to thirty-three, there are sixteen on one side and fifteen on the other), which consist of (1), a pair of septa adjoining the dorsal directive pair, and having the dorsal septum larger than the ventral; (2), thirteen pairs of septa situated towards the ventral aspect of the body, and having the ventral septum larger than the dorsal; and (3), a pair consisting of two macrosepta and lying between the two above mentioned groups. The distinction then between *Epizoanthus parasiticus* and *Epizoanthus axinellæ* on the one hand and the true *Zoanthus* on the other, is that in the latter the two systems are separated by microsepta, in the former by macrosepta, so that a pair of septa is madeup of one septum from either system.

The remarks made by me on the septal canals and mesenteric filaments of *Zoanthus* apply equally to *Epizoanthus parasiticus*. The reproductive organs were well developed, and seemed to lie only on the macrosepta, and that without exception; they were testes in the specimen which I examined in transverse section.

The individual animals of the *Epizoanthus* colony were united at the base by a tolerably thick crust, in which numerous canals run from one polyp to another; all the canals extend with repeated anastomosis in one and the same layer of the cœnenchyma. Hence if we cut a colony through longitudinally, the cœnenchyma is separated by the vascular stratum into a broader external and a narrower internal layer; the character of the tissue is the same in both, except that the inner layer is without branched fibres. The gastric spaces of all the polyps reach as far as the vascular stratum, in which lies a very large canal surrounding the opening of the shell like a ring (Pl. III. fig. 9).

The hollow of the shell enclosed by the cœnenchyma is lined by a chitinous membrane, which lies firmly attached to the thin layer of the cœnenchyma, and has a structure of its own. Two lamellæ are separated from one another by an interspace, and are connected by perpendicular septa parallel to one another which divide the interspace into numerous tubes and smaller prismatic spaces. I leave it an open question whether this chitinous membrane is the last remains of the Gasteropod shell or a cuticular formation secreted by the superficial epithelium of the *Epizoanthus*.

The mode of life of *Epizoanthus parasiticus* is the same as that of *Epizoanthus papillosus* and *Epizoanthus cancrisocius*, the former of which was described by Gray in the Proceedings of the Zoological Society, 1867, p. 237, the latter by Studer in the Monatsberichten der Berliner Academie, Jahrg., 1878, p. 547. Both forms settle on Gasteropod shells, occupied by a hermit crab, and completely absorb the calcareous parts of the shell. The upper section of the wall of *Epizoanthus papillosus* appears to be of the same nature as that of *Epizoanthus parasiticus*. I draw this inference from Gray's words in the description given of the individual polyps, "The apex when expanded is flat, with close, radiating white lines." It is therefore still a question whether these are merely allied

species or whether *Epizoanthus papillosus* and *Epizoanthus cancrisocius* are identical with *Epizoanthus parasiticus*.

Family SPHENOPIDÆ.

Solitary Zoantheæ with the posterior end of the body rounded.

Sphenopus, Steenstrup.

Sphenopidæ with thick wall, the uppermost layers of which are encrusted with sand granules; with strong mesodermal sphincter.

Gray, in his system of the Zoantheæ (Proc. Zool. Soc., 1867, p. 236), has erected several genera, in which the individual polyps remain solitary, and are either firmly attached to the bottom or stick in the sand by means of the rounded body-end, viz., the genera *Isaurus*, *Pales*, *Orinia*, and *Sphenopus*. As no thorough anatomical studies have been made as yet of all these forms, it is doubtful in the meantime whether they ought to be placed among the Zoantheæ or not. *Sphenopus* is the only one of which I can affirm that it belongs to the Zoantheæ, as the macrosepta and microsepta are visible in regular order, and the œsophagus has only one œsophageal groove.

Sphenopus arenaceus, n. sp. (Pl. II. fig. 10, Pl. XIV. fig. 8).

The greater part of the wall is encrusted with sand granules, and so transformed into a kind of carapace; tentacles small and pointed, about sixty in number, distributed in two rows; thirty macrosepta and the same number of microsepta.

Habitat.—Cape York. (? The title of the label enclosed with the preparation was nearly entirely destroyed by the rough surface of the animal, and could not be exactly made out.) One specimen.

Dimensions.—Length, 4·5 cm.; breadth, 2·8 cm.

Colour.—(Determined from the spirit specimen) brown-red.

The wall of *Sphenopus arenaceus*, a new species, which I erect here from a single specimen among the Challenger material, is encrusted with foreign bodies to a degree which I have never found in any other Zoanthea; it forms a firm unyielding capsule, in which the soft parts are completely concealed when the animal is strongly contracted. The form of the *Sphenopus* then becomes irregularly oval, rather smaller at the rounded posterior end of the body than at the anterior. The wall is inverted a little way at the anterior end, though its nature does not undergo any change.

The surface is regularly rough like shagreen, as the sand granules are nearly all of equal size. The granules force their way so deeply into the wall that only a thin layer of soft tissue remains on the endodermal side; it is broadest in the front, and becomes narrower as it runs backwards, till the wall at the aboral body-pole consists almost entirely of

a layer of sand 5 millimetres thick (even in Pl. II. fig. 10 the soft part of the wall is too large in proportion to the layer of sand granules). Where the sand grains are absent the fundamental substance is homogeneous and furnished with two different forms of cells, small branched cells and larger roundish ones, the latter being entirely filled with strongly refractive concrement-like granules. The tissue between the sand granules (Pl. XIV. fig. 8), on the other hand, appears rather fibrous, and even the corpuscles of connective tissue are fusiform in shape. The direction of the fibres and the fusiform cells is parallel to the surface of the body. In most parts the sand granules are so thickly compacted that the fundamental substance is entirely covered.

There are no ectodermal vessels in the wall, but the supporting fibres are very numerous; they are richly furnished with granular protoplasm, are very fine and branched on the endodermal side, whilst towards the ectoderm they become lost among the sand granules.

The mesodermal circular muscle, which is strongly developed as in the other Zoantheæ, is not confined merely to the inverted part of the wall, but extends a good way down into the outer section. It is strongest where it begins close to the oral disk and lies in the non-encrusted section of the wall, it then becomes narrower and gradually approaches the endoderm, till the lower end almost touches the epithelium. It consists of bundles of fibrillæ, which give repeatedly waved figures in transverse section; several bundles are united into roundish bundles of the second order, which remain farther apart from one another.

Whilst the wall is very thick and firm, all the inner parts consist of delicate, easily torn lamellæ. The oral disk only is tolerably strong, and foreign bodies (sponge spicules, sand granules) are enclosed here and there in its supporting lamella. It is covered by a smooth layer of ectodermal radial muscles, and the margin bears two rows of tentacles; I could not determine the number of the tentacles accurately because of the strong contraction, but there were probably about sixty of them.

Before the oral disk passes into the œsophagus, which is of considerable size, it rises into a thin, sharp-margined lip, which is repeatedly indented at the edge. A large number of longitudinal ridges of the œsophagus, which correspond to the origins of the perfect septa, spring from these indentations.

The œsophageal groove is remarkably distinct; it is distinguished by its depth, and is enclosed by two broad folds, almost as hard as cartilage. Gray probably had these folds in mind when he specially mentions that in *Sphenopus marsupialis* "the laminæ of the stomach have a cartilaginous edge." They extend a little way beyond the lower margin of the stomach and form a projection, resembling the prow of a boat.

The arrangement of the septa agrees essentially with that already described in detail for *Zoanthus*, sp.? Two small directive septa lie at the dorsal end of the œsophagus, two large directive septa at the ventral end, which is easily recognised by the œsophageal

groove; two pairs, with dorsal macrosepta and ventral microsepta, adjoin the former on either side; twelve pairs, with ventral macrosepta and dorsal microsepta, adjoin the latter. The small dorsal and the large ventral septal regions are therefore separated on either side by microsepta. There are in all thirty macrosepta and thirty microsepta.

The following observations seem to me to justify these statements. From the dissection of individual septa, it was evident to me that the œsophagus is surrounded by two kinds of septa, viz., macrosepta, which are attached along the entire length of the œsophagus; and microsepta, which end on the oral disk before it becomes raised into the oral lip. In all of them the muscular fibres which rise obliquely are very distinct, the longitudinal fibres less so.

The only example of *Sphenopus arenaceus* which I was able to examine was bisected longitudinally parallel to the sagittal plane, so that only the one half (Pl. II. fig. 10) contained the œsophageal groove and the septa fastened to it. At the end of the œsophageal groove three macrosepta followed one another before I liberated the first microseptum by dissection, whilst the adjoining part of the other half begins with a microseptum, and the macrosepta and microsepta come alternately. If we then compare the transverse section through *Zoanthus* (Pl. XIV. fig. 3), we find a similar arragement of the septa in the region of the œsophageal groove, except that in *Sphenopus* the outermost of the four macrosepta placed in a row in *Zoanthus* is wanting. As it falls in the line through which the section has been taken in dividing the animal, it has most likely been destroyed.

At the dorsal end we first meet with a microseptum, then with a macroseptum; after which, on dissection, I found the septa arranged in the following order, two microsepta, one macroseptum, one microseptum, one macroseptum, one microseptum, one macroseptum. In the adjoining portion of the other half, I found one microseptum, one macroseptum, one microseptum, one macroseptum, two microsepta, one macroseptum. If we compare this arrangement with fig. 3 of *Zoanthus*, and consider the two pairs of microsepta discovered by dissection to be homologous with the two lateral pairs of microsepta in *Zoanthus*, we should likewise meet with the same corresponding conditions if we assume that one of the small directive septa and the adjoining macroseptum have been destroyed in making the section.

Finally, as regards the number of the septa, I determined them according to the lines of insertion which shone through the œsophagus; in this way we can settle the number of the macrosepta, with which the number of microsepta corresponds, presupposing, of course, that they are arranged in the same way as in *Zoanthus*. I found this to be the case in at least half of the septa dissected.

The reproductive organs and mesenteric filaments were cemented by mucus into a badly preserved mass, and were not adapted for examination.

Tribe VI. CERIANTHEÆ.

Actiniaria with numerous unpaired septa and a single ventral œsophageal groove; the septa are longest on the ventral side and gradually diminish towards the dorsal aspect; the two septa attached to the bottom of the œsophageal groove (directive septa) are remarkably small, and are distinguished in this way from the other ventral septa.

