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A Revision of the Medusæ belonging to the Family Laodiceidæ.

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THIS is an old family-name to which I have given a new definition. Although the character selected is a conspicuous one, it has not hitherto taken an important position in classification, but has been chiefly used as a character for distinguishing certain genera. This character, now selected for the family, is the presence of cordyli, commonly called sensory clubs, on the margin of the umbrella.

Some of the genera which possess cordyli were placed by Hæckel amongst the Thaumantidæ, of which the Laodiceidæ formed a subfamily, and was distinguished from the other subfamilies not by the presence of cordyli, but by the number of radial canals. The other genera, on account of their having branched radial canals, were placed in the Cannotidæ, a family which Maas (1904) has recently revised.

In the family Laodiceidæ I have placed the following genera:—*Laodice*, *Staurophora*, *Ptychogena*, *Staurodiscus*, *Toxorchis*, and *Melicertissa*. The characters of these genera have been revised, but the revision has not led to a transference of species. The species of all the genera have been subjected to an impartial examination, which has resulted in a reduction of their number. For the purpose of making

this revision as complete as possible I have briefly given the characters of new species of *Stauroph*ora and *Ptychogena*.

A cordylus is an organ of a well-marked character, and when once recognized it is not likely to be mistaken for anything else on the margin of the umbrella. It is quite distinct from marginal bulbs and tubercles or sprouting tentacles and cirri. Its shape varies slightly in different genera, but it always has a clear translucent appearance, without any coloration, and is free from nematocysts. It is also without otoliths and such concretions as are generally found in sense-organs. Its function, however, has not yet been definitely found out, but it is generally regarded as a sensory organ. The first adequate description of a cordylus was given by Brooks (1895), to whom the sensory theory is due.

Hartlaub's positive statement (1897) that the cordyli of *Staurophora* develop into tentacles led me to carefully examine early and intermediate stages of *Laodice*. If cordyli are the forerunners of tentacles one would naturally expect to see them in the earliest stage or in the very early stages; but they do not make their appearance until the Medusa has at least trebled the original number of its tentacles.

After searching the margins of the umbrella of several dozen young *Laodice*, I did find two specimens which showed cordyli being converted into tentacles. They showed, however, an exception to the normal course of development of a tentacle which needs an explanation.

When there is ample room between two tentacles one finds a cordylus, a cirrus, and a tentacular bud in a single row and isolated from one another. The tentacular bud increases in size until it becomes a bulb, from which sprouts out the tentacle. Under this condition there is not the slightest indication of a cordylus becoming converted into a tentacle. The stalk of the cordylus arises direct from the margin of the umbrella and does not touch the tentacular bulb.

In most young specimens the interval between two tentacles has frequently the appearance of being overcrowded, owing to the marginal appendages developing faster than the margin of the umbrella. The tentacular buds arise alongside of, or even underneath, the stalk of a cordylus, so that a cordylus is often seen on the side, or on the top, of a tentacular bulb. One specimen was seen with a number of buds and bulbs with tentacles developing; each bulb had a cirrus on its outer side and a cordylus on its inner side. It was evident that the tentacular bud had forced its way up between the cirrus and

the cordylus. On the development of the bud into a bulb the cirrus and cordylus were carried up on to the side of the bulb. It is rare to find a cirrus and cordylus on the side of a basal bulb of a large tentacle, so that these organs either change their position or disappear. They cannot develop into a tentacle, because the tentacle is already formed.

In the two specimens showing the cordyli being converted into tentacles it was fairly evident that the tentacular bud made its appearance right underneath the already fully developed cordylus. There were a sufficient number of bulbs with cordyli to trace out the various stages of growth. One bulb showed very distinctly the conical apex of the sprouting tentacle beneath the translucent stalk of a cordylus, and later stages showed the translucent cells of the cordyli becoming opaque as the tentacles advanced in size. The cordylus in the process of conversion becomes very large, and finally loses its characteristic shape. It seems to me that the cells of the cordylus are converted into tentacular cells, and as soon as that process is completed the rounded end of the cordylus becomes pointed and indistinguishable from an ordinary half-grown tentacle.

As the conversion of cordyli into tentacles was only seen in two young stages, it is probably due to the cordyli being in the way of rapidly growing tentacles, and consequently they were absorbed.

A time comes when tentacular growth stops and the bulbs remain in an arrested state of development. This, I think, accounts for some adult specimens having their cordyli upon small bulbs and also upon bulbs with ocelli.

Family Laodiceidæ, L. Agassiz, 1862.

Character of the Family.—Leptomedusæ with cordyli, commonly called sensory clubs, on the margin of the umbrella.

Genus Laodice, Lesson, 1843.

Generic character.—Laodiceidæ with four radial canals; with a central stomach and mouth; with ocelli on the basal bulbs of the tentacles.

This is the best-known genus of the family. Although I have excluded several species which were formerly placed in the genus and reduced others to synonyms, still I am not quite satisfied with the result, owing to the difficulty of

finding suitable characters for the determination of the species. As the means of distinguishing the species the following characters are used :—

a. The presence or absence of cirri.
b. The presence or absence of a spur at the base of the tentacles.
c. The number of cordyli between the tentacles.
d. The shape of the gonads.

Laodice undulata (Forbes & Goodsir), 1851.

Thaumantias undulata, Forbes & Goodsir, 1851, p. 313, pl. x. fig. 7.
Thaumantias confluens, Forbes & Goodsir, 1851, p. 314, pl. x. fig. 8.
Thaumantias mediterranea, Gegenbaur, 1856, p. 237, Taf. viii. figs. 1–3.
Cosmetira punctata, Hæckel, 1864, p. 334.
Laodice calcarata, Browne, 1898, p. 823, pl. xlix. fig. 4.
Laodice cruciata, Maas, 1904, p. 18.

