144549

M. le professeur G. Gilson 1019

hommage de l'auteur.

2- Hydrozoaires

15

A REVISION OF THE MEDUSÆ BELONGING TO THE FAMILY *MITROCOMIDÆ*

BY

P. L. KRAMP
(ZOOLOGICAL MUSEUM, COPENHAGEN)

WITH 1 PLATE AND 52 FIGURES IN THE TEXT

REPRINTED FROM
"VIDENSKABELIGE MEDDELELSER FRA DANSK NATURHISTORISK FORENING"
VOL. 92

COPENHAGEN
BIANCO LUNOS BOGTRYKKERI A/S
1932

A REVISION OF THE MEDUSÆ BELONGING TO THE FAMILY *MITROCOMIDÆ*

A REVISION OF THE MEDUSÆ BELONGING TO THE FAMILY *MITROCOMIDÆ*

BY

P. L. KRAMP

(ZOOLOGICAL MUSEUM, COPENHAGEN)

WITH 1 PLATE AND 52 FIGURES IN THE TEXT

REPRINTED FROM
"VIDENSKABELIGE MEDDELELSER FRA DANSK NATURHISTORISK FORENING"
VOL. 92

COPENHAGEN
BIANCO LUNOS BOGTRYKKERI A/S
1932

Denne Afhandling er af det matematisk-naturvidenskabelige Fakultet antaget til offentlig at forsvares for den filosofiske Doktorgrad.

København, den 16. Februar 1932.

Knud Jessen

h. a. dec.

A Revision of the Medusæ belonging to the Family *Mitrocomidæ.*

By

P. L. Kramp.

With Plate X.

Preface.

While working up the Hydromedusæ of the Museum at Brussels I found a new species of *Mitrocomidæ* which could not be fitted into any of the genera known up to then and as defined by Browne (1910). It was evidently closely related to *Mitrocomella polydiademata*, but it had only 8 lithocysts. I called it *Trissocoma brownei* (Kramp 1930). The find of this new species induced me to examine other representatives of the *Mitrocomidæ* in our collections at the Zoological Museum of Copenhagen, and I soon realized that a thorough revision of the family was desirable. I knew that Mr. E. T. Browne was particularly well acquainted with the group, and I also knew that the type specimens of some of the more important species were to be found in England, either in the British Museum, or in Mr. Browne's collection where I would also find well-preserved specimens of many British species. My plan was to go to England, to examine the material in question, and discuss the various systematic problems with Mr. Browne. I accordingly wrote to Mr. Browne, who readily assented to my plan, and with a grant from the Rask-Örsted Foundation I set off to England in October 1930. Before leaving Copenhagen, I carefully examined such species as were represented in our own collections, and took with me sections and other microscopical preparations for comparison. After an examination of the specimens in the British Museum, where Mr. A. Knyvett Totton most kindly gave me every assistance, I went to Berkhamstead, where Mr. Browne received me as his guest, and there I spent some most interesting and enjoyable weeks, studying specimens and literature, and discussing matters relating to medusæ. I am glad to have this opportunity to express my gratitude to Mr. Browne for many years' friendship and good advice in my studies on medusæ, and especially for his help in the present work. His specimens and notes were entirely at my disposal, and during our discussions on the difficult problems his great experience secured results which could not have been obtained without his participation.

My previous studies on coelenterates have been greatly encouraged by my Chief at the Zoological Museum of Copenhagen, Dr. Th. Mortensen, and I wish to thank him most heartily for his interest in my work.

The paper is divided into the following chapters:

I. Introduction, with remarks on principles of Classification.

II. History of the family *Mitrocomidæ*.

III. Species to be excluded from the *Mitrocomidæ*.

IV. Comparative Morphology, dealing with each set of organs separately, their general appearance, structure, and number, with remarks on their systematic importance and comparison with similar organs in other Leptomedusæ. As the specimens are merely preserved in alcohol or formaline, they are not in suitable condition for studies on the histological structures, which are therefore only occasionally touched upon in the descriptions of the organs.

V. Geographical Distribution.

VI. Genera and Species of *Mitrocomidæ*. New diagnoses of the genera, with short descriptions of the species. Remarks on history, nomenclature, development, abnormalities, and occurrence. Discussion of limitation of genera and species. I quite agree with Browne that definitions of genera should be kept as wide as possible, so that there is a chance of including new species without an alteration of the generic definition. When the description of a species is entirely derived from the literature, it has been rearranged in order to conform with the other descriptions. In the lists of synonyms are included all important references; for full lists up to 1910, see M. Bedot: Matériaux pour servir à l'histoire des Hydroïdes (1901—1925). — One new species is described: *Tiaropsidium japonicum* n. sp.

VII. Taxonomic Discussion. An attempt to classify the genera and species in a natural way. It is still difficult to determine the systematic position of the family within the Order of the Leptomedusæ as long as the other families are more or less badly defined.

I. Introduction

with Remarks on Principles of Classification.

