On Eloactis mazeli.

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With Figures 1–4 in the Text.

Jourdan was the first to describe *Eloactis mazeli*. In 1880 he published *Recherches zoologiques et histologiques sur les Zoanthaires du golfe de Marseilles* (1), and in this paper *E. mazeli* is described under the name of *Ilyanthus mazelii*. Jourdan obtained his specimen from the muddy sand of the north-eastern part of the Gulf from a depth of 60–80 metres. He compares its external characters with those of Peachia, Ilyanthus, and Halcampa ; the following is a translation :—

"In form it approaches Peachia, from which it differs through the absence of gonidial tubes. In the absence of terminal pores and in the smoothness of the column it resembles Ilyanthus, while its cylindrical form recalls that of Halcampa, though it differs from this genus in that it lacks tubercles and a terminal swelling. Its buccal disc is conical, of an orange tint striped with darker lines which run from the mouth to the bases of the tentacles. These last are twenty in number and are arranged in two cycles ; they are white with brown apices and the inner ones are smaller than the external ones."

"The column is cylindrical, and is orange-red with paler lines which run down from the summit in the spaces intervening between the outer tentacles. The basal region is lighter in colour and more membranous ; it is non-adhesive, and the lower part of the column wall is often pushed in, giving the base the appearance of being sunk in. Longitudinal and transverse sections of the basal region show that this sunken portion has no aperture."

Jourdan could not study the structure much owing to the state of preservation of his one specimen, also he was working in the early days of the serial-section method. He was therefore unable to make out the arrangement of the mesenteries, and thus could not place the animal in its correct systematic position.

In 1884 Andres, in *Le Attinie* (2), gave the following description of

E. mazeli, placing it in the Heteractiniæ with *Eloactis globosa*, *Ropalactis*, *Ragactis*, *Heteractis*, and *Stauractis*.

The base, he says, is "slightly adherent, often with a rounded vesicle resembling a physa. Column long, cylindrical, sulcated by 20 invections of slight depth, often minutely rugose; membranous, delicate, scarcely adhesive. Disk small. Tentacles few, bicyclic 10 : 10; the length of the tentacles of the external cycle twice that of the tentacles of the internal cycle; not entirely retractile, rounded at the tips; outwardly deflexed. Peristome low, rounded, concave and grooved. Mouth often prominent. No acontia. Gonidia somewhat open. Pharynx often protruded and resembling numerous angular lobes. Size fairly large." . . .

Delage and Hérouard (6), in 1901, described *Eloactis mazeli* thus: Eloactis is an Actinian which appears to vary in form because of its marked contractility; the base is only slightly adherent, if at all; the column is smooth or rugose according to the state of contraction; it is deeply grooved longitudinally; the tentacles are few in number and arranged in two cycles; they terminate in a rounded swelling rich in nematoblasts; there is no sphincter.

Delage and Hérouard also place it in the Heteractidæ (Andres) Heteractinæ, 11th family; but they say that the family is probably highly artificial, uniting provisionally several Actinians, concerning the anatomy of which very little is known. They all have a smooth and striated but not verrucose column, and tentacles arranged in various ways, but not branched, and armed by swellings rich in nematoblasts.

In 1892, Garstang described a living specimen of this interesting anemone from the Devonshire coast (*Trans. Devon. Assoc.*). Since then several specimens have been dredged from the neighbourhood of the Eddystone and the South Devon coast (cf. p. 68). Almost all were damaged, only the summit of the scapus and oral crown being present, and even these were greatly distorted and contracted. Under these conditions the tentacles were much shortened and strongly capitate; the coloration of these specimens was usually of little intensity. Some of the specimens still showed signs of life.

The present paper embodies the results of an investigation of specimens dredged off South Devonshire, and of one perfect specimen from the Mediterranean. It is sought—

(1) To establish the identification of the British specimens as specimens of *E. mazeli* (Jourdan).

(2) To demonstrate the affinities of Eloactis with certain other Actinian types.

External Characters of E. mazeli (Jourdan).