Laodice calcarata, A. Agassiz, 1862.

Laodicea calcarata, A. Agassiz, 1862, p. 350.
Lafoea calcarata, A. Agassiz, 1865, p. 122, figs. 184–194.
Laodice calcarata, Hæckel, 1879, p. 134.
Laodice calcarata, Brooks, 1895, p. 287, pl. xvii.

Laodice ulothrix (Hæckel), 1877.

Cosmetira ulothrix, Hæckel, 1877.
Laodice ulothrix, Hæckel, 1879, p. 133, Taf. viii. figs. 5–7.
Laodice ulothrix, Mayer, 1900, p. 49; Mayer, 1904, p. 14, pl. iv. fig. 30.

In 1851 Forbes and Goodsir described as new species *Thaumantias undulata* and *Thaumantias confluens*, which they found on the west coast of Scotland. I consider *T. confluens* to be an earlier stage of *T. undulata*. It is quite evident from the description and figure that *T. undulata* belongs to the genus *Laodice*. The specimens were seen alive, and in their description the authors state that each tentacle "springs from a bulbous base, bearing a small but distinct black ocellus. Between each pair of tentacula is a minute, transparent, mobile, pedunculated tubercle. [The figure shows these tubercles, which have the appearance of roughly drawn cordyli.] Down the four gastrovascular canals, very nearly from their divergence to the margin of the umbrella, run the four linear genital glands, tinged with rose-colour. They are very peculiarly formed, each hanging from the surface of the subumbrella in the shape of a pair of undulated membranous curtains, strikingly reminding us of the appearance presented by *Staurophora*, but differing in their nature ; for, in the animal we are describing, they are

assuredly distinct from the stomach-lobes. The stomach is rather large and quadrangularly campanulate, rose-coloured, and slightly fimbriated at the margins." The umbrella is hemispherical, about 1½ inches (38 mm.) in diameter. The tentacles are about 160 in number. The authors do not mention or figure cirri, which should have been present in the specimens.

The *Laodice* which I have found on the British coasts I called *Laodice calcarata*, and used the name before I had seen the paper by Forbes and Goodsir. Otherwise I should have no doubt called the British form *Laodice undulata*. The fact that Forbes and Goodsir mention the presence of one "pedunculated tubercle" between every two tentacles, by which they evidently mean a cordylus, shows, I think, clearly that they had found a *Laodice*, and, so far as I know, there is only one species of *Laodice* on the British coasts.

Forbes and Goodsir say nothing whatever about cirri, which they would have seen if the living specimens had been carefully examined. In preserved specimens cirri are sometimes scarce and also the cordyli, as these organs are rather fragile. In the second species, *Thaumantias confluens*, the figure of the margin of the umbrella does show two or three projections between the tentacles. They may possibly represent the bases of broken off cirri and a cordylus. The authors state that this species has also pedunculated tubercles.

To Gegenbaur the credit must be given for the first adequate description with good figures of a *Laodice* when he described *Thaumantias mediterranea*, 1856.

It is futile to consider *Medusa cruciata* of Forskål, 1775, as a *Laodice*, because the essential character of the family is not mentioned or figured. Hæckel, moreover, has caused utter confusion by placing several species clearly belonging to other genera as synonyms of *Laodice cruciata*. The law of priority is carried too far when it is extended to species which have never been either described or figured, so as to indicate the character of the family or genus.

In the above list of references there are six distinct specific names; three of them may be safely regarded as synonyms. I have made several endeavours to find a single character or combinations of characters whereby the remaining three species—*L. undulata*, *L. calcarata*, and *L. ulothrix*—could be distinguished from each other and readily recognized. When the descriptions and figures of these species have been analyzed one finds that new figures, with more detailed descriptions based upon more specimens, are needed. It is

solely for that reason that I have refrained from joining all the above-mentioned species under one name.

The normal number of cordyli between every two tentacles in the British form is one, and one is also found in the Mediterranean form. *Laodice ulothrix*, according to Hæckel's figure, has two cordyli, but Mayer has described specimens with one cordylus between every two tentacles. *Laodice calcarata*, according to Agassiz, has one or two cordyli between the tentacles, but Brooks mentions specimens with only one. It is evident that there is one cordylus between every two tentacles and that some specimens may have one or two; but there is no evidence that any of the North-Atlantic species have always two cordyli between every two tentacles. The same is the case with the cirri, either one or two between every two tentacles. Allowances must be made for development and also for breakage in preserved specimens. Brooks records a variety of *Laodice* without cirri from the Bahamas, but Mayer records specimens with cirri from the same region.

The ocelli are certainly very variable in number. In some specimens every tentacle is provided with an ocellus, whereas in others comparatively only a few tentacles have ocelli. Gegenbaur figures an ocellus at the base of the cordylus in *L. mediterranea*, and Brooks also mentions a variety with ocelli in the same position from the Bahamas. The ocellus belongs really to a tentacular bulb in an arrested state of development, upon which the cordylus is situated. I have found that the British form of *Laodice* has a very variable number of irregularly distributed ocelli, so that they are of little use for a specific character.

The length of the gonads along the radial canals is useless for a specific character, as the length depends upon growth.