Morphology and Classification must be the Foundation of Biology and Oecology. Several biologists have been guilty of deplorable mistakes because they have not paid sufficient attention to this fundamental principle; it is a hopeless task trying to unravel and understand the biology and oecology of animals without being sure how to identify the species and without taking into consideration their morphological structure. The medusæ are particularly interesting animals from biological points of view, and they are of considerable importance as indicators of sea-currents (Kramp 1924, 1927, and 1930). In several cases it is, however, necessary to take up for thorough investigation the limitation of species or varieties, in order to be sure not to confound two or more different forms with different geographical distribution and biological habits.

When the species are properly described and identified, they must be classified into genera and families. A natural classification of the Leptolinæ (Anthomedusæ and Leptomedusæ) is difficult, because the asexual generation (the hydroids), must be included in the system, and in numerous cases the hydroid is unknown. When both generations are known, we often find that hydroids of very similar appearance give rise to very different medusæ, whereas, on the other hand, medusæ which seem to be closely related are derived from hydroids of quite different structure. In several cases, however, the resemblance between two or more species or genera of medusæ is only a superficial one, and a careful study of their morphology may reveal unexpected differences which may serve to guide us towards a better understanding of their systematic positions. When, on the other hand, similarly constructed organs are found in species of quite different general appearance, we must consider the systematic importance of that structure, which can only be done by means of comparative-morphological studies of as many species as possible.

During the 19th century the medusæ were studied by several prominent authors who described a large number of species and tried to classify them. A detailed account of the history of the Coelenterata was given by C. Chun in Bronn's Klassen und Ordnungen des Thier-Reichs (Bd. II, Abt. 2, Kap. I and III, 1889—1892), in which the various attempts on classification are treated at some length. At first the polyps and the medusæ were classed separately; the division of the latter into two main groups (now usually termed *Hydromedusæ* and *Scyphomedusæ*) was soon realized, but the groups were defined in different ways by the various authors. The most important characters, by which the distinction between the two main groups was carried out, are the following: The external aspect of the gonads (Eschscholtz 1829: Cryptocarpæ and Phanerocarpæ); the "eyes" being naked or covered by lappets (Forbes 1848: Gymnophthalmata and Steganophthalmata); the presence or absence of a velum (Gegenbaur 1856: Craspedotæ and Acraspeda); the generative elements discharging themselves externally or into the body cavity (L. Agassiz 1862: Hydroidæ (incl. Trachymedusæ and Siphonophora) and Discophora (incl. Narcomedusæ)); the absence or presence of gastric filaments (Claus 1877: Hydroidmedusen and Acalephen); the nerve-ring being continuous or broken (Eimer 1878: Cycloneuræ and Toponeuræ); the sexual organs originating from the ectoderm or from the endoderm (O. & R. Hertwig 1879: Ectocarpæ and Entocarpæ); the absence or presence of an ectodermal pharynx (Goette 1887: Hydrozoa (incl. Hydrocorallia and Siphonophora) and Scyphozoa (Scyphomedusæ and Anthozoa)). — It will be observed that, in course of time, there was an increasing tendency towards a distinction between the two main groups of medusæ according to minor structures, especially after O. & R. Hertwig had published their detailed investigations of various types of medusæ (1878).

Whereas minor structures were comparatively early taken into consideration for distinction between the main groups of the coelenterates, the subdivision into smaller groups (families and genera) was continually carried out by means of the superficial aspect; accordingly the construction of families and genera was for a long time rather artificial, and we are still sticking to some of these artificial groups, many of which are due to Haeckel (1879—80).

Haeckel (1879) was the first to divide the Craspedotæ into *Lep-*

tolinæ and *Trachylinæ* according to the structure of the marginal sense organs. His further division of the Leptolinæ into two orders: *Anthomedusæ* and *Leptomedusæ*, seems well founded, though the limit is not quite as sharp as formerly supposed. The families within each of these orders, as defined by Haeckel, are more or less artificial, based upon superficial characters and regardless of structures of great systematic importance, and the division into genera is almost entirely based upon geometrical principles such as numbers of sense organs or tentacles. Haeckel's classification has been much criticized by subsequent authors, but still in some of the most recent textbooks his families are retained with no or small alterations (Hartlaub in Nordisches Plankton 1907—1917, Mayer in Medusæ of the World 1910, Broch in Kükenthal's Handbuch der Zoologie 1924).

Further studies by recent authors have increased our knowledge of the structure of medusæ to a considerable degree and brought us nearer to the possibility of establishing a satisfactory classification, but the importance of comparative-morphological investigations has not been equally estimated by all of these authors.

During the period from 1889 to 1913 E. Vanhöffen published a series of papers with beautiful figures and more or less adequate descriptions of many interesting medusæ. In his first papers he turned himself very polemically against other medusologists, especially Haeckel and Claus, and established new classifications. Now and again he touched upon the systematic importance of minor structures, but the comparative-morphological principle was never carried through in his classification and, in spite of his many scornful words against Haeckel, he really followed the same principles, subdividing the groups according to superficial characters and numbers of organs. His papers after 1908 contain no discussions on classification.