I have made no further anatomical investigations of the Cerianthеæ, and cannot even complete the statements which were formerly made by von Heider (Sitzungber. d. Wiener Akad. Math. Naturw. Cl., Bd. lxxix. Abth. 1, p. 204, Jahrg., 1879), and my brother and myself (Actinien, p. 107). From these we cannot even certainly determine what position the animals occupy in the circle of the Actiniaria, and whether or not they ought to be placed in one of the known principal divisions. They are distinguished from all the forms previously discussed, except the Edwardsiæ, by the fact that they want the paired arrangement of the septa—at least up to the present it has not been observed in them. They come nearest the Zoantheæ, as they have only one œsophageal groove; the septa also appear not to be disposed in a circle, but in the region of a limited zone of growth, which, however, lies dorsally, not ventrally as in the Zoantheæ. In this case the largest septa are found in the region of the œsophageal groove, and the septa gradually decrease in size from that point to the opposite end of the sagittal axis; two pairs of very small septa lie under the œsophageal groove, to which the name of directive septa is given more from their position than from their anatomical constitution.

Family CERIANTHIDÆ.

Cerianthеæ with a double corona of tentacles, marginal principal tentacles and circumoral accessory tentacles, posterior end of the body rounded, without sphincter.

Cerianthus, Delle Chiaje.

Cerianthidæ with aboral pore, with a sheath consisting of mud, sand granules, and nematocysts, in which the posterior end of the animal lies as if in a case.

Cerianthus americanus.

Cerianthus americanus, Verrill, Memoirs Boston Soc., vol. i. p. 32, 1866.

Habitat.—Station 321. February 25, 1876. Lat. 35° 2′ S., long. 55° 15′ W. Depth, 13 fathoms. One specimen.

Dimensions.—Length of the animal (in the contracted condition), 12 cm.; breadth of the oral disk, 3·5 cm.; length of the inner tentacles, 2–2·5 cm.; of the outer tentacles, 4–5 cm.

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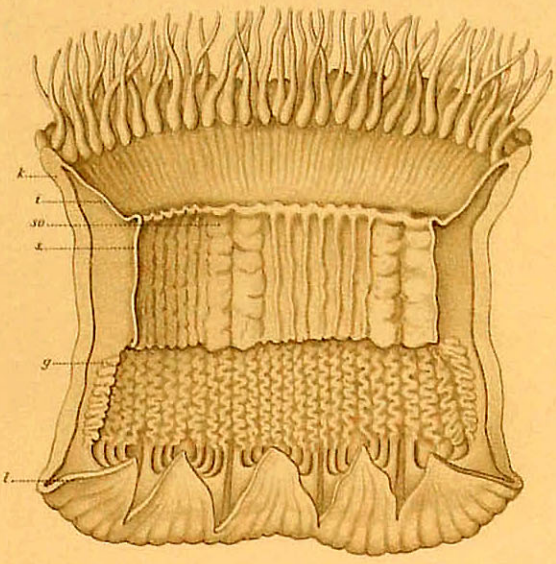

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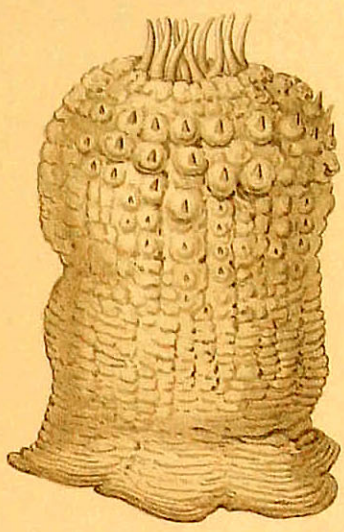

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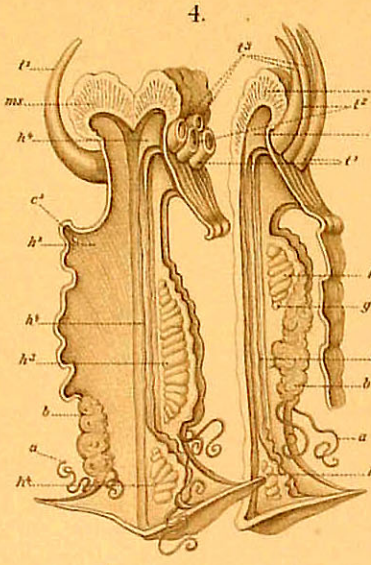

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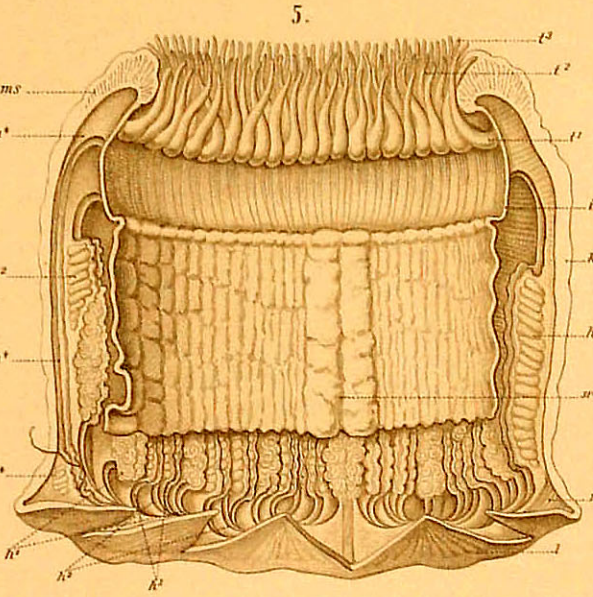

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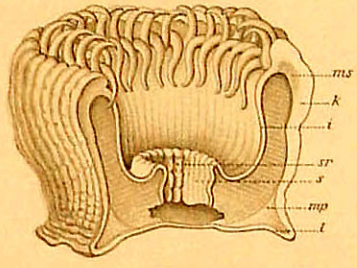

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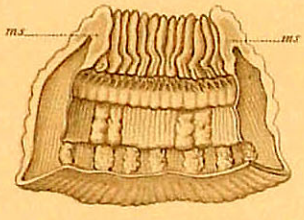

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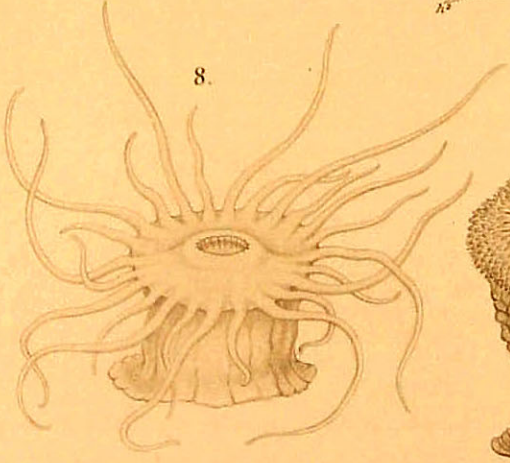

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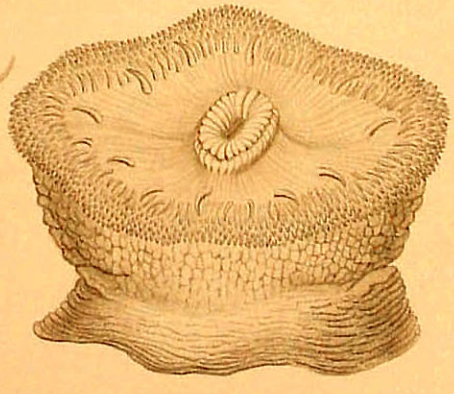

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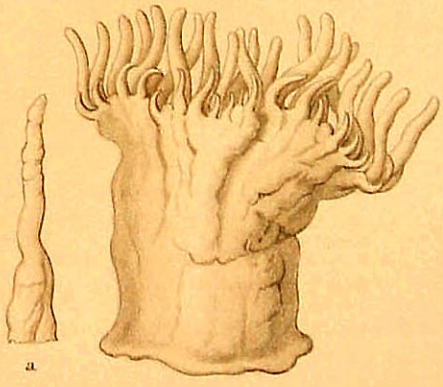

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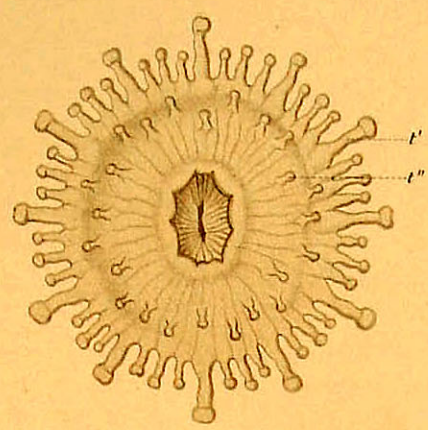

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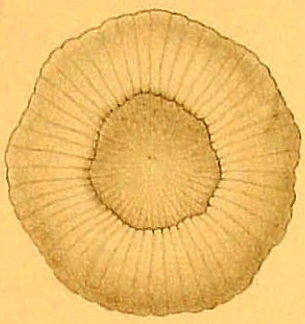

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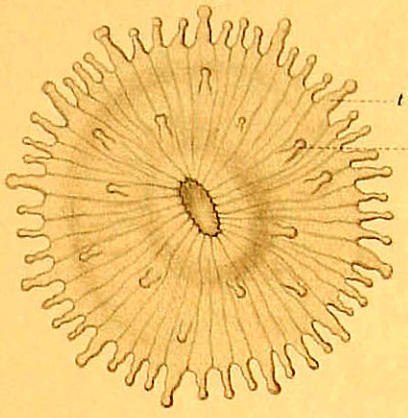

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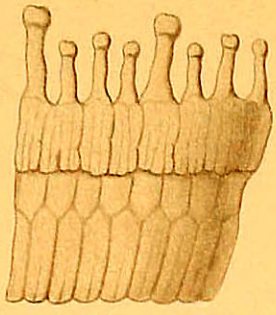