The following description of the external characters of *E. mazeli* (Jourdan) is based on an examination of a preserved specimen from Naples. Length of scapus, 47 mm.; it tapers gradually downwards. Diameter at summit of scapus, 11 mm.; diameter at base, 7 mm. The base, which is slightly enlarged, is very similar to that of Peachia, being invected somewhat in the centre to a depth of several mm. Upper margin well demarcated, surface of scapus without tubercles, but very much folded and wrinkled and thrown into numerous complex ridges. Tentacles, 20 in two alternating cycles of 10 each, the outer the longer. In this specimen they are contracted, rather stout, tapering slightly upwards and then expanding into a globular or ovate head. Length of outer tentacles 10 mm., inner 4 or 5 mm. Colour, greenish white (in spirit). The tentacles are mottled with dark purplish brown blotches. These become larger and confluent higher up, and in the contracted tentacles appear as slightly raised vesicles or blisters. On the head of the tentacle these marks are of a paler brown suggestive of a less degree of contractility. The disk is narrow and concave; the mouth pointed and prominent.

Internal Structure of the Italian Specimen of E. mazeli.

The mesenteries are twenty in number, and are all perfect and fully developed. Their arrangement is very simple, the mesenteries arising in pairs and two of these pairs are directives (Fig. 1). The longitudinal muscles of each pair are on the faces which look towards the intramesenterial spaces, except in the case of the four directive mesenteries whose longitudinal muscles are on the faces which are turned towards the adjacent intermesenterial spaces. There is only one siphonoglyphe, and this is deep and well defined. The surface of the stomatodæum possesses numerous ridges which increase the digestive area. The body wall consists of ectoderm, mesoderm, and endoderm in almost equal proportions. The ectoderm has a corrugated appearance on its outer surface owing to the body wall being slightly contracted. The mesoglœa is fibrillar, especially towards the inner surface, as in Halcurias.

Jourdan, in his description of the internal characters of Eloactis, also shows the fibrillar nature of the mesoderm: "Sur les coupes transversales le picrocarmin colore vivement le mesoderme et permet d'y distinguer deux zones, l'externe composée de tissu conjonctif lache, l'interne formée de tissus lamineux" ("In transverse sections, the mesoglœa is deeply stained