O. Maas expressed his programme in his very first paper, when he said (1893 p. 18, concerning the *Trachynemidæ*): "Ich nehme als Hauptprincip der Eintheilung nicht die Zahl der Höhrbläschen und als Unterprincip nicht die Zahl der Tentakeln an, sondern gehe von der Beschaffenheit der Tentakel bei der Bildung der Genera aus", and similar expressions were used when other groups were concerned. Maas clearly saw that Haeckel's classification was unsatisfactory, but he was too cautious to establish a new system based upon the previous insufficient knowledge; he realized that thorough morphological investigations of many species and genera were necessary to obtain a sound basis for classification, and he held this principle in view in all his work. His descriptions and figures were always elaborate and reliable, though important structures frequently escaped his attention; but his attempts on classification were, however, few and termed by himself provisional. He dissented from Vanhöffen in the classification of the Rhizostomata and the Narcomedusæ, and he cancelled (1904) the artificial family *Cannotidæ* Haeckel. In his works on special groups of medusæ Maas often used the expression that a satisfactory classification of the group cannot yet be established, thereupon he will immediately proceed into the description of the genera and species.

Besides Vanhöffen and Maas the following authors have greatly increased our knowledge of the medusæ: Cl. Hartlaub (since 1884), A. G. Mayer (since 1894), E. T. Browne (since 1895), and H. B. Bigelow (since 1904). Hartlaub has carried out some excellent revisions of species and genera, especially of *Pandeidæ* and *Margelidæ*, and Mayer has described several new species, partly from living specimens, but none of these two authors have tried to revolutionize the higher classification by means of comparative-morphological studies on minor structures; in the main they both kept to Haeckel's and Vanhöffen's systems.

Browne and Bigelow have not merely described a great number of interesting species; they have also carried out a good amount of classificatory work. Browne demonstrated that *Willia* is an Anthomedusa (1897) and revised the fam. *Williadæ* (1905 c); he established the new family *Laodiceidæ* to comprise Leptomedusæ with marginal clubs (cordyli) and revised the genera and species belonging to that family, and he has given a provisional revision of the *Mitrocomidæ* (1910, see below).

Bigelow mainly follows the older classifications (Gegenbaur, Agassiz, Haeckel) with the modifications proposed by later authors, especially Maas, but his own careful morphological studies have enabled him to improve the diagnoses of several groups, and new alterations are also occasionally proposed (see Bigelow 1909 p. 10). His opinion of systematic work is summarized in the following words (1918 p. 391, concerning the Narcomedusæ): "What is most needed now is not so much a continued discussion of family relationships, as an attempt to fill in the gaps in our knowledge of the actual genera and species concerned. . . . (then) a sound phylogenetic classification will follow automatically". I quite agree with Bigelow in this respect, but I think it would be wise now and again to test the empirical results of our investigations by applying them to attempts on classification on the comparative-morphological principle and so point out the gaps which particularly need to be filled in.

Several other authors have contributed to our present knowledge of the morphology of the medusæ. I shall only call attention to Linko's excellent studies on the structure of the eyes of the Hydromedusæ (1900 b).

Quite recently (since 1924) T. Uchida has carried out some adequate morphological investigations of Japanese medusæ and revised the classification of some groups. I will presently come back to some of his results and ideas; be it sufficient to say here that he has put forth several fruitful thoughts, though sometimes his conclusions are a little premature, and he often makes use of purely external characters in his definitions of the groups. For practical purposes external characters are most convenient, but their reliability as distinguishing marks must be tested by their coexistence with other structures.

Comparative-morphological investigations of older times usually set out from the existing classification of the animals and selected for thorough examination a few types within each of the larger systematic groups, afterwards generalizing the results as relevant to other types anticipated to belong to the same groups. As far as the medusæ are concerned, such generalizations have frequently turned out to be erroneous. Morphological investigations of as many species as possible are necessary to determine which species and genera are similarly constructed, and to which structures a systematic importance may be applied. In some cases it is evident beforehand that a certain structure has or has not a systematic value, in other cases we do not know in advance. Characters which denote a degree of development will usually not be of great systematic importance, but in some cases they may be so. A considerable importance may, on the other hand, generally be applied to characters which denote a direction of development. The criterion of the systematic importance of a structure is whether that structure leads to a classification which looks natural in conjunction with other characters. I also wish to point out that we are not allowed to anticipate that one special character has the same systematic importance in all groups.

Results of morphological investigations of medusæ belonging to different groups are published in some of my previous papers (Kramp 1919, 1920, 1924, 1926, 1928, Kramp & Damas 1925). All these papers deal with collections brought home by various expeditions and worked up separately; it is therefore rather accidental which species and groups have been the subject of these investigations, and I am far from able to enter upon a general discussion of the classification, but I have been fortunate enough to make some interesting observations which it might be useful to summarize on this occasion.