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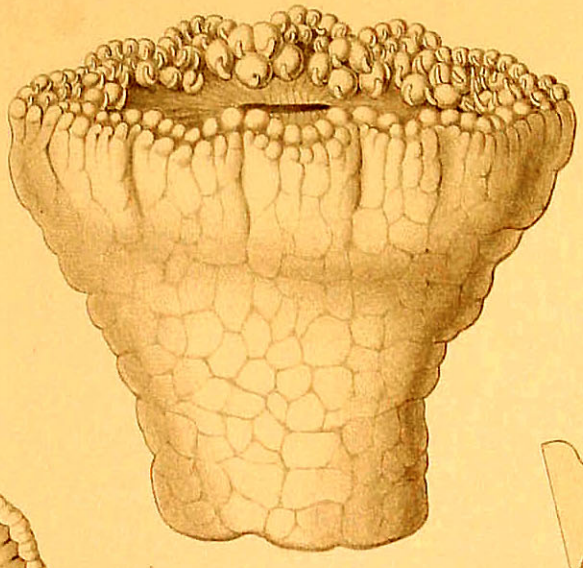

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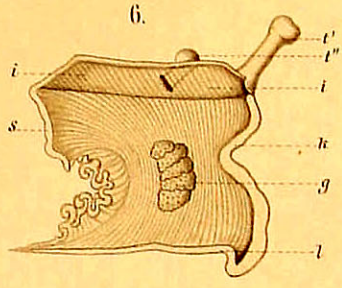

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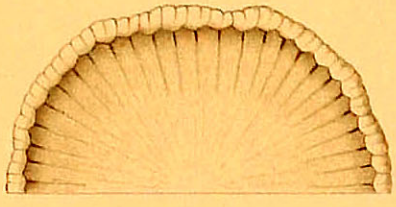

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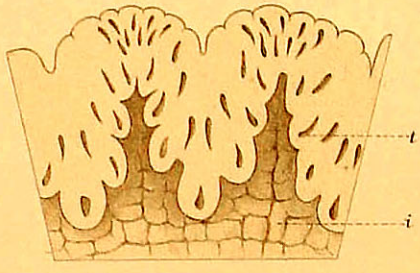

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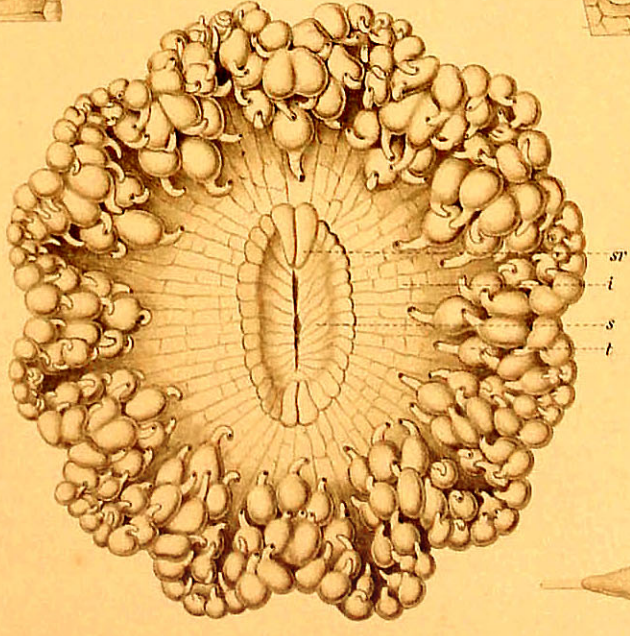

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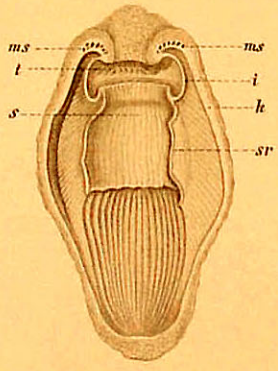

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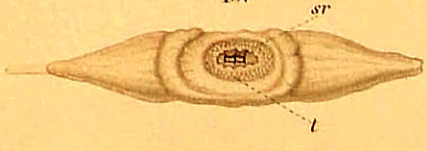

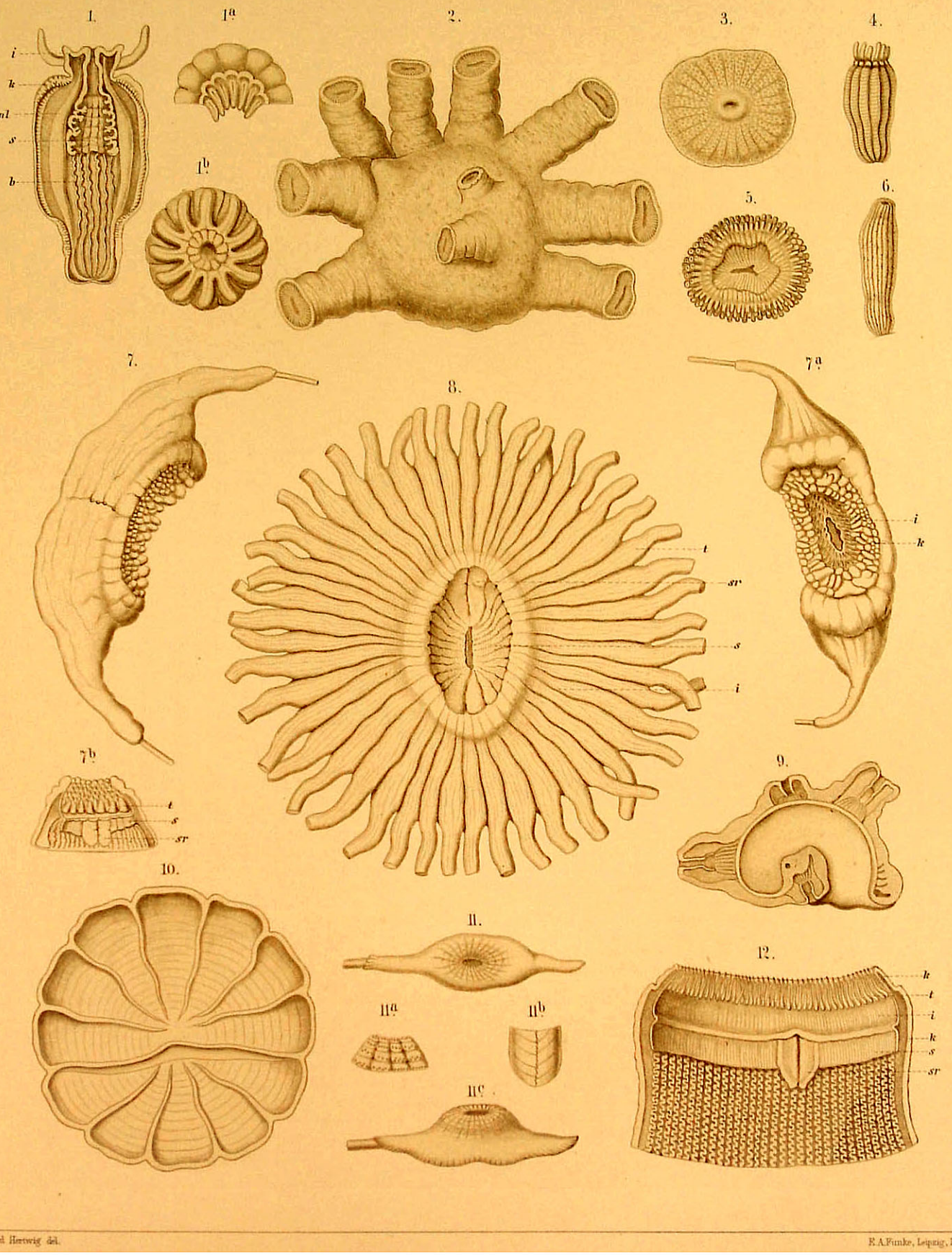
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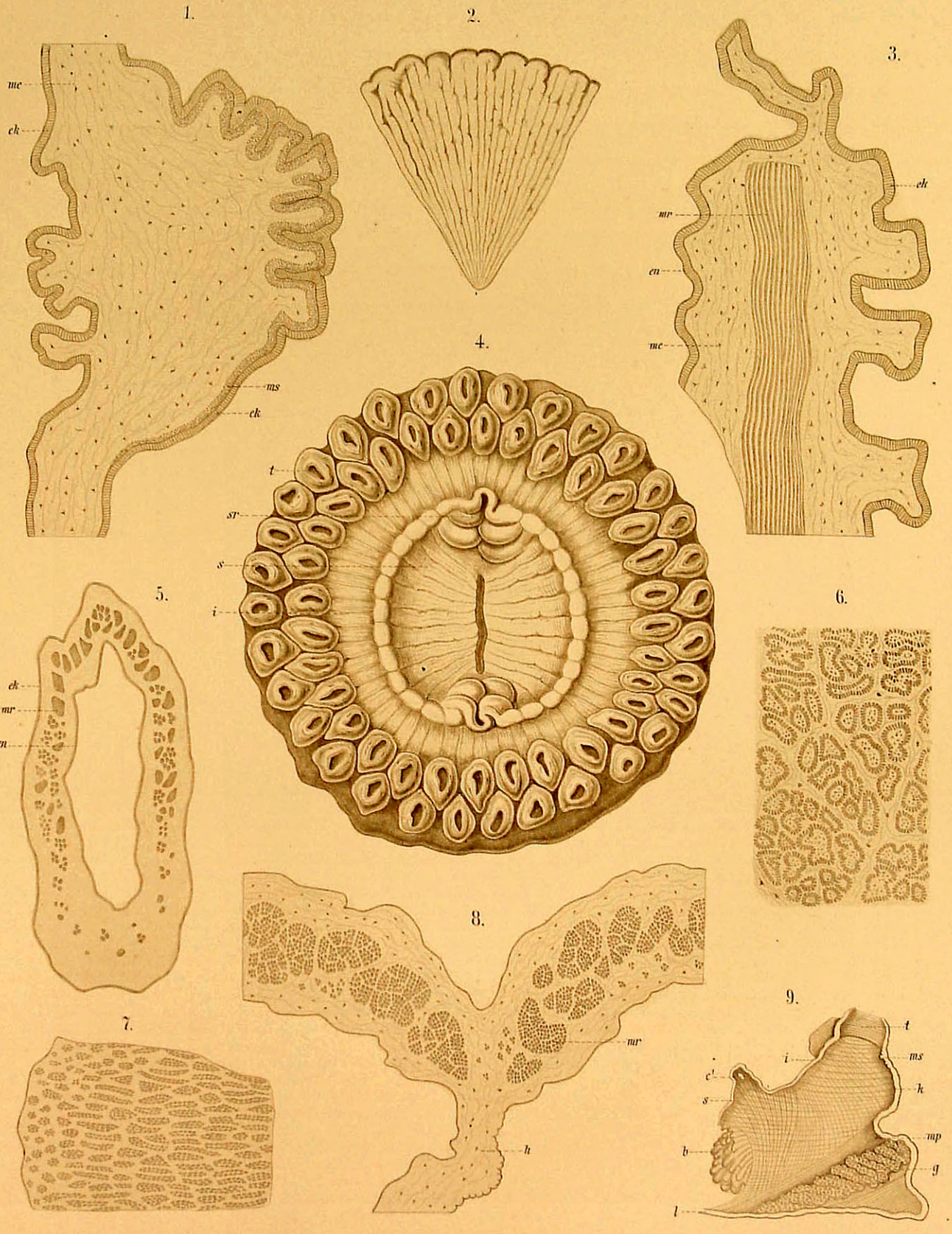
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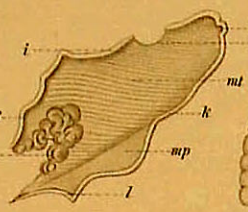