There is certainly a difference in colour, but colour unfortunately usually disappears after preservation, and, moreover, the descriptions do not always state whether the colour described is that of the living medusa or of a specimen in alcohol or some other fluid. I have seen large living specimens of the British form which were quite colourless, and other specimens from the same locality with pink gonads. There is, however, a tendency for the European forms to have pinkish gonads and the American forms to have dark yellowish to brown gonads. Mayer describes *L. ulothrix* from the Bahamas as being dull pink, brownish, or greenish white, so that it appears to me that colour is of little use as a specific character.

On bringing together the characters of the three species

found in the North Atlantic and Mediterranean, one finds that between every two tentacles there are always one cordylus (rarely two) and either one or two cirri. The ocelli are variable in number and not quite constant in position, and their colour is variable—dark brown, dark violet, or black. The colour of gonads and other organs is also variable—dark yellow, brown, pink, or pale violet. The tentacles are numerous and have, when fully developed, an endodermal basal spur, which is variable in length and shape. The gonads, when mature, form undulating bands upon the radial canals.

Distribution. North Atlantic; Europe, British coasts (*L. undulata*, Forbes and Goodsir; *L. calcarata*, Browne).

Mediterranean (*L. mediterranea*, Gegenbaur; *L. cruciata*, Maas).

Canary Is. (*L. ulothrix*, Hæckel).

Bahamas (*L. ulothrix*, Mayer).

North Atlantic; American coast (*L. calcarata*, Agassiz, Brooks, Hargitt).

Tortugas, off Florida (*L. ulothrix*, Mayer).

The Hydroids belonging to Laodice calcarata *and* Laodice undulata.

A. Agassiz (1865, p. 124) gives a brief description with a figure of the hydroid which he believed to belong to *Laodice calcarata*. It is necessary, however, to criticize this connexion of the hydroid with the medusa, as it is a matter of some importance.

Agassiz discovered a small hydroid which he considered to belong to the genus *Lafoea*, hence the name *Lafoea calcarata*. The hydroid is a small creeping form and was found just below low-tide mark in Buzzard's Bay, Naushon. The hydranths are arranged "in a quincunx manner on both sides of a long slender creeping stolon, which does not branch." The figure shows that the perisarc is tube-like, and there is no evidence of an operculum. The hydroid has a few very large gonothecæ, inside of which develop medusæ. The medusa on liberation has "two long tentacles, two slightly developed ones, and four more hardly perceptible in the middle of the space between the chymiferous tubes (radial canals)." The basal bulbs of the two tentacles and the other six tentacular buds each have one dark pigment-spot. This medusa on liberation from its hydroid has only two long tentacles, no cirri, and no cordyli.

The next stage mentioned is much older than the earliest

stage. As there is no evidence to show that Agassiz reared the medusæ in an aquarium, I presume that this later stage was taken out of the sea. It has sixteen tentacles and a cirrus between every two tentacles. The basal bulbs of all the tentacles are provided with ocelli; but there are no cordyli. It seems to me that the similarity between the above two stages is the presence of ocelli, and it is well to remember that there are other genera besides *Laodice* with dark ocelli on the basal bulbs.

Metschnikoff (1886, p. 83, Taf. iv. figs. 17–31, Taf. v. fig. 1) has given an excellent description of the development of the ova of *Laodice cruciata* and splendid figures of the hydroids which he reared from the ova. His work is entirely embryological, and no description of the medusa is given. I presume he means *Laodice cruciata* according to Hæckel, and that his species was really *Laodice mediterranea* of Gegenbaur; for this is the only species of *Laodice* among Hæckel's many synonyms. The hydroid which Metschnikoff reared is similar to *Cuspidella humilis*, Hincks.

Hincks (1868) described three species of *Cuspidella*—*C. humilis*, *C. costata*, and *C. grandis*. The descriptions are based upon the shape of the hydrothecæ. It is evident to me that the shape of the hydrotheca of *Cuspidella* and its allies is not sufficient to base specific characters upon, and that the structure of the hydranth must be taken into consideration, and also the gonosome. It is quite likely that *Cuspidella costata* is only another form of *C. humilis*. For the purpose in view it is sufficient to know that Metschnikoff reared from the ovum of *Laodice* a hydroid belonging to the genus *Cuspidella*, which is distinguished generically from Agassiz's *Lafoea* by the presence of an operculum on the top of the hydrotheca.

During June 1906 I received a letter from Miss M. Delap, of Valencia Island, stating that she had kept a colony of *Cuspidella costata* under observation and had seen the colony liberate medusæ. Later on I received drawings of the hydroid and its medusa and also specimens. The hydrotheca is like Hincks's figure and has a few transverse rings and an operculum. The gonotheca is somewhat similar to the hydrotheca, but is about twice the length and is without transverse rings. The figure drawn by Miss Delap shows two medusa-buds inside the gonotheca and a medusa just escaping through the operculum. The medusa on liberation has two opposite perradial tentacles and two opposite perradial tentacular bulbs. On each side of the two tentacles there is a cirrus, adradial in position, and cirrus-buds occupy

the other four adradial positions. The umbrella is nearly as broad as high, about 1 mm., and has a few nematocysts scattered over the exumbrella. The four perradial tentacular bulbs have black ocelli on their inner side. The medusa on liberation is without cordyli.

Metschnikoff figures two specimens of the young hydroid, one with a short hydrotheca and the other with a long hydrotheca; both are without transverse rings, which are generally considered to be lines of growth. Miss Delap's figure is similar to Metschnikoff's hydroid with a short hydrotheca, but shows the transverse rings.