The *Codonidæ* Haeckel are derived from hydroids belonging to at least three different families: Corynidæ, Pennariidæ, and Tubulariidæ (incl. Corymorphidæ), all of which belong to the suborder Capitata (Kühn 1910). In accordance herewith attempts have been made to subdivide the Codonidæ into two or more subfamilies or families. Uchida (1927 p. 167) will keep the Tubulariidæ separate on account of their bilaterally symmetrical body, but this is not characteristic of all members of the group. Adult specimens of *Euphysa flammea* (Linko) are quadrilaterally symmetrical and have four equally developed tentacles; the species was therefore referred by Linko (1904 p. 212) and Hartlaub (1907 p. 12) to the genus *Sarsia* in spite of its lack of ocelli. I have demonstrated (1925 p. 245) that the four tentacles are successively developed, and I also observed four narrow, but conspicuous, perradial, longitudinal muscle bands in the manubrium. Later on I found similar muscle bands in *Euphysa tentaculata* and *E. aurata* (1926 pp. 23 and 26) and in "*Sarsia*" *japonica* Maas (1928 p. 32); in this latter species the four tentacles are equally developed even in the youngest stages known. Several other structures show the close relationship between these four species (1926 pp. 19—26 and 1928 p. 33) which together with some other species constitute the genus *Euphysa* and may be arranged into a progressive developmental series (1928 p. 34). *Steenstrupia nutans* has four broad perradial muscle bands (1926 p. 29); in *Hybocodon prolifer* the ectodermal muscle-layer surrounds the manubrium, but is somewhat more strongly developed in the perradial parts, and a similar arrangement is observed in *Euphysora bigelowi* (1928 p. 38). In the species of Sarsiidæ examined up to now the ectodermal muscles are equally developed all round the manubrium. In the manubrium of male specimens of *Sarsia princeps* the external surface of the mesosarc is provided with longitudinal ridges so as to give room for an increased number of muscle fibres (1926 p. 3). Future studies will show whether a special arrangement of the ectodermal muscles in the manubrium is characteristic of the Tubulariidæ in contradistinction to the Sarsiidæ.

Hartlaub (1907) denies the presence of a ring of nematocysts around the mouth in *Euphysa* and *Steenstrupia*, nor does he mention it in the descriptions of *Margelopsis;* as a matter of fact, it is present in all these genera as well as in *Ectopleura* and *Hybocodon* (1925 p. 252; 1926 pp. 24, 26, 29, 36; 1928 p. 31) and in *Euphysora bigelowi* and *annulata* (1928 pp. 38 and 39). An oral armature of nematocysts thus seems to be characteristic of the Tubulariidæ in contradistinction to the Sarsiidæ. In *Hybocodon* the oral nettle-ring is divided up into roundish, prominent knobs which may be regarded as forerunners of oral tentacles as in *Cytæis;* for several reasons I consider it highly probable that *Cytæis* must be removed from the Margelidæ and placed among the Tubulariidæ; the gonad encircles the manubrium, and in the latter there are four perradial muscle bands. In the papers mentioned above (1925, 1926, 1928) several other structures of the Sarsiidæ and Tubulariidæ are carefully studied, but it is premature to draw systematic conclusions from these studies.

It is now generally agreed that the family *Cladonemidæ* Haeckel is an altogether artificial group; it is, however, not easy to insert its members into the right places among the other Anthomedusæ. On the present occasion I shall only mention the genus *Zancleopsis*, established by Hartlaub (1907 p. 115) who placed *Zancleopsis dichotoma* (Mayer) in the family Cladonemidæ *sensu* Haeckel on account of its branched tentacles; but at the same time he stated that "keine andere Cladonemide steht den Codoniden so nahe wie diese". Uchida (1927 p. 167) is sure that *Zancleopsis*, like *Zanclea*, should be referred to the Codonidæ (Sarsiidæ). In 1928 (p. 40) I described a new species, *Zancleopsis tentaculata;* the distinctly cross-shaped base of the manubrium, the complete perradial divisions of the folded gonads, and the out-turned mouth edge with indications of lips contradict a relationship with the Codonidæ and point towards the Pandeidæ; there are two large and two small tentacles with basal bulbs of peculiar structure. A very similar medusa with four small tentacles shaped exactly as the two small ones in *Z. tentaculata* was described by Uchida (1927 p. 204) as *Cnidotiara gotoi* n. g., n. sp. and referred by him to the Tiaridæ (= Pandeidæ).

The principal characters by which Haeckel distinguished the family *Margelidæ* were the possession of oral tentacles and the longitudinal division of the gonads into four or eight separate parts. In some species, however, there is a ring-shaped gonad encircling the manubrium, and oral tentacles are not absolutely confined to the Margelidæ; moreover the nettle-armature may be constructed in different ways. Later authors, especially Vanhöffen (1891 p. 3) and Uchida (1927 pp. 214 and 219) point out the solid tentacles in the Margelidæ (*sensu* Haeckel). Paying no regard to the fact that tentacles can be "solid" in different ways, they include *Cytæis* in this group. In *Cytæis* the endoderm of the marginal tentacles consists of several rows of cells which meet in the axial line without leaving any central cavity; many typically "hollow" tentacles are "solid" in their distal part in the same way. Apart from *Cytæis*, all Margelidæ have true solid tentacles with the endoderm consisting of a single row of cylindrical cells (1928 p. 48, fig. 22 b). When *Cytæis* is referred to the Tubulariidæ (see above) the possession of true solid marginal tentacles thus really seems to be characteristic of the Margelidæ, though the clustered tentacles in *Margelopsis* among the Tubulariidæ are similarly constructed.