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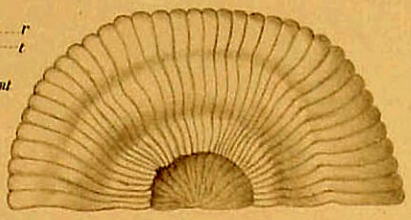

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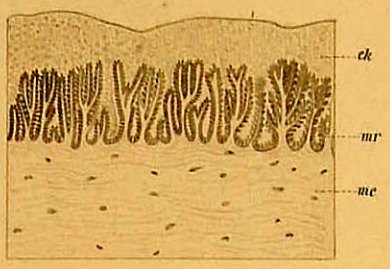

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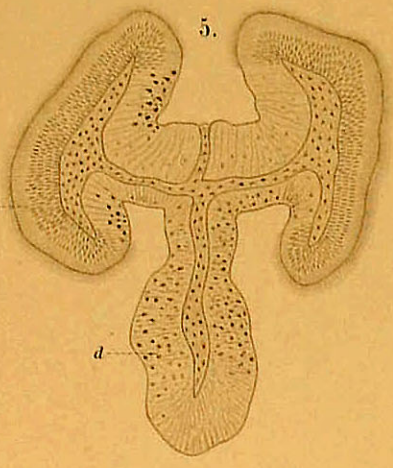

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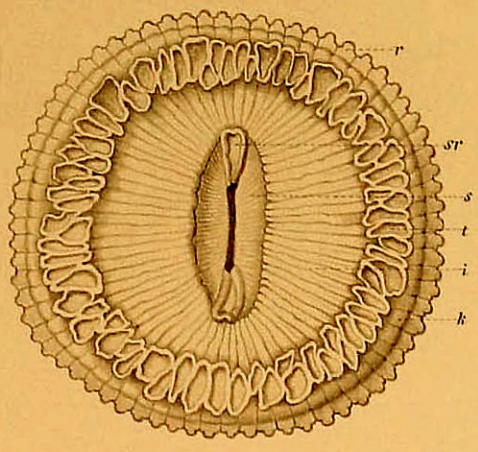

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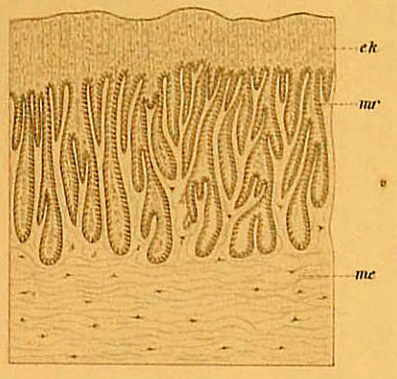

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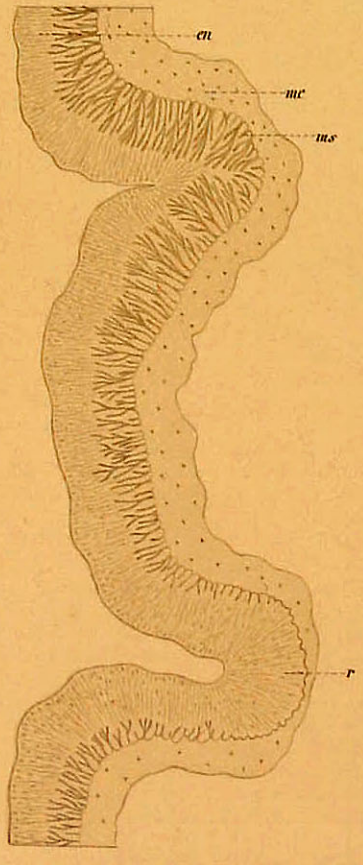

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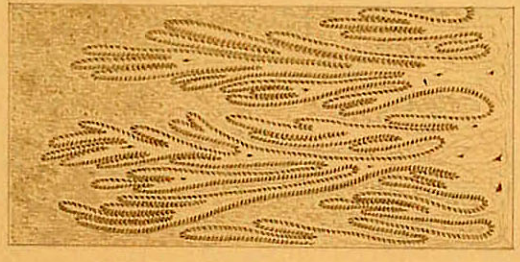

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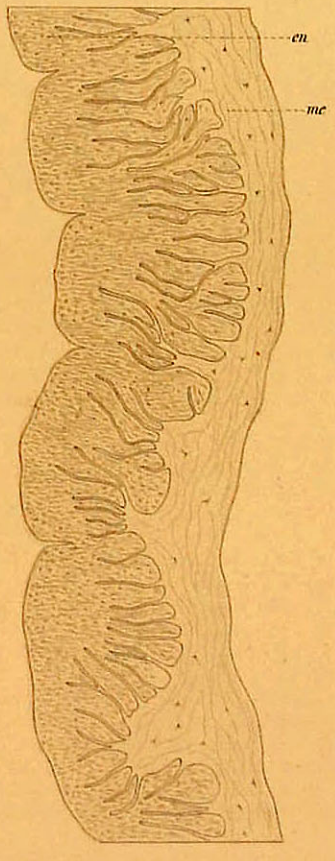

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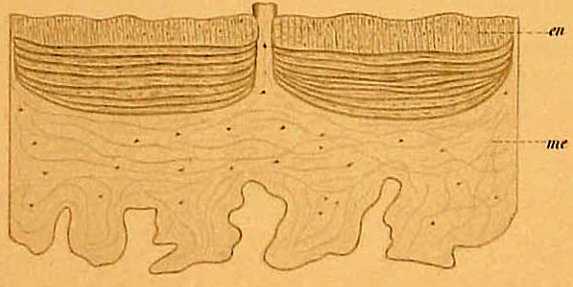

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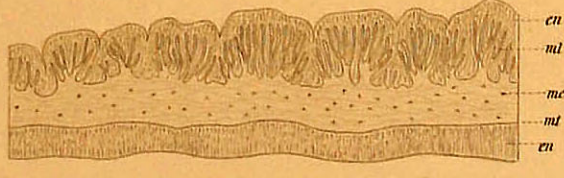