The comparison of *Cuspidella costata* with *Lafoea calcarata* of Agassiz shows that the two hydroids are not of the same genus. The hydrotheca of *Lafoea calcarata* is without an operculum, and its gonotheca is also without an operculum and is quite different in shape. Agassiz's hydroid is not a *Cuspidella*, and it is not a true *Lafoea*, because it liberates medusæ. *Lafoea* has a peculiar gonosome, which until recently was regarded as a distinct hydroid, generically known as *Coppinia*. Moreover, the medusæ liberated from these two hydroids are not similar. Agassiz's medusa has two tentacles and six tentacular buds, all with ocelli, and no cirri. Miss Delap's medusa has two tentacles and two tentacular buds, all with ocelli, and four cirri. Either Agassiz's hydroid does not belong to *Laodice calcarata*, or if it does, then the adult medusæ found on the American coast and on the British coast should show specific differences, sufficiently conspicuous to distinguish one from the other.

I have in my collection of British medusæ some young stages of *Laodice* taken in tow-nets at Valencia in 1897 and at the Scilly Isles in 1899 and 1903. The earliest stage, about 1·25 mm. in diameter, has four perradial tentacles, each with a black ocellus on the basal bulb, four interradial, eight adradial, and a few scattered buds or bulbs, all without ocelli. Between every two bulbs there is generally a cirrus; but there is not the slightest trace of a cordylus. As development proceeds tentacles sprout out from the bulbs, more buds or bulbs appear, and more cirri come into existence. It is not until the umbrella is 3–4 mm. in diameter that cordyli are clearly recognizable. (Many of the early stages were examined alive.)

Laodice is the only medusa on the British coasts with black ocelli on the inner side of the basal bulbs and with cirri, so that these early stages, without cordyli, are not likely to belong to another genus. The presence of black ocelli and cirri in the medusa liberated from *Cuspidella costata* indicates

a *Laodice*, and there is no reason for supposing that after a little further development it would not become similar to the earliest stage in my series of young *Laodice*.

The absence of cirri in the medusa liberated from *Lafoea calcarata* seems to indicate that it is not a *Laodice*. The later stage, with cirri, described by Agassiz, has the characters of a *Laodice*, and agrees with one of my early stages before the cordyli begin to develop; but, as I have already pointed out, there is no evidence that this particular specimen was reared from the hydroid.

Laodice indica, Browne, 1905, p. 136, pl. i. fig. 5, pl. iv. figs. 7–11.

This species is very much like *Laodice undulata*, but the tentacles are without a basal spur. Cirri present. One cordylus between every two tentacles.

Distribution. Indian Ocean, Ceylon.

Laodice marama, Agassiz and Mayer, 1899, p. 162, pl. iii. figs. 7–8.

This species closely resembles *Laodice indica*, but can be distinguished from it by the presence of usually two or three cordyli between every two tentacles. Cirri present. The tentacles have long tapering basal bulbs and are without a spur. The size of the umbrella and the general appearance of the gonads suggests the description having been based upon a young immature stage.

The presence of cirri distinguishes this species from *L. pulchra*.

Distribution. Pacific Ocean, Fiji.

Laodice pulchra, Browne, 1902, p. 280.

In this species there are generally three to four cordyli between every two tentacles, and they are situated upon small bulbs. Cirri absent. The tentacles are without a basal spur. Gonads arranged in a series of short folds along both sides of very large radial canals.

Distribution. South Atlantic, Falkland Islands.

Laodice Maasii, nov. nom.

Laodice fijiana, var. *indica*, Maas, 1905, p. 25, Taf. ii. figs. 14–15, Taf. v. figs. 32–35.

It was not without some hesitation that I decided upon giving a new name to the *Laodice* described by Maas in the

report on the 'Siboga' medusæ. Maas believes his specimens to be either identical with, or closely related to, *Laodice fijiana* of Agassiz and Mayer. If not identical, he suggests that they should be regarded as a variety under the name of *indica*. In describing the specimens Maas took the opportunity to criticize the genus *Laodice* and its allies. His is an excellent criticism, and after I had independently investigated the literature on the species I was pleased to find myself in agreement with him.

Laodice Maasii is twice to three times the size of *L. fijiana*, with more than twice the number of tentacles, and with many more cordyli. The gonads extend much further along the radial canals. Both species are provided with ocelli on about two thirds of the basal bulbs of the tentacles. Taking the above characters alone there is no reason for not imagining the smaller *L. fijiana* growing to a larger size and possessing more tentacles, more cordyli, and longer gonads. Then it would resemble *L. Maasii*. The medusa figured by Agassiz and Mayer does not look at all like Maas's medusa. The gonads of *L. fijiana* are adjacent to the stomach and on conspicuous diverticula of the radial canals, whereas in Maas's medusa the diverticula are not visible in the figures, though the author states that there are outgrowths along the radial canals. It is a question of degree between a slight outgrowth and a conspicuous one. There is, however, one character by which the two species can be distinguished. Maas figures and describes the tentacles with basal spurs, which are not present in *L. fijiana*.

Distribution. East Indian Archipelago.

Laodice fijiana, Agassiz and Mayer, 1899, p. 163, pl. iii. figs. 9–10.

This species has a very few cordyli; only about eight are present, though the tentacles number about seventy. Cirri absent. Tentacles without a basal spur. The gonads are upon short lateral diverticula of the radial canals. The scarcity of cordyli and the presence of conspicuous diverticula on the radial canals carrying the gonads appear to be the principal characters of this species.

Distribution. Pacific Ocean, Fiji.

The following species are excluded from the genus *Laodice*:—

Laodice cruciata, Hæckel, 1879.