Uchida divides the Margelidæ into two families: Cytæidæ with the marginal tentacles placed singly, and Bougainvilliidæ with tentacles in clusters. This seems to me an artificial distinction; be it only remembered that in *Lizzia blondina* there is only one tentacle on each of the interradial bulbs, and in certain geographical areas very few specimens attain more than one tentacle on each perradial bulb (1926 pp. 54—55). The Margelidæ are more naturally divided according to the structure of the oral nettle-armature which has been studied by Hartlaub (1911). In *Podocoryne* and *Rathkea* the mouth-arms are simple or branched dilatations from the perradial corners of the mouth, armoured with clusters of nematocysts; they may remain open, groove-shaped (1925 p. 269), or they may attain a tentacle-like appearance, but if so they are hollow; *Turritopsis* and *Oceania* have four perradial lips bordered with knobs of nematocysts. In *Bougainvillia*, *Nemopsis*, *Lizzia*, *Köllikeria*, and *Chiarella* the mouth opening is simple, and at some distance above the mouth there are four simple or branched oral tentacles. In *Köllikeria* and in some species of *Bougainvillia* the endoderm of the oral tentacles consists of several rows of cells meeting in the axial line and leaving no central cavity; in *Bougainvillia macloviana* and *Lizzia blondina* the oral tentacles only contain one row of endoderm cells, except in the basal part (1928 pp. 48—49 and 50). The Margelidæ with oral tentacles above the mouth almost coincide with the Bougainvilliidæ of Uchida, except that *Rathkea* must be referred to the same group as *Podocoryne*. — Uchida (1927 p. 150) gives a wrong description of the development of the tentacles in "Bougainvilliidæ with four tentacle clusters", stating that in any stage of development the number of tentacles in each cluster is odd; as a matter of fact, in *Bougainvillia* the tentacles appear alternately on either side of the first one (1925 pp. 258—261, 1928 p. 49).

I agree with the authors who divide the old family *Tiaridæ* into two, Pandeidæ and Bythotiaridæ, but not on account of the presence of centripetal canals in the latter (Uchida 1927 p. 169); in *Bythotiara* and *Heterotiara* there are no centripetal canals (at least, such are only observed in a few abnormal specimens, 1926 p. 97, 1928 p. 59). The structure and insertion of the tentacles are much more characteristic of the group (1924 p. 13, 1928 pp. 59—60).

As Hartlaub (1913) has thoroughly studied the gonads of the "Tiaridæ", I have mainly paid attention to the tentacles, which are always hollow, but otherwise constructed in different ways (1920 p. 7; 1925 pp. 274, 283; 1926 pp. 66—96; 1928 pp. 55, 59). The structure of the tentacles and their basal bulbs may prove to be of systematic importance, but it is too early to make definite statements in this respect.

The *Pandeidæ* is an interesting group from a classificatory point of view. Hartlaub (1913 p. 239) rightly points out the difficulty in determining which genera and species are the more primitive; as primitive characters may be considered: simple gonads with a smooth surface, small oral lips with a smooth edge, lack of "mesenteries", narrow radial canals with smooth edges, small number of tentacles, lack of abaxial spurs on the tentacle bulbs. One or more of these primitive characters may, however, be combined with high development in other respects (1926 p. 66). As will presently be pointed out, similar combinations of primitive and specialized characters are also found in the Mitrocomidæ. Careful studies of the minor structure of the various organs may possibly lead to a natural classification of the Pandeidæ. I wish to call attention to the occurrence in *Tiaranna rotunda* and *Bythotiara murrayi* of some peculiar small marginal appendages which, in my opinion, are forerunners of the cordyli in the Laodiceidæ (1920 p. 7, 1919 p. 5, 1924 p. 14). It is interesting that they occur in one species of each of the two closely related families.

Among the most characteristic features of the Pandeidæ is the possession of four oral lips without nettle-armature but with a thin out-turned edge; the same structure of the mouth is found in the Leptomedusæ. Moreover the cross-shaped base of the manubrium which is attached to the subumbrella along the borders of radiating grooves; the same is the case in most Leptomedusæ (1919 p. 6).

In the Anthomedusæ the gonads are in the walls of the stomach, but in some species they extend some way out along the radial canals; this is, however, effected in two different ways. In some of the Margelidæ: *Bougainvillia macloviana*, the male *Bougainvillia ramosa*, and in *Nemopsis*, it is the upper, proximal parts of the gonads which grow outwards along the radial canals, and one might fancy that a further outgrowth that way might terminate in an emancipation from the stomach walls and so lead to the conditions in the Leptomedusæ, where the gonads are in the walls of the radial canals; but I do not think that the gonads of the Leptomedusæ have arisen in that way. In 1919 (p. 6) I have discussed the probable course of development from the gonads of the Pandeidæ to those of the Laodiceidæ, from which it appears that the distal parts of the gonads in the latter (the parts nearest to the bell margin) correspond to the distal parts of the Pandeid gonads (the parts nearest to the mouth). In most of the Laodiceidæ the emancipation of the gonads from the stomach is not completed, and the corners of the manubrium are drawn out into funnel-shaped extensions reaching almost to the distal parts of the gonads. By means of lateral, longitudinal folds these funnels may, in some species, be divided into a ventral and a dorsal part (described in details in *Laodicea undulata* and *Ptychogena lactea*, 1919 pp. 17, 19, and 32); it is noteworthy that this interesting structure is present in much the same way in the highest developed forms of these two genera, but not in the more primitive *Ptychogena crocea* (1925 pp. 291 and 292) in which, on the other hand, the entire cavity of each of the funnels is connected with the stomach cavity through a vertical slit which can be closed by means of two vertical folds (1925 p. 290). A closing mechanism which can separate the stomach cavity from the radial canals is also found in some other Leptomedusæ e. g. *Melicertum octocostatum* and *Tima bairdi* (1919 pp. 53 and 103).