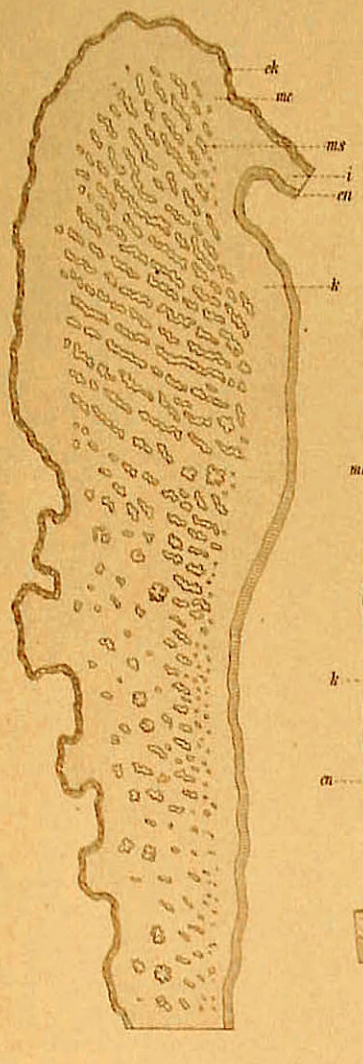
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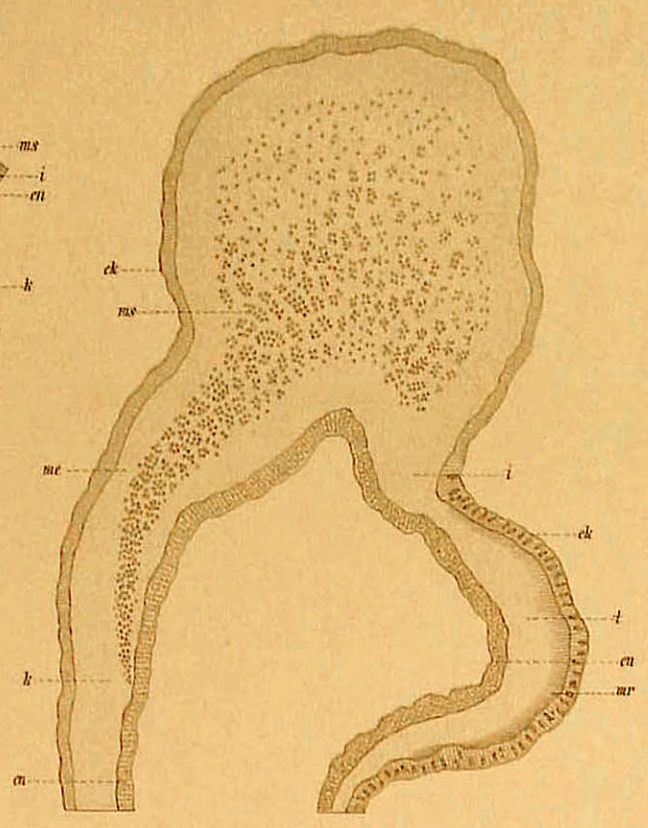
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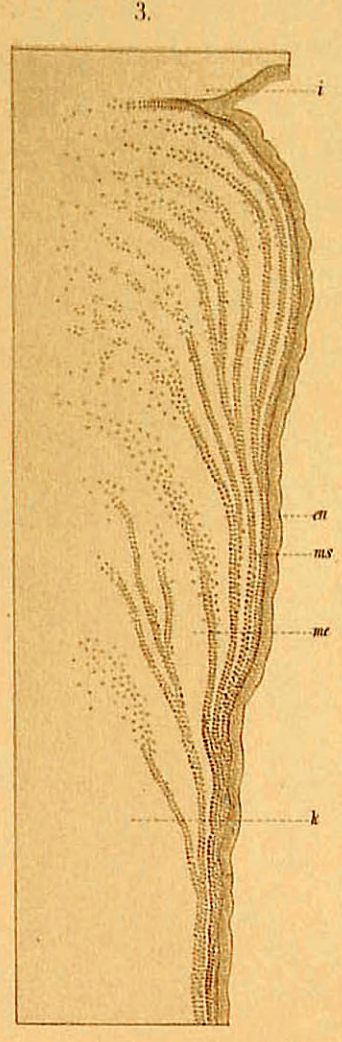
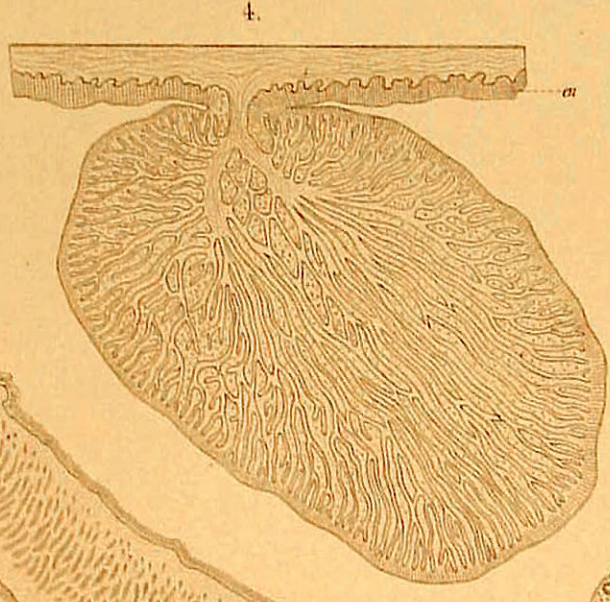
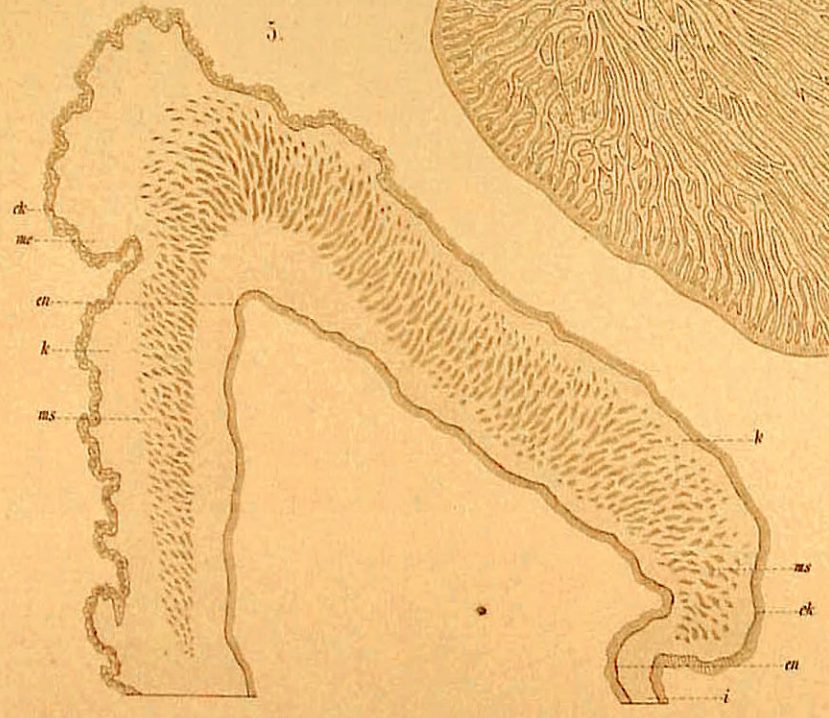

3.
i
en
ms
mc
k


4.
en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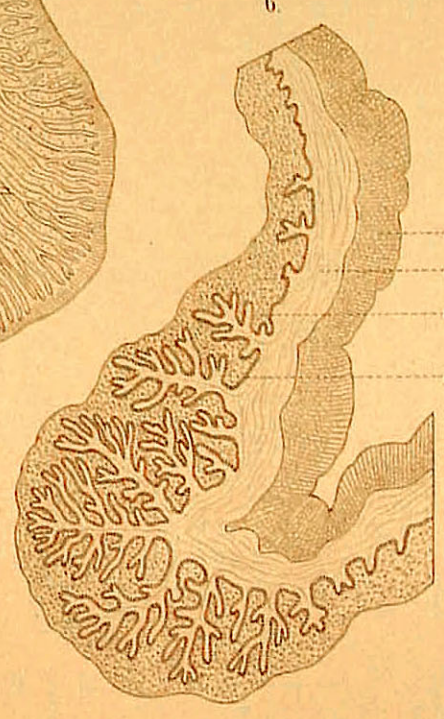
ek
mc
en
k
ms
k
ms
ek
en
i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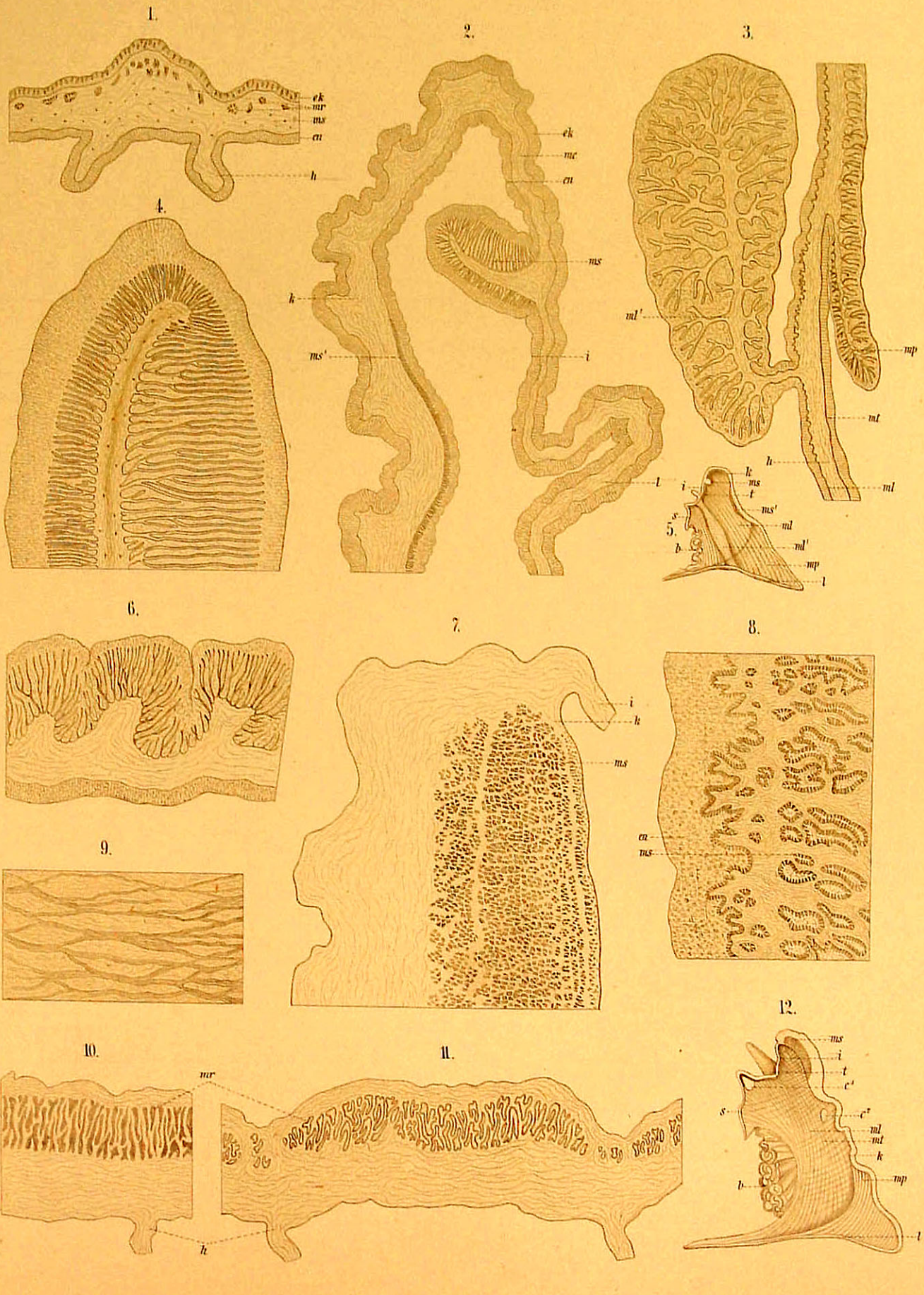
ek
mc
en
ms