I think it would be a distinct advantage if this specific

name were regarded as obsolete. In the first place, it is impossible to identify the original *Medusa cruciata* of Forskål, as its description and figures are too indefinite. In the second place, Hæckel has produced great confusion by putting under the name of *Laodice cruciata* several species which clearly belong to other genera. I have criticized in detail Hæckel's synonyms in the Proc. Zool. Soc. (1896, p. 482), and it is not necessary to do so again. There is only one genuine *Laodice* amongst the lot, namely *Thaumantias mediterranea*, Gegenbaur.

Cosmetira salinarum, du Plessis, 1879, p. 39, pl. xii.

Laodice salinarum, Hæckel, 1880, p. 636.

This species was found by du Plessis in brackish-water ditches in a salt-marsh near Cette. Du Plessis says that "it is curious that it is a miniature copy of a much larger species, *Cosmetira punctata*, which occurs in the sea near Cette." *Cosmetira punctata* is a synonym of *Laodice mediterranea*. The description given by du Plessis is rather vague, and the photograph, which is the only figure, is too fuzzy to show any details. From the description I rather think that the medusa is more likely to be an *Olindias* or one of the Olindiadæ. It was found suspended by the long tentacles from the lower surfaces of masses of algæ. This points to the tentacles having adhesive disks. The tentacles are provided with rings of nematocysts, and between the tentacles at regular intervals are some little reddish sacs, which have a pigment-spot and some crystalline concretions. The sensory clubs of the Laodiceidæ are without otoliths or crystalline concretions. There is no clear evidence that this medusa belongs to the Laodiceidæ, and it should be searched for again and properly described. Maas (1905) has also expressed an opinion to the same effect.

Laodice cellularia, A. Agassiz, 1862, p. 350; id. 1865, p. 127, figs. 195–196.

Thaumantias cellularia, Hæckel, 1879, p. 129; Murbach and Shearer, 1803, p. 172, pl. xvii. fig. 2.

Agassiz, in his original description of this species, was doubtful whether it belonged to the genus *Laodice*, for the examination of the tentacles could not be made sufficiently accurate to determine this point. Murbach and Shearer have again found this medusa. They definitely state that specimens preserved in formalin do not show ocelli or cirri. As nothing

is said about sensory clubs, it may be presumed that these organs are also absent, and therefore the medusa is not a *Laodice*. Whether it is a *Thaumantias* or not depends upon the result of a revision of the Thaumantidæ and Eucopidæ. *Thaumantias cellularia* inhabits Puget Sound and the straits between Vancouver Island and British Columbia.

Laodice Chapmani, Günther, 1903, p. 425, pl. ix. figs. 1–3.

Maas has already expressed an opinion that this species is not a *Laodice*. It certainly does not look like one, and the absence of cordyli excludes it from the Laodiceidæ. The description is based upon a single specimen found in the North Atlantic.

Laodice neptuna, Mayer, 1900, p. 48, pl. xx. figs. 50–52.

This medusa was found at the Tortugas, off the coast of Florida. It has been well described and figured by Mayer, who does not mention the existence of cordyli; consequently I exclude it from the Laodiceidæ. In general appearance this medusa does not look like a *Laodice*, but more like a medusa belonging to another family at an intermediate stage in development.

Genus Staurophora, Brandt, 1835.

Staurophora, Hæckel, 1879.
Staurostoma, Hæckel, 1879.

Generic character.—Laodiceidæ with four radial canals; with a narrow cross-shaped stomach and mouth extending across the subumbrella; with ocelli on the basal bulbs of the tentacles.

Although Brandt established the genus *Staurophora*, it was Louis Agassiz who, in his description of *Staurophora laciniata*, first gave an accurate account of a *Staurophora*, and clearly demonstrated the existence of a mouth and stomach. One of his figures shows distinctly a cordylus, though no mention is made of this organ in the description. Agassiz was perfectly right in associating his species with Brandt's genus *Staurophora*.

Hæckel has certainly misinterpreted Brandt's figures of *Staurophora* in considering the lobes of the stomach to be blind lateral branches of the radial canals; hence his placing *Staurophora* in the family Cannotidæ. This error led to his introducing a new genus, *Staurostoma*, for Agassiz's species, which was placed amongst the Thaumantidæ. Hartlaub and

Maas have also expressed their disapproval of Hæckel's *Staurostoma*.

The most interesting character of *Staurophora* is the position of the stomach, mouth, and the gonads. How they obtained their present position will be more readily understood after considering the position of these organs in *Laodice*. It appears to me that *Staurophora* is descended from a *Laodice*-like medusa.

In *Laodice pulchra* the radial canals are extremely large and the gonads are situated upon them. The gonads are arranged in a series of short folds forming a row on each side of the canals, close to the subumbrella. They extend along the whole length of the enlarged canals right up to the central stomach, where they very nearly meet the gonads belonging to the adjacent canals. In my original description of *Laodice pulchra* the enlarged portions of the radial canals were regarded as lobes of the stomach, and not as radial canals. I considered the very short canals between the lobes and the circular canal to be the true radial canals. This species certainly has the appearance of possessing a very large four-rayed stomach with gonads extending along the lobes and a large central mouth with the margin in folds.

If one were to slit open along the middle the enlarged portions of each radial canal of *Laodice pulchra*, and imagine the cut margins to be the margins of a mouth, then the position of the mouth, stomach, and gonads would be similar to those of *Staurophora*.

I think the mouth of *Staurophora* has arisen by the outgrowth of a central mouth along the enlarged portions of the radial canals of a *Laodice*-like medusa, and consequently those portions of the radial canals have been converted into a four-rayed stomach. The gonads have not changed their position, but in *Staurophora* they have lengthened slightly and meet in the centre of the cross.