In many Leptomedusæ the proximal parts of the radial canals are more or less funnel-shaped, but it is only among the Laodiceidæ that we find the funnels extending outwards along the gonadial parts; in all other families the gonads are completely emancipated from the manubrium. We must assume, however, that this complete emancipation marks a further stage in the development from the Pandeidæ through the Laodiceidæ.

In most Leptomedusæ the gonads are on the lateral sides of the radial canals, being separated in the median, ventral line, but in some genera (*Obelia*, *Phialidium*, *Octocanna*, and perhaps in other forms too) there is only one gonad on each radial canal, completely encircling the ventral edge of the latter (1919 pp. 94 and 95, 1925 p. 308). This may prove to be of systematic importance.

The classification of the Leptomedusæ needs a revision, most families being badly defined. Among the most characteristic structures of the *Laodiceidæ* are the hollow marginal clubs or cordyli. A typical cordylus is distinctly club-shaped and destitute of nematocysts, but in some species, preferably among the lower organized forms, they are provided with nematocysts in the distal end and, besides, they are more or less cylindrical (*Chromatonema rubrum* (1919 pp. 4 and 9, 1920 p. 8), *Ptychogena crocea* (1925 p. 291), *Ptychogena antarctica* (Browne 1910 p. 30), *Staurodiscus tetrastaurus* (Mayer 1910 Pl. 22 fig. 8)). As to the occurrence of very similar organs in *Tiaranna* and *Bythotiara*, see above.

The *Thaumantiadæ* is an artificial group which needs a revision. It is probable that *Melicertum* and *Orchistoma* should be excluded from the Thaumantiadæ, not so much on account of their increased number of radial canals as because the entire dorsal wall of the stomach is attached to the subumbrella (1919 p. 53). The *Mitrocomidæ* will be thoroughly dealt with in the following pages. As to the classification of the *Eucopidæ* and the *Æquoridæ* I will only state that I do not agree with the authors who subdivide the Eucopidæ according to the number of lithocysts in conjunction with the mere presence or absence of a stomachal peduncle, though the shape and structure of the stomachal peduncle may prove to be of systematic importance.

The examples mentioned above serve to illustrate the value of thorough morphological investigations of many species as a means to classify the medusæ in a natural way. The classification according to the structure of the medusæ should, of course, be controlled by means of the corresponding hydroids, when they be found and described. As long as our knowledge of the connection between medusæ and hydroids is so deficient as it is now, we must, however, restrain from attempts to establish a system which pretends to be common to both generations. It is even not certain that the two generations have followed the same lines of development (see below, p. 338).

I will now take up for discussion the morphology and classification of one special group of medusæ, the *Mitrocomidæ* which are characterized as Leptomedusæ with open marginal lithocysts. It is my hope, in future, to extend my comparative-morphological studies to comprise other groups and so, perhaps, to contribute to a satisfactory classification of the medusæ, and also to the reliable limitation of the species which is necessary for biological purposes.

II. History of the Family Mitrocomidæ.

The *Mitrocomidæ* are Leptomedusæ with open marginal lithocysts.

The systematic importance of the open lithocysts, already described by Haeckel in *Mitrocoma annæ*, was first recognized by Metschnikoff (1886 a p. 241) who established the family "*Lafoeidæ*" for the following species: *Tiaropsis multicirrata* (Sars), *T. diademata* L. Agassiz (= *T. multicirrata*), *T. mediterranea* nov., *Mitrocoma annæ* Haeckel, and *Halopsis cruciata* A. Agassiz (= *Phialis cruciata* Haeckel, now *Mitrocomella cruciata*), to which he added (1886 b p. 81) *Halopsis ocellata* A. Agassiz.

Maas (1893 p. 60) adopted the family and added two new species: *Mitrocoma duplex* (probably an abnormal *M. annæ*) and *Halopsis megalotis* (= *Cosmetira megalotis*), and "perhaps" *Euchilota ventricularis* McCrady and *Mitrocomium cirratum* Haeckel. In 1905 (pp. 29—30) Maas further added the two species *Tiaropsis rosea* Agassiz & Mayer and *T. punctata* Mayer.