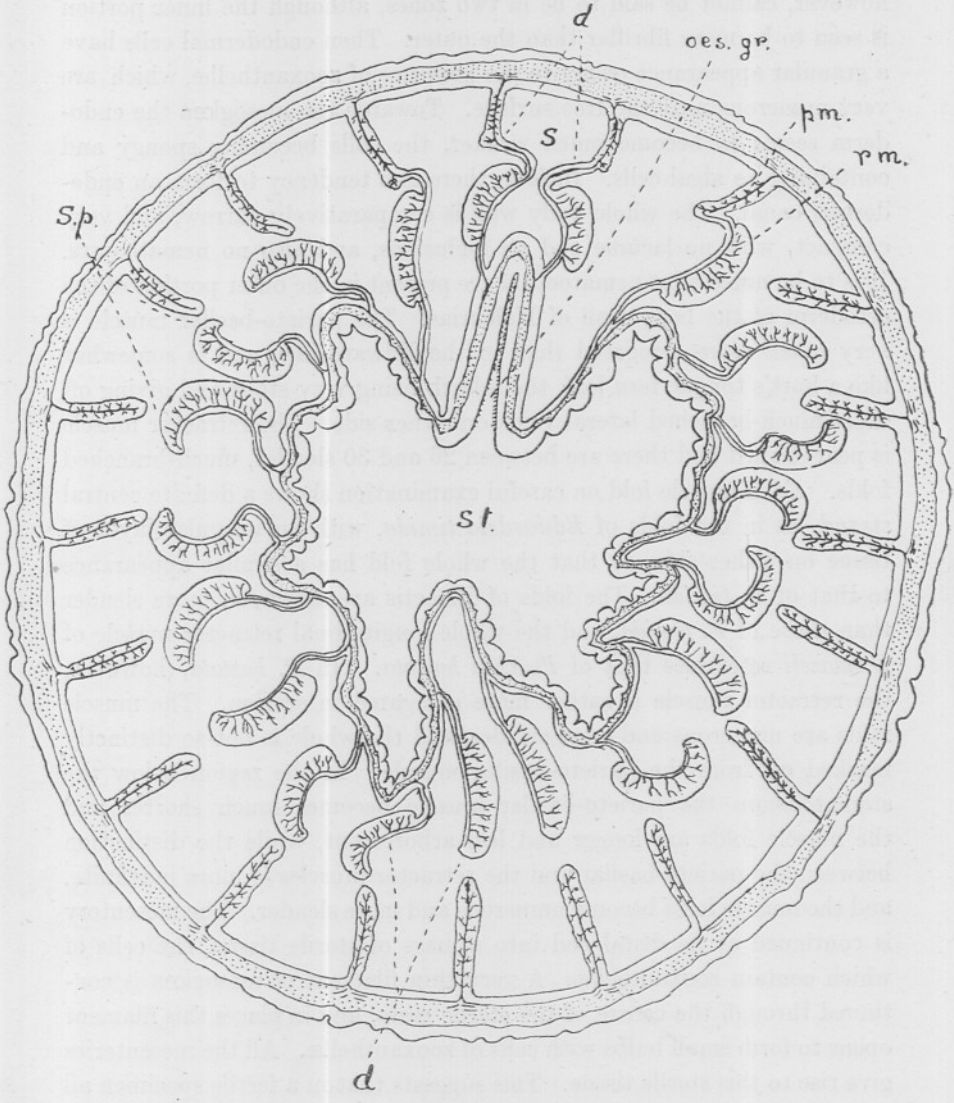

FIG. 1.—Transverse section through the column, showing stomatodæum with œsophageal groove, and septostomes in all the mesenteries except in the sulcar directive and in two sulco-lateral mesenteries: *d.* directive mesenteries, *œs.gr.* œsophageal groove or siphonoglyphe, *p.m.* parietal muscle, *r.m.* retractor muscle, *s.* sulcus, *s.p.* septostomes, *st.* stomatodæum.

by picrocarmine showing two zones, the outer composed of loose conjunctive tissue, and the internal zone of laminated tissue"). The mesoglœa, however, cannot be said to be in two zones, although the inner portion is seen to be more fibrillar than the outer. Then endodermal cells have a granular appearance owing to the presence of zooxanthellæ, which are very numerous near the free surface. Towards the mesoglœa the endoderm seems to become much weaker, the cells becoming spongy and containing no algal cells. In fact, there is a tendency to form an endodermal canal. The whole body wall is comparatively narrow, and very compact, with no lacunæ and no inclusions, and also no nematocysts. It is to be noted that nematocysts are present in the outer portion of the ectoderm of the body wall of Halcurias. The parieto-basilar muscle is very much more elongated than in the Edwardsidæ, and is somewhat like a hart's tongue fern leaf, the midrib being very stout and giving off short much-branched lateral veins on either side. The retractor muscle is pear-shaped and there are between 26 and 30 slender, much-branched folds. Each muscle fold on careful examination shows a definite central strand, as in the folds of *Edwardsia timida*, with an irregular layer of tissue on either side, so that the whole fold has a similar appearance to that of *E. timida*. The folds of Eloactis are, however, more slender than those of *E. timida*, and the whole longitudinal retractor muscle of *E. mazeli* resembles that of *Peachia hastata*. In *P. hastata*, however, the retractor muscle is rather more elongated in section. The muscle folds are numerous and more slender, and the whole is not so distinctly marked off from the parieto-basilar muscle. In the region below the stomatodæum the parieto-basilar muscle becomes much shorter and the muscle folds are longer and less arborescent, while the distinction between the parieto-basilar and the retractor muscles is more indefinite, and the muscle folds become numerous and more slender. The mesentery is continued at its distal end into a mass of sterile tissue, the cells of which contain zooxanthellæ. A very thin filament of mesoglœa is continued through the centre of the sterile mass, and in places this filament opens to form small bulbs with cells of zooxanthellæ. All the mesenteries give rise to this sterile tissue. This suggests that in a fertile specimen all the mesenteries would behave alike and would thus give rise to twenty gonads. In Halcurias also all twenty mesenteries are fertile. There is one œsophageal groove as in Halcurias, but in *Eloactis mazeli* the groove is deep and well defined; whereas in Halcurias the siphonoglyphe is said to be neither very deep nor well defined. In *E. mazeli* the ectoderm of the siphonoglyphe consists of large elongated columnar cells containing