1.
ek
mr
ms
en
h
2.
ek
mr
en
ms
k
ms'
i
l
3.
ml'
mp
ml
h
ml
4.
5.
k
ms
i
t
ms'
s
ml
b
ml'
mp
l
6.
7.
i
k
ms
8.
en
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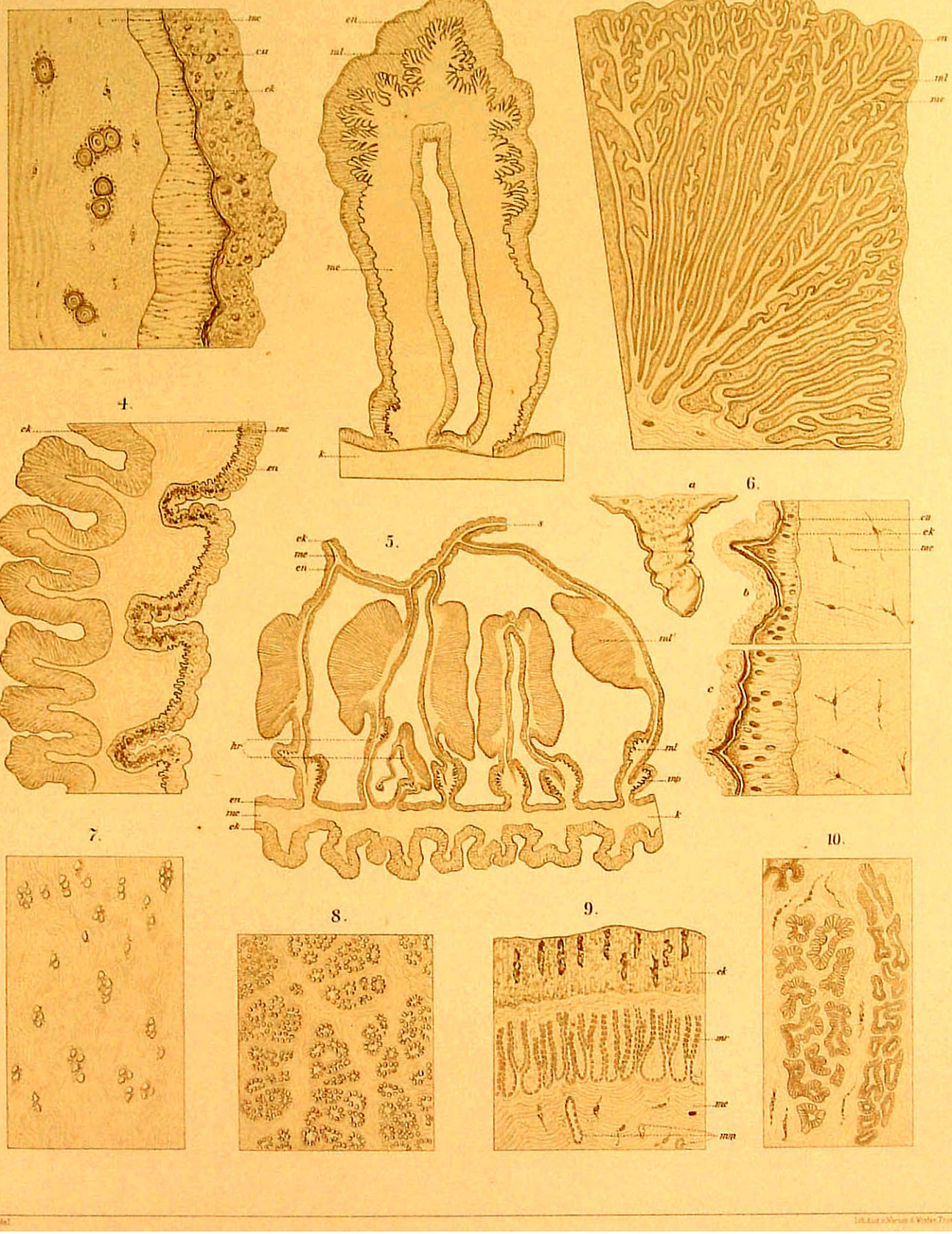
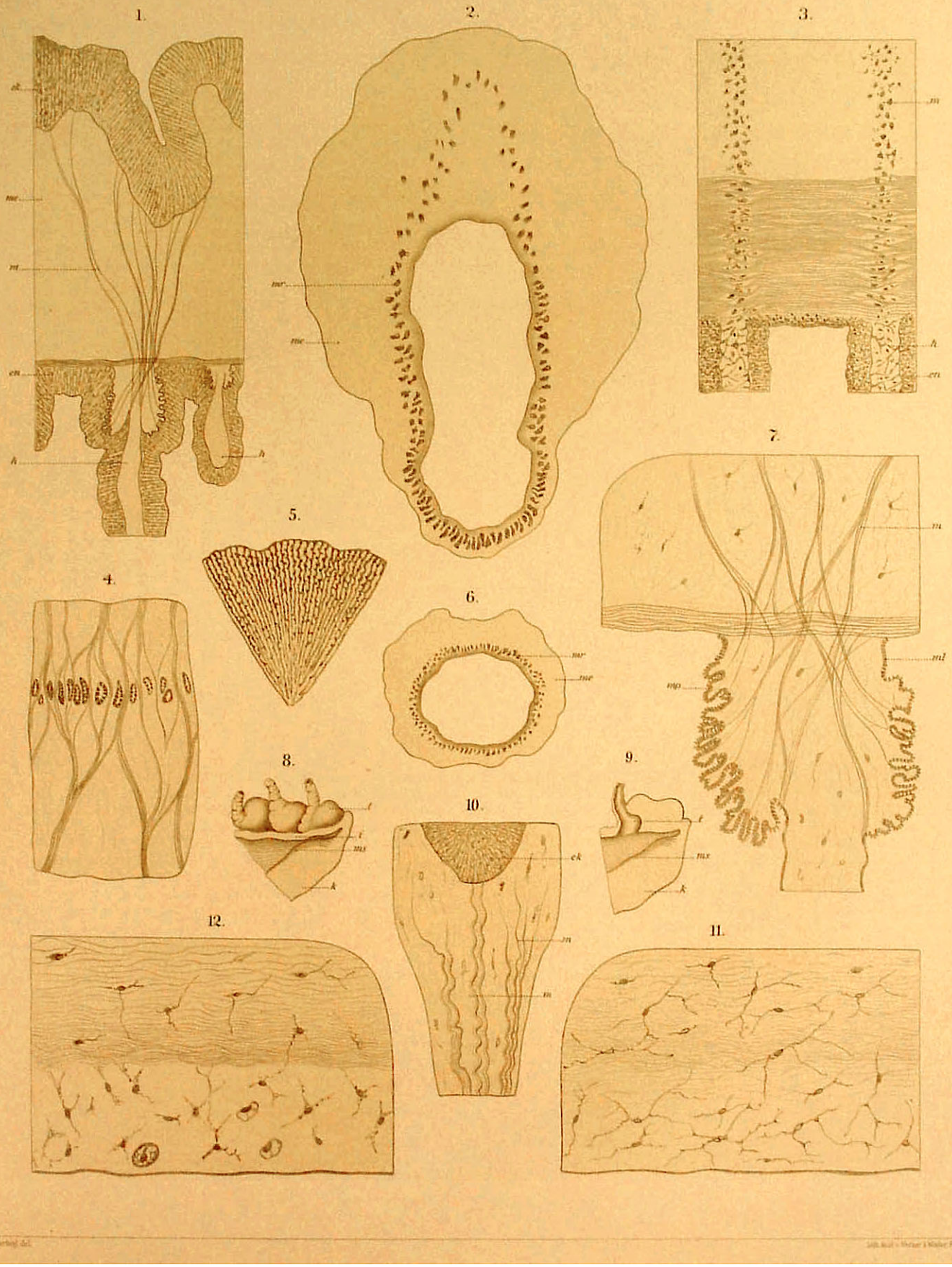
k
h
mp
l

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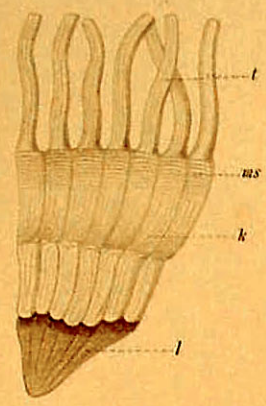
10.
11.
12.


1.
t
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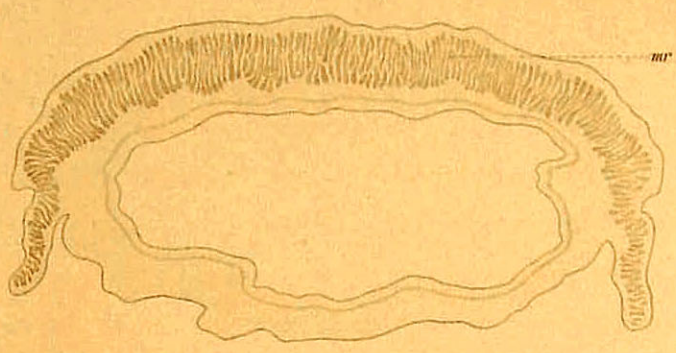
k
l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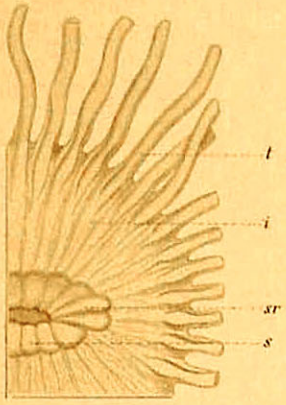
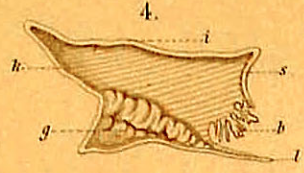
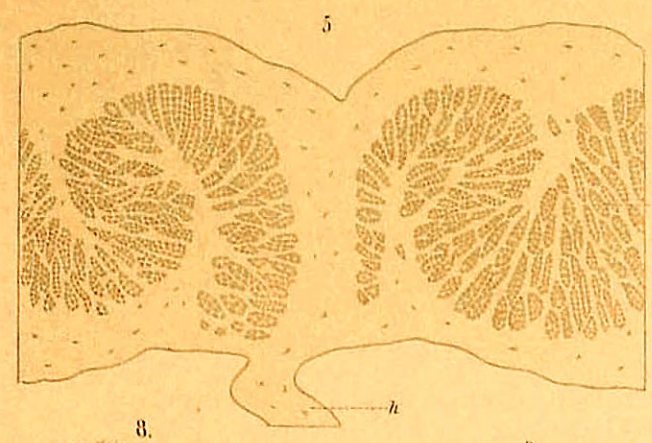
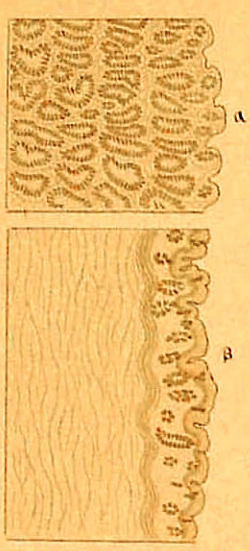

3.
t
i
sr
s

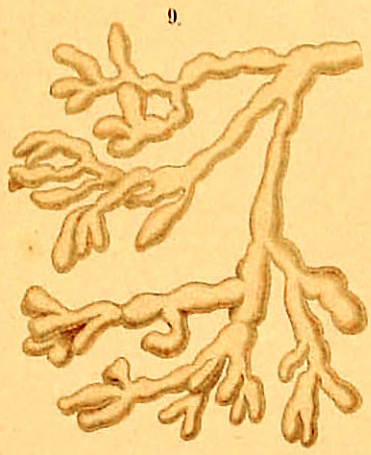

4.
i
k
s
g
b
l


5
mr
h

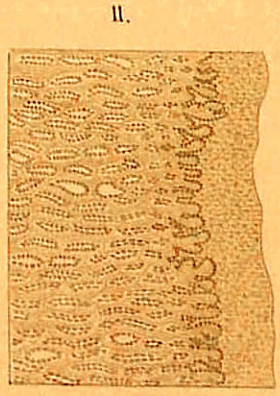

6.
α


7.
α
β


8.