Torrey (1909 p. 16) changed the family name into *Mitrocomidæ*, because the medusæ in question bear no relation to the hydroid-family *Lafoeidæ*, and at the same time he described as a new species *Mitrocoma discoidea*, and *Tiaropsidium kelseyi* as a new genus and species.

In the same year Hartlaub (1909 p. 83) stated that *Cosmetira pilosella* Forbes has open lithocysts.

Browne (1910 pp. 32 ff.) gave a provisional revision of the family, comprising the following genera: *Cosmetirella* nov., *Cosmetira* Forbes, *Tiaropsis* L. Agassiz, *Mitrocomella* Haeckel, and *Mitrocoma* Haeckel, but provisionally excluded *Halopsis* until it should be demonstrated that its lithocysts were open (demonstrated by Bigelow 1914 b p. 102). Browne did not then recognize *Tiaropsidium* Torrey as a proper genus distinct from *Tiaropsis*.

Since that time the family *Mitrocomidæ* has been adopted by all authors except Mayer (1910) who did not apply more systematical importance to the open lithocysts than that of a generic character; consequently the species belonging to the *Mitrocomidæ* were placed in several different groups in his monograph.

In my paper on the Leptomedusæ of the Ingolf Expedition (Kramp 1919 p. 59) I gave a tabular synopsis of the genera, based upon Browne's definitions, but adding *Halopsis* and the genus *Halistaura* which had been established by Bigelow (1913 p. 30) for *Laodicea cellularia* A. Agassiz. — Mayer had united the three Haeckelian genera *Mitrocoma*, *Mitrocomella*, and *Mitrocomium*, and unfortunately I followed him in this respect; so far as *Mitrocomium* is concerned this now proves to be wrong, as it does not even belong to the same family.

Recently (Kramp 1930 p. 22) I somewhat altered the above synopsis as I thought I saw two different types of cirri in *Mitrocomella polydiademata* and also in my new *Trissocoma brownei;* but I have now found that these two species have the same kind of cirri as found in the other species of *Mitrocomella* and in *Mitrocoma* and *Halopsis*, whereas an entirely different type occurs in *Cosmetira*, as described by Hartlaub (1909). The genus *Trissocoma* becomes a synonym of *Mitrocomella* in the present paper.

Browne's revision (1910) only comprised the definitions of the genera, with a few remarks on the species. The present revision is extended to comprise the species. The final result has been that the family *Mitrocomidæ* consists of the following nine genera: *Mitroco-*

mella Haeckel, *Mitrocoma* Haeckel, *Halopsis* A. Agassiz, *Cosmetira* Forbes, *Cosmetirella* Browne, *Halistaura* Bigelow, *Tiaropsis* L. Agassiz, *Tiaropsidium* Torrey, and *Octogonade* Zoja (see the synopsis p. 377).

III. Species to be excluded from the Mitrocomidæ.

Mitrocomium cirratum Haeckel. — The possession of open lithocysts is included by Mayer (1910 p. 286) in the definition of the genus *Mitrocoma*, and to that genus he also refers *Mitrocomium cirratum*. Though Mayer examined this species himself during a stay at Naples, he did not notice that its marginal vesicles are closed, which I have myself proved by sections. Accordingly the species belongs to the family *Eucopidæ*.

Mitrocomium assimile Browne (1905 a p. 137, Pl. I fig. 3). — I have seen the type specimen from the University Museum, Liverpool, and I can state that the lithocysts are closed.

Mitrocomium lendenfeldi (*Mitrocomium annæ* Lendenfeld 1884 p. 606, Pl. 29 figs. 58—60; *Mitrocoma lendenfeldi* Mayer 1910 p. 290). — Nothing is said of the lithocysts being open or closed; the species seems to be allied to *Mitrocomium*.

Mitrocoma sp. juv. Vanhöffen (1912 a p. 367). — A young, abnormal medusa (three radial canals) from Port Natal; it cannot be identified.

Tiaropsis macleayi Lendenfeld (1884 p. 605, Pl. 23 fig. 37). — Lendenfeld says nothing about the lithocysts being open or closed (only that they are large), and nothing about ocelli at the base of the lithocysts; on the other hand, some of the numerous tentacles are said to have a basal ocellus. The description and figure are very inadequate, and it is impossible to state the systematical position of this species which ought, therefore, to be altogether cancelled from the system as an indeterminable species.

Tiaropsis oligoplocama Romanes (1876 b p. 525 and 1877 Pl. 15 fig. 4) must be regarded as an obsolete species, for no description is given, and the small figure is useless for identification.

Cosmetira salinarum du Plessis (*Laodice salinarum* Haeckel 1879 p. 636) is regarded by Browne (1907 p. 468) to be one of the *Olindiadæ*.

The following, more or less doubtful species will be mentioned later on under their generic names: *Mitrocoma minervæ* Haeckel, *Mitrocoma duplex* Maas, *Halopsis* (*Mitrocomella*) *cruciata* A. Agassiz, *Tiaropsis punctata* Mayer.