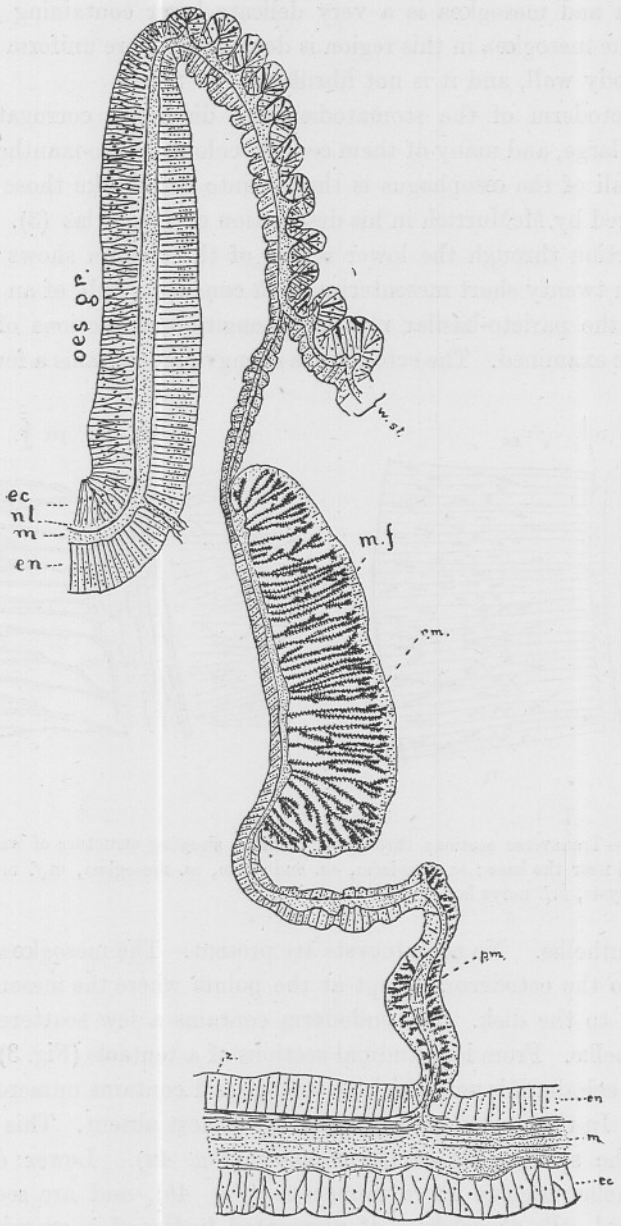

FIG. 2.—Transverse section through a mesentery, showing the muscles, also the structure of the wall of the stomatodæum and of the wall of the œsophageal groove: *ec.* ectoderm, *en.* endoderm, *m.* mesoglœa, *m.f.* muscle fibres, *œs.gr.* œsophageal groove or siphonoglyphe, *p.m.* parietal muscle, *r.m.* retractor muscle, *n.l.* nerve layer, *z.* zooxanthellæ, *w.st.* wall of stomatodæum.

large nuclei, and they are slightly granular and ciliated. Between the ectoderm and mesoglœa is a very delicate layer containing the nerve cells. The mesoglœa in this region is denser and more uniform than that of the body wall, and it is not fibrillar.

The ectoderm of the stomatodæum is distinctly corrugated. The cells are large, and many of them contain colonies of zooxanthellæ. The whole wall of the œsophagus is thrown into ridges like those described and figured by McMurrich in his description of Halcurias (3). A transverse section through the lower region of the column shows the body wall with twenty short mesenteries, each consisting only of an elongated form of the parieto-basilar muscle. Longitudinal sections of the oral disk were examined. The ectoderm is spongy and contains a few colonies