The earliest stages of *Staurophora laciniata* are very similar to those of a young *Laodice*. They have a small central stomach and mouth and four radial canals. A. Agassiz has traced the development of the mouth of *S. laciniata*, and his figures clearly show how the mouth grows out to form a perradial cross.

There is no disputing the fact that in *Staurophora* the gonads are upon the walls of the stomach and occupy the position of the gonads of an Anthomedusa. There is, however, very good evidence that *Laodice undulata* comes from a calyptoblastic hydroid belonging to the genus *Cuspidella*, and there are also Laodiceidæ with gonads on the radial

canals far away from the stomach; so that the position of the gonads of *Staurophora* does not justify its removal to the Anthomedusæ nor allow one to look upon the enlarged radial canals of *Laodice* as lobes of the stomach. Hartlaub (1897) has suggested that *Staurophora* is related to the Tiaridæ, because the early stages bear a resemblance to *Tiara*.

Staurophora Mertensii, Brandt, 1835; id. 1838, p. 400, Taf. xxiv.–xxv.; Hæckel, 1879, p. 149.

This is the type species of the genus, and as it has not been taken since the days of Brandt, a fresh description to meet modern requirements and detailed drawings are much needed.

Brandt's figures show that the cross-shaped stomach and mouth, which extend right across the subumbrella, have a large number of short lateral lobes. These lobes form the characteristic feature of the species, as they are arranged in a definite manner, either alternating or in pairs, and have a definite shape.

Distribution. North Pacific; Norfolk Sound and off the Aleutian Islands.

Staurophora arctica (Hæckel), 1879.

Staurostoma arctica, Hæckel, 1879, p. 131; Levinsen, 1892, p. 145; Aurivillius, 1896, p. 194; Linko, 1900, p. 4, Taf. ii. figs. 22–25; 1904, p. 218; 1907, p. 151.

This species, according to Hæckel, has the gastro-genital cross extending completely across the subumbrella, but the mouth extends for only half that distance, so that the distal half of each ray is a closed tube.

Linko (1900) states that all the tentacles (over 400 in number) are equal in size and similar, and that on their inner side, close to the velum, there is blackish ocellus. He figures a long cordylus between every two tentacles and also a sensory vesicle above the velum, one opposite every tentacle. So far as I know, a sensory vesicle has not been yet found in any other species of the Laodiceidæ. It is a small vesicle, with a single otolith, embedded in the ectoderm, and situated just at the juncture of the velum with the subumbrella.

Distribution. Arctic Ocean; Spitzbergen (*Hæckel*). Barents Sea, Kolafjord and Ekaterinen Haven in Lapland (*Linko*). West coast of Greenland (*Levinsen*).

Staurophora laciniata, L. Agassiz, 1849.

Staurophora laciniata, L. Agassiz, 1849, p. 300, pl. vii.; A. Agassiz, 1865, p. 136, figs. 215–219; Wagner, 1885, p. 80, Taf. iv.; Fewkes, 1886, p. 958; Fewkes, 1888, p. 233; Hartlaub, 1897, p. 484, Taf. xvi. *c*, Taf. xxii.; Broch, 1905, p. 7.
Staurostoma laciniata, Hæckel, 1879, p. 130; Hargitt, 1905, p. 43.
Staurophora Keithii, Peach, 1867, p. 358, pl. ii.
Thaumantias melanops, M'Intosh, 1890, p. 40, pl. viii.; Hartlaub, 1904, p. 103.

This species has the mouth extending along the whole length of the stomach, and the tentacles form alternating series of large and small ones, but the difference in size is very slight. Both this species and *S. arctica* require further examination, and careful drawings should be made of the organs on the margin of the umbrella, especially of the tentacles. It is not yet definitely proved that the latter is a distinct species.

Peach states that his specimens agreed in every detail with L. Agassiz's description of *S. laciniata*, except that the four rays of the stomach meet to form a perfect cross, whereas Agassiz figures an imperfect cross. This slight difference is not a specific character, though Peach attached great importance to it.

M'Intosh described under the name of *Thaumantias melanops* an abnormal Hydromedusa without stomach or mouth. Hartlaub (1904) has examined M'Intosh's specimen, and states that it is a typical *S. laciniata*.

Hartlaub (1897) records the capture of a large specimen at Heligoland, but he is a little uncertain whether it belongs to *S. arctica* or *S. laciniata*. He also obtained some very early stages, about 2 mm. in diameter, and kept them alive for several weeks in an aquarium. They fed on copepods and grew at a great rate. It was whilst watching the development of these young stages that Hartlaub saw cordyli develop direct into tentacles. The figures of these young stages do not show cordyli, but only tentacular buds.

Distribution. Arctic Ocean; White Sea (*Wagner*). North Atlantic; America, Boston Harbour (*L. Agassiz*); Nahant (*A. Agassiz*); Woods Holl (*Hargitt*). Lat. 38° N., long. 68° W. (*Fewkes*). Bay of Fundy; Grand Manan Is. and Frye's Is. (*Fewkes*, 1888). Europe; Norway (*Broch*). Scotland, east coast (*Peach*, *M'Intosh*). Heligoland (*Hartlaub*).

Staurophora falklandica, sp. n.

This new species was taken by the Scottish Antarctic

Expedition (S.S. 'Scotia') in Stanley Harbour, Falkland Islands. A description of it, with figures, will be given in the Report on the Medusæ collected by the expedition, to be published in the 'Transactions of the Royal Society of Edinburgh.'