9.


β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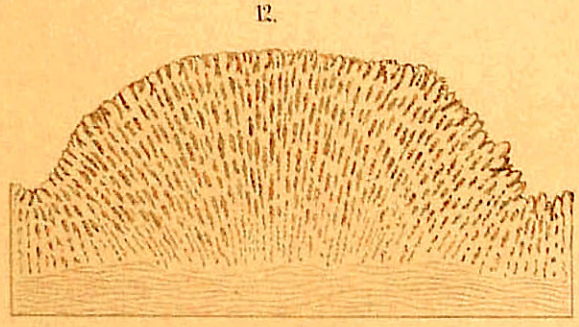
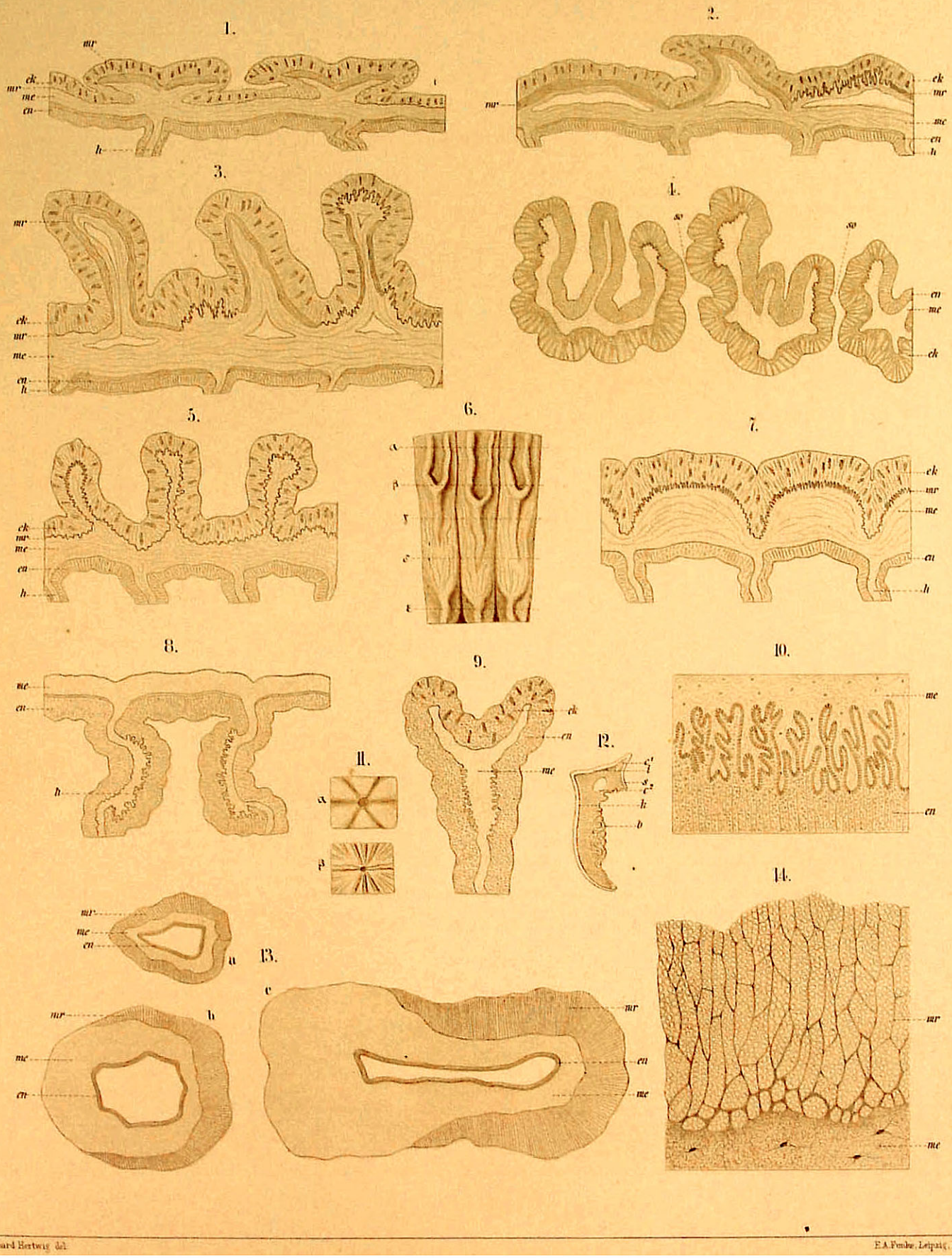

12.


ek
10.
en


γ
δ


1.
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mr
me
en
h
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mr
ek
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h
3.
mr
ek
mr
me
en
h
4.
so
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me
ek
5.
ek
mr
me
en
h
6.
α
β
γ
ε
ζ
7.
ek
mr
me
en
h
8.
me
en
h
9.
ek
en
me
10.
me
en
11.
α
β
12.
ek
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h
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mr
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a
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b
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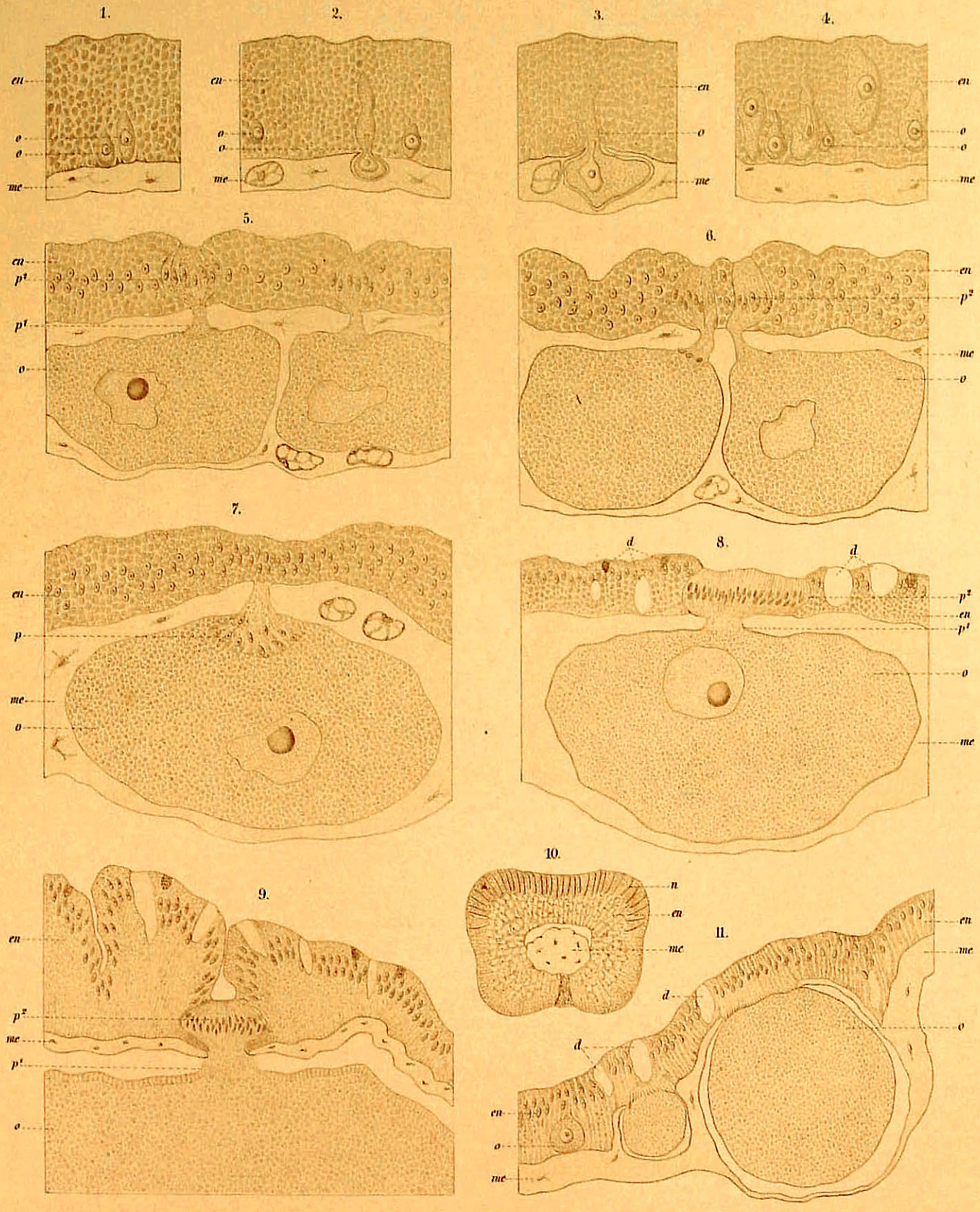
en
c
mr
en
me
14.
mr
me