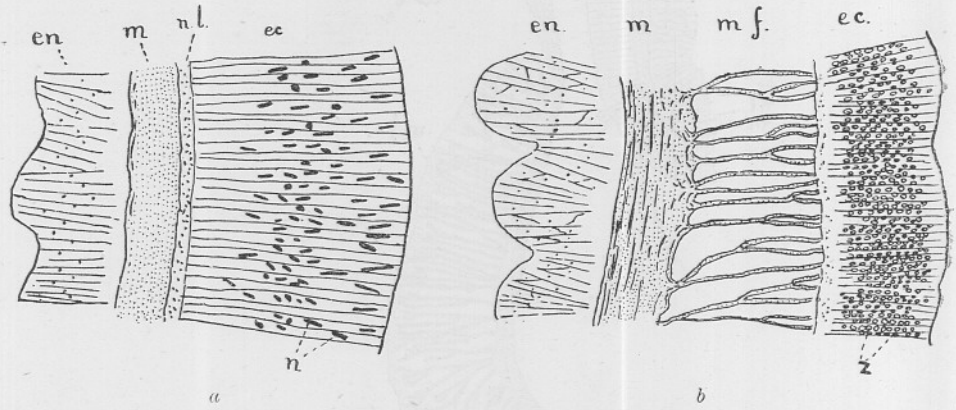

FIG. 4.—Transverse sections through a tentacle, showing structure of wall: (*a*) near the tip, (*b*) near the base; *ec.* ectoderm, *en.* endoderm, *m.* mesoglœa, *m.f.* muscle fibres, *n.* nematocysts, *n.l.* nerve layer, *z.* zooxanthellæ.

of zooxanthellæ. No nematocysts are present. The mesoglœa sends up folds into the ectoderm, except at the points where the mesenteries are attached to the disk. The endoderm contains a few scattered cells of zooxanthellæ. From longitudinal sections of a tentacle (Fig. 3) it is seen that the ectoderm is very thick at the tip, and contains numerous nematocysts. In this region zooxanthellæ are almost absent. This ectoderm causes the swollen tip of the tentacle (Fig. 4*a*). Lower down the zooxanthellæ become more numerous (Fig. 4*b*), and are seen in the ectodermal cells as colonies of pigmented bodies of a greenish yellow colour. The presence of these algal colonies accounts for the blotches described on the exterior of the tentacles. Near the base the ectoderm is less thick, and in places contains neither nematocysts nor

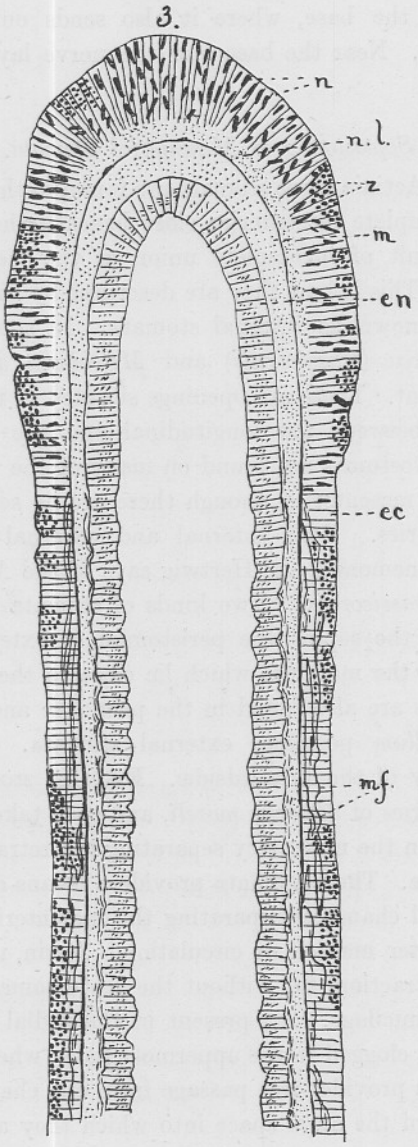

FIG. 3.—Longitudinal section through a tentacle: *ec.* ectoderm, *en.* endoderm, *m* mesoglœa, *m.f.* muscle fibres, *n.* nematocysts, *n.l.* nerve layer, *z.* zooxnathellæ.

zooxanthellæ. There is a definite nerve layer at the base of the ectoderm in the region around the tip where there are numerous nematocysts to control. The mesoglœa is dense, but becomes more fibrillar towards the base, where it also sends out branches which very often divide. Near the base also the nerve layer becomes much thinner.

Septostomes or Mesenterial Stomata.