It is very much like *S. laciniata*, but has a series of long tentacles and a series of very short rudimentary tentacles.

Genus Ptychogena, A. Agassiz, 1865.

Generic character.—Laodiceidæ with four radial canals; with a central stomach and mouth; with the basal bulbs of the tentacles without ocelli.

Ptychogena lactea, A. Agassiz, 1865.

Ptychogena lactea, A. Agassiz, 1865, p. 137, figs. 220-224; Hæckel, 1879, p. 147; Hargitt, 1905, p. 45.
Ptychogena pinnulata, Hæckel, 1879, p. 148; Hæckel, 1882, p. 7, pl. ii.; Grönberg, 1898, p. 465; Levinsen, 1892, p. 145.
Ptychogena pinnulata, var. *intermedia*, Linko, 1904, p. 217.

This species was first discovered by A. Agassiz, who found it abundant for a few days in Massachusetts Bay, about 1864, and it has not again been recorded for the North-American coast. This single record rather indicates that this medusa is not a native of that region, but has probably drifted down south from the Arctic regions.

According to Hæckel *P. pinnulata* differs from *P. lactea* in the shape of the gonads. Those of the latter have fewer lateral diverticula, but some of the longer ones are slightly branched.

Linko has found in Barents Sea a form which he considers to be a variety intermediate between *P. lactea* and *P. pinnulata*. This variety has gonads shaped like *P. lactea*, but with about as many diverticula as *P. pinnulata*. It agrees in colour with *P. lactea*. I do not think that the differences in the shape and size of the gonads are, taken by themselves, sufficient for a specific character, and Linko's variety shows a connexion between the two species. The differences in shape and size are more likely due to the development of the gonads.

This species is probably a scarce Arctic medusa which drifts south into the North Atlantic. There is no trustworthy evidence that it is a deep-sea form.

Distribution. Arctic Ocean: Greenland (*Grönberg*). Barents Sea (*Linko*). North Atlantic: America, Massachusetts Bay and Nahant (*A. Agassiz*). Iceland (*Levinsen*). Between

Ireland and Iceland, lat. 59° 7′ N., long. 13° 32′ W., lat. 42° 8′ N., long. 63° 39′ W. (*Hæckel*).

Ptychogena antarctica, sp. n.

This new species was taken off Cape Adare, Victoria Land, by the 'Southern Cross' Expedition. There is only one specimen, which unfortunately has a large hole through the top of the umbrella. The stomach and mouth are completely gone and only the distal halves of the four gonads remain. The margin of the umbrella is in perfect condition. The basal bulbs of the tentacles are laterally compressed, and there are no ocelli. They belong to the same type of bulb as that figured by Agassiz and Hæckel for *P. lactea*, and are not like the basal bulbs of *Staurophora* or *Laodice*.

The gonads are large, with broad lateral folds. In the region of the gonads the radial canals show a wavy margin corresponding to the principal folds of the gonads, but the canals have no lateral diverticula like *P. lactea*. The shape of the gonads is intermediate between *P. lactea* and *P. longigona*.

The new species can easily be distinguished from *P. lactea* by the absence of diverticula on the radial canals and by the colour of the tentacles, which are red. It is not so easy to distinguish it from *P. longigona*, because the organs on the margin of the umbrella of *P. longigona* have not been described in detail or figured. The gonads of the *P. antarctica* have much broader lateral folds and do not extend so far along the radial canals.

A description with figures of *P. antarctica* will appear in the Report on the Medusæ collected by the 'Discovery' and 'Southern Cross' Expeditions.

Ptychogena longigona, Maas, 1893, p. 64, Taf. vi. figs. 7–9.

Maas, in the description of this species, states that it has "Randkolben," by which I presume he means cordyli. As he has omitted to figure the margin of the umbrella, it is necessary to rely upon the brief description. The gonads are very long, extending the whole length of the radial canals, and are arranged in a series of lateral folds or lobes, but the radial canals have no lateral diverticula as in *P. lactea*.

Distribution. North Atlantic, off the north-west coast of Scotland.

Genus STAURODISCUS, Hæckel, 1879.

Generic character.—Laodiceidæ with four main radial canals, each with lateral branches.

The two genera *Staurodiscus* and *Toxorchis* are distinguished from the other genera of the Laodiceidæ by the presence of branched radial canals. It was on account of the branching of the canals that Hæckel placed these genera in the Cannotidæ. The Cannotidæ, as a distinct family, has now ceased to exist; its destruction was due to a revision of its genera by Maas (1904). *Staurodiscus* and *Toxorchis* were transferred by Maas to the Berenicidæ, to which he gave an emended definition.

Berenice is the type genus of the Berenicidæ. One species (*B. rosea*) is without marginal bulbs, but the other (*B. Huxleyi*) has bulbs. I am uncertain whether these bulbs are cordyli or only tentacular bulbs; if they should turn out to be cordyli, then the species should be transferred to the genus *Staurodiscus*.

Staurodiscus tetrastaurus, Hæckel, 1879.

Staurodiscus tetrastaurus, Hæckel, 1878, p. 145, Taf. ix. figs. 1–3; Mayer, 1900, p. 46, pls. xviii.–xix. figs. 47–49; Maas, 1904, p. 440.
Staurodiscus heterosceles, Hæckel, 1879, p. 146.

In this species each of the radial canals has a pair of lateral branches which do not join the circular canal. The gonads develop upon the blind branches and also upon the portion of the main canal between the branches and the circular canal. There are eight to sixteen tentacles and two or three cordyli between every two tentacles. Cirri absent. A black ocellus at the base of all the tentacles and cordyli. Mayer describes young stages as well as adult, and states that the ocelli are endodermal.