1.
en
e
e
me
2.
en
o
o
me
3.
en
o
me
4.
en
o
o
me
5.
en
p²
p¹
o
6.
en
p²
me
o
7.
en
p
me
o
8.
d
d
p²
en
p¹
o
me
9.
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p²
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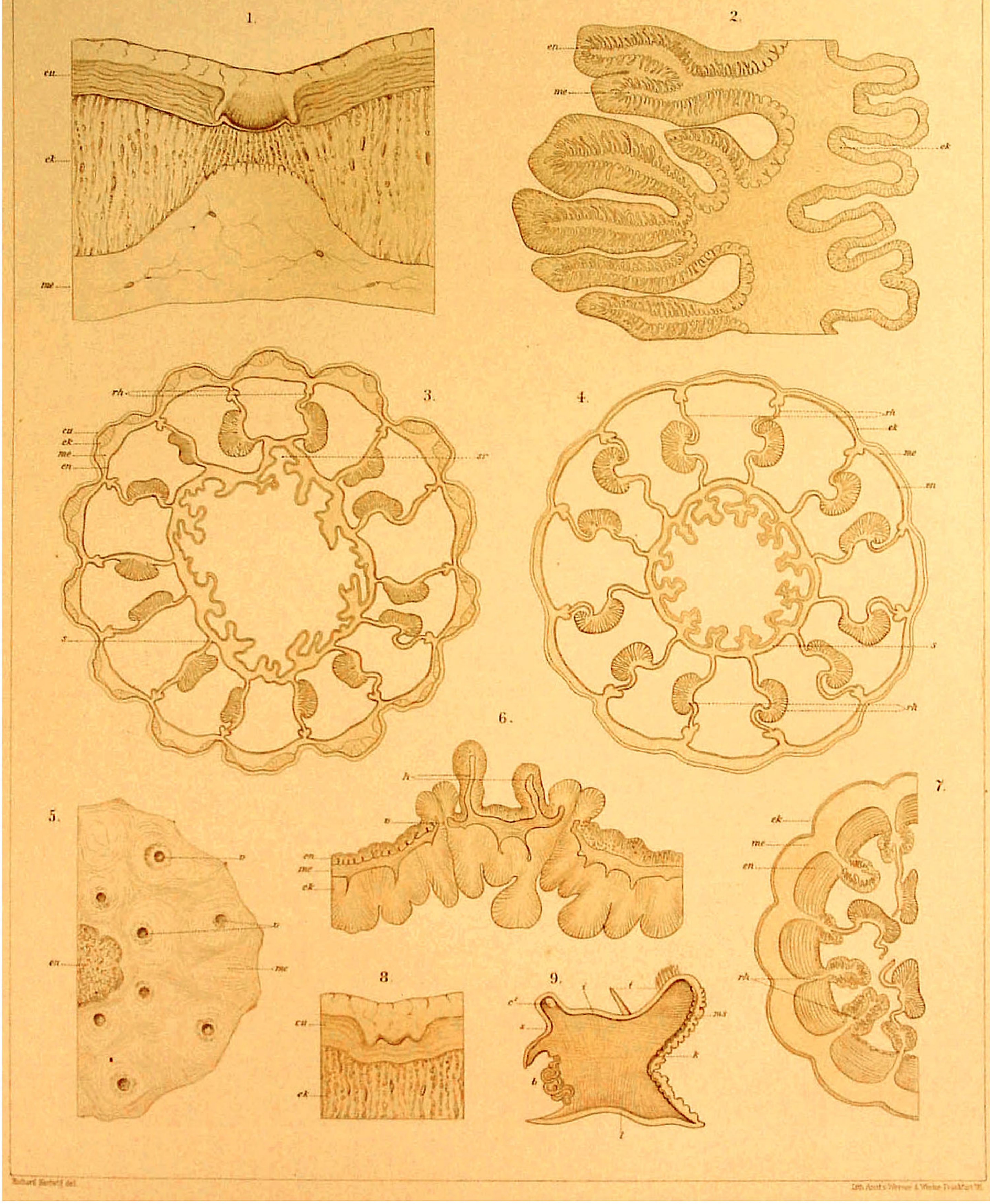
p¹
o
10.
n
en
me
11.
en
me
d
o
d
en
o
me


1.
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2.
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ek
3.
rh
cu
ek
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en
zr
s
4.
rh
ek
me
en
s
rh
5.
v
v
en
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6.
h
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me
en
rh
8.
cu
ek
9.
c'
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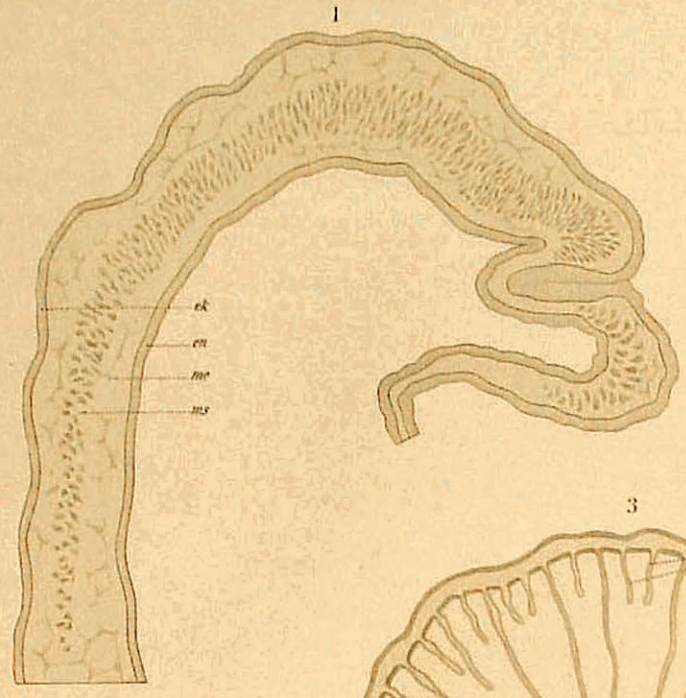
l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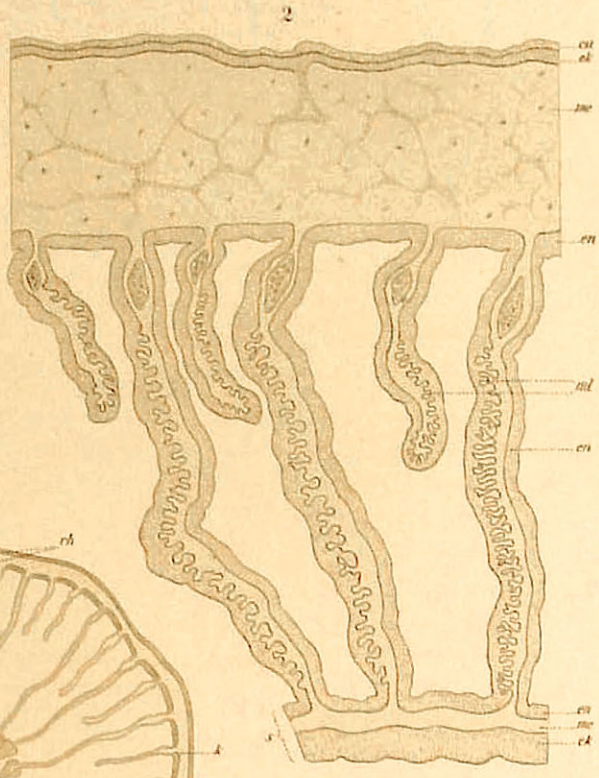
2
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mf
en
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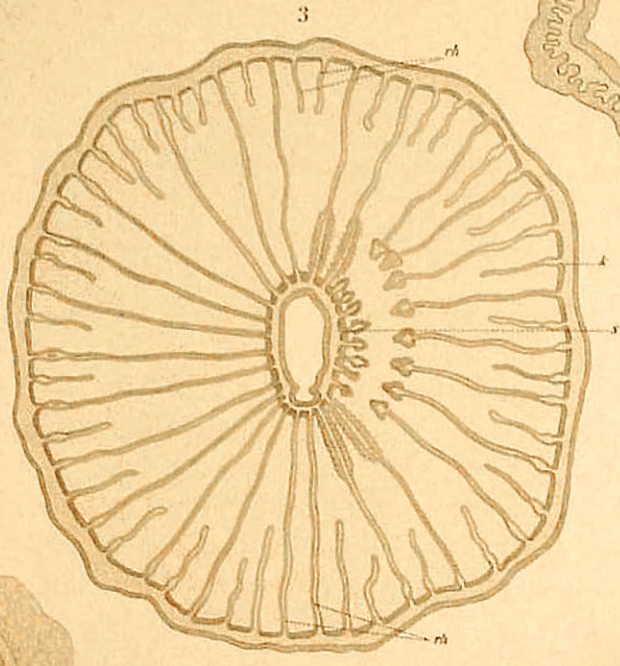
me
ek


3
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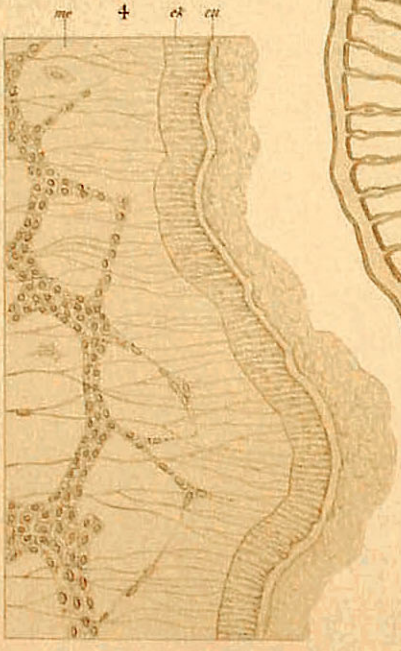
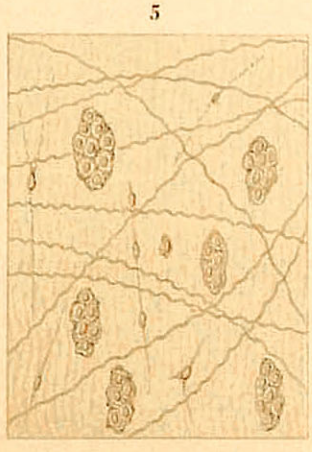
s
rh


me
4
ek
cu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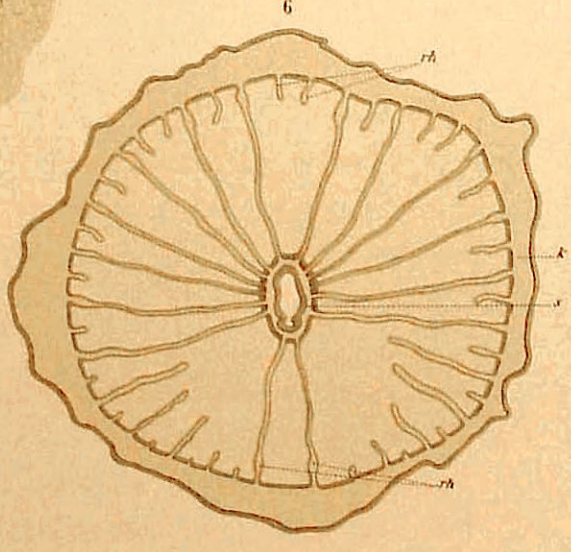
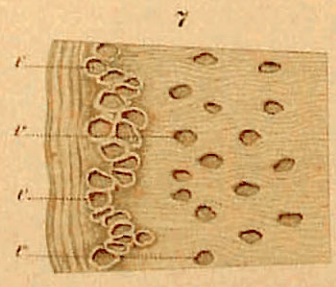

6
rh
s
rh


7
t
t
t
t


8