"In the genus Actinia these stomata are found in the uppermost inner angles of the complete mesenteries close beneath the mouth, and are probably the result of incomplete union of the mesentery with the stomatodæum." This is how they are described by Professor Bourne in (5). They are known as internal stomata. In some other Actiniæ, e.g. *Tealia coriacea* (*crassicornis*) and *Metridium dianthus*, external stomata are present. These are openings situated in the upper third of each mesentery between the longitudinal and the parietal muscles. In *Metridium* septostomes are found on many of the imperfect as well as on the perfect mesenteries, though there are no septostomes on the directive mesenteries. Both internal and external septostomes are present in some anemones, e.g. Hertwig says of the Actinian which he named *Dysactis crassicornis*, "Two kinds of stomata are found on the muscular part of the septa—the peristomial or external stomata are very large, whilst the marginal which lie close to the wall are small." These septostomes are also found in the primitive anemones, e.g. *Halcampa chrysanthellum* possesses external stomata. No septostomes were found in any of the Edwardsidæ. External stomata are present in all the mesenteries of *Eloactis mazeli*, and each takes the form of an elongated slit down the mesentery separating the retractor muscle from the parietal muscle. These stomata provide a means of communication between the radial chambers separating the mesenteries, and probably thus ensure a better method of circulation. Again, undoubtedly they facilitate rapid retraction, for without the septostomes there would be a danger of the mucilage, etc., present in the radial chambers of the cœlenteron getting clogged in the uppermost parts, whereas the presence of the septostomes provides free passage from one chamber to another, not only by way of the axial space into which they all open, but also *via* these stomata.

Systematic Position of Eloactis mazeli.

Delage and Hérouard (6) have temporarily placed this anemone in

the 11th family of the Heteractinæ with several other anemones whose internal structure is unknown.

The elongated form of the body, the absence of a definite sphincter muscle, and the presence of a small number of mesenteries, are characters of Eloactis which show that it is related to the primitive, rather than to the more advanced anemones: the latter do not possess an elongated body, but are characterized by the presence of a definite sphincter muscle and a large number of mesenteries. The Edwardsidæ and the Halcampidæ are two of the most primitive families whose members have an elongated body form, no definite sphincter muscle, and a small number of mesenteries. The Edwardsidæ have eight mesenteries, whereas in *E. mazeli* there are twenty; therefore Eloactis cannot be placed with Edwardsia, the sole genus of that family.

The family Halcampidæ has been defined by McMurrich in the paper already referred to (2), as "Actiniæ with a small number of mesenteries, six, ten, or twelve pairs being all present; longitudinal muscle pennons narrow, but strong; no special sphincter muscle; conchula present or absent; base usually rounded and vesicular." In this family, therefore, McMurrich places Halcurias and Peachia as well as the genus Halcampa. Eloactis, with a small number of mesenteries and no sphincter, may be placed in the Halcampidæ. It may be closely compared with *Halcurias pilatus*, as described by McMurrich, and both are found to possess the following characters:—

Column cylindrical; ten pairs of mesenteries, all of which are perfect. There is no special sphincter muscle, and the tentacles are not covered after contraction.

There is one siphonoglyphe, and on the surface of the stomatodæum are numerous ridges.

All the mesenteries bear reproductive organs.

The mesogloea is fibrillar, especially towards the inner surface.

Halcurias has an adherent base, whereas the members of the Halcampidæ have a rounded and vesicular base. *Eloactis mazeli* and *Eloactis producta* have indications of a slightly adherent base; but in these three forms this character is outweighed by the small number of the mesenteries and the structure of their muscles.

The structure of *E. mazeli* shows that this form is slightly more highly specialized than *Halcurias pilatus*. In the latter, the four pairs of mesenteries situated in the sulco-lateral and lateral intermesenterial spaces are less extensively developed than the other six, and the siphonoglyphe is neither deep nor well defined. On the other hand, *E. mazeli* has

all its mesenteries fully developed and has a deep and well-defined siphonoglyphe ; also the distribution of nematocysts is different in the two forms. Eloactis possesses twenty highly specialized tentacles, all well armed with nematocysts, and these are present only on the tentacles, especially on their ovate heads. *H. pilatus* does not possess such highly specialized tentacles ; they are more numerous, and nematocysts are present on the disk and body wall as well as on the tentacles. Thus the tentacles are not so well adapted as feeding and defensive organs, and the division of labour is not so complete as in *E. mazeli*.

Peachia is probably still more advanced :—

It has a single deep siphonoglyphe like *E. mazeli*, but the longitudinal retractors of the perfect mesenteries of Peachia are more elongated (in section), and there is a better developed system of musculature than in *E. mazeli*.

Eloactis mazeli is therefore an elongated anemone, with twenty highly specialized tentacles, ten pairs of perfect and fully-developed mesenteries, and a deep and well-defined siphonoglyphe, and is probably intermediate in position between Halcurias and Peachia.

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