Distribution. North Atlantic: Canary Is. (*Hæckel*). Tortugas (*Mayer*).

Staurodiscus nigricans, Agassiz and Mayer, 1899, p. 164, pl. iv. figs. 11–12.

This species has radial canals with a pair of lateral branches, which do join the circular canal. The gonads are upon the branches and the portion of the main canal between the branches and the circular canal. Twelve tentacles present and six or seven cordyli between every two tentacles. Cirri and ocelli absent.

Distribution. Pacific Ocean; Fiji (*Agassiz and Mayer*).

Genus Toxorchis, Hæckel, 1879.

Generic character.—Laodiceidæ with six main radial canals, each one widely forked or with lateral branches.

Toxorchis arcuatus, Hæckel, 1879, p. 157, Taf. ix. figs. 6–8.

This species has only been seen by Hæckel. His figures show that each radial canal is widely forked, with gonads in the fork of the canals. The margin of the umbrella is provided with twenty-four tentacles, and between every two tentacles there are a cirrus and a cordylus. The basal bulbs of tentacles have ocelli.

Distribution. North Atlantic; Canary Is. (*Hæckel*).

It is probable that the genus *Cladocanna*, Hæckel (1879, p. 160), will ultimately become a synonym of *Toxorchis*. There are two species, *C. thalassina* (Péron, 1809), which has not been well described, and *C. polycladia*, which Hæckel has described but not figured. The latter species has six radial canals with several lateral branches, each of which is again dichotomously divided. The tentacles are very numerous and between them are cirri and marginal clubs. If the marginal clubs turn out to be cordyli, then I would suggest that the species be placed in the genus *Toxorchis*. Maas (1904) considers *C. polycladia* to be identical with *C. thalassina*, and doubtfully refers it to the genus *Toxorchis*.

Genus Melicertissa, Hæckel, 1879.

Generic character.—Laodiceidæ with eight radial canals, without lateral branches.

This genus Hæckel placed in the Thaumantidæ, in the subfamily Melicertidæ, containing genera with eight canals. This subfamily will probably disappear on the completion of the revision of the Thaumantidæ.

Melicertissa clavigera, Hæckel, 1879, p. 135, Taf. viii. figs. 8–12.

This is another species which has only been seen by Hæckel. **It has only eight tentacles, and between every two tentacles there are three cordyli but no cirri.** The basal bulbs of the tentacles and cordyli have ocelli.

Distribution. North Atlantic: Canary Is. (*Hæckel*).

Melicertissa malayica (Maas), 1905.

Melicertidium malayicum, Maas, 1905, p. 28, Taf. v. figs. 29–31.

This species is readily recognized by the large number of tentacles (about one hundred and fifty). There is roughly one cordylus to every two tentacles, but not between every pair of tentacles; the total number of cordyli is about half that of the tentacles. The cirri are rather scarce. About one fourth of the tentacles are provided with ocelli. The gonads are on the proximal half of the radial canals.

Distribution. East Indian Archipelage (*Maas*).

Maas placed this species in the genus *Melicertidium* as it agreed with Hæckel's definition of the genus, which happened to be an erroneous one. I have recently emended the genus *Melicertidium*. The species belonging to it have eight radial canals and numerous tentacles, but they are without cirri or marginal bulbs of any kind.

The following genera and species have for the present been excluded from the Laodiceidæ :—

Octonema eucope, Hæckel, 1879, p. 127.

The genus *Octonema* was established by Hæckel for a single species found at Honolulu, Sandwich Is. According to Hæckel's classification, the genus is distinguished from *Laodice* by the presence of only eight tentacles. The species has a large number of marginal bulbs, knobs, and cirri. Unfortunately there is no figure of this medusa, so that the exact meaning of "Randkolben" remains doubtful. Hæckel also states that a black ocellus is situated on the outer side of the basal bulb of the tentacles. The Laodiceidæ usually have the ocelli on the inner side of the basal bulbs, and there is no trustworthy evidence to show that any species of the family has ocelli on the outer side. It is quite probable that *Octonema eucope* belongs to another family.

Octonema gelatinosa, Mayer, 1900, p. 8, pl. vi. figs. 20–21.

The description of this species is based upon a single specimen taken in Charleston Harbour, U.S.A. It has the appearance of a young stage, with only four tentacles and twenty marginal bulbs. Each bulb has an ocellus, which, according to the description, is situated in the endoderm. There are eight marginal clubs, and a figure shows that their

distal end is provided with cells which look like nematocysts. Cordyli proper are without nematocysts, so that these bulbs are more likely to be tentacular bulbs.

Octorhopalon fertilis, von Lendenfeld, 1884, pp. 919, pl. xlii. figs. 14–15.

This is a little medusa, 2 mm. in diameter, having eight tentacles and eight marginal clubs, and was found by Lendenfeld at Port Jackson, Australia. The description is rather concise and the figures have been badly reproduced, so that they do not help out the short description. The author states that cirri are absent, but nothing is said about ocelli, though in the figure there are indications of an ocellus on the inner side of the basal bulbs of the tentacles.

The gonads are very large, extending along the whole length of the radial canals and also round the base of the stomach. They are folded transversely.

Before one can classify this medusa among the Laodiceidæ there are two points which require further elucidation. Is it a young stage with gonads just appearing or a fully grown adult? **Are the clubs true cordyli?** The clubs in one figure have the appearance of cordyli lying across the velum; in the second figure they project outwards and have the appearance of auditory clubs, which should contain an otocyst.

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