IV. Comparative Morphology of the Mitrocomidæ.

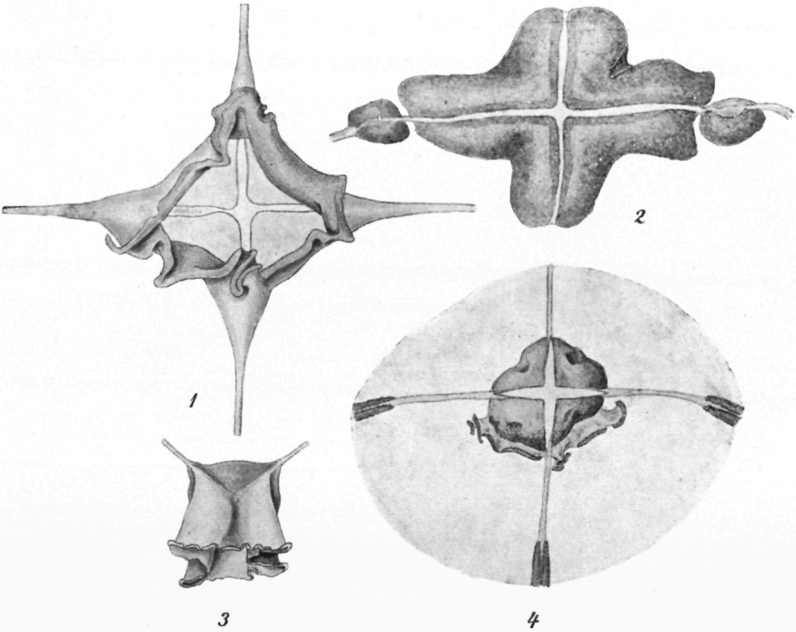
Size. — The family of the *Mitrocomidæ* comprises fairly small as well as large species. The diameter of adult specimens ranges from 4 mm (*Mitrocomella sinuosa* and *M. brownei*) to about 90 mm (*Halistaura cellularia*). The size at which the specimens of one and the same species attain sexual maturity is, however, very variable and, as in medusæ of other families, we occasionally find rather small individuals with prematurely developed sexual products.

Umbrella. — In a living specimen the umbrella may assume many different shapes according to state of contraction (see the series of figures of *Tiaropsis* in L. Agassiz 1849 Pl. 6 figs. 1—8). When we describe the shape of the umbrella as hemispherical, watch-glass shaped, etc., we mean the appearance when the medusa is at rest. Well preserved specimens will, as a rule, approximately attain the shape of the living specimen at rest, but owing to shrinkage, uneven muscular contraction, pressure, etc., preserved medusæ are often so deformed that it is difficult to tell what they were like while swimming in the sea. Descriptions of shape of umbrella, based only on preserved specimens, must therefore always be taken with due reservation. In most species of *Mitrocomidæ* the umbrella is more or less hemispherical or somewhat flatter, evenly rounded, and its gelatinous substance moderately thick, thus resembling most other Leptomedusæ. An indication of a stomachal peduncle is only found in *Tiaropsis multicirrata*.

The epithelium of the exumbrella is very thin, and the subumbrella epithelium is not much thicker except towards the umbrella margin, where the ectodermal cells are cubical or even a little higher than broad, and where the annular muscle fibres of the subumbrella are fairly conspicuous (see figs. 27 and 29—32, pp. 332 and 333). Also in this respect the *Mitrocomidæ* resemble most other Leptomedusæ. In some species the swimming movements are known to be very energetic.

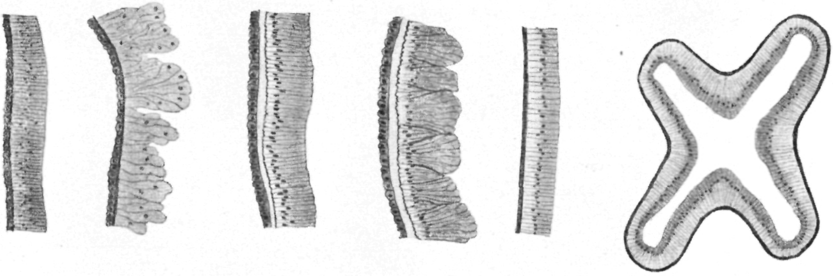
Velum is well developed, usually fairly broad, and with rather strong muscles.

Manubrium. — In all *Mitrocomidæ*, as also in many other Leptomedusæ, the stomach is attached to the subumbrella along the borders of radiating grooves, corresponding in number to the radial canals. Thus, in the four-rayed forms, the dorsal wall of the stomach is separated from the subumbrella by four triangular pouches, in *Octogonade* by eight, and in *Halopsis* by a larger number of similar pouches. As in many other Leptomedusæ the perradial corners of the stomach are drawn out into short, conical funnels which gradually pass into the radial canals. These funnels are more or less conspicuous in the different species, and besides their appearance is subject to consider-



Figs. 1—4. Manubrium. — Fig. 1. *Tiaropsidium japonicum*, oral view, type-specimen. — Fig. 2. *Tiaropsidium roseum*, aboral view of manubrium and two young gonads, specimen from Mauritius. — Fig. 3. *Mitrocomella polydiademata*, lateral view, specimen from west coast of Jutland. — Fig. 4. *Cosmetirella davisi*, aboral view, specimen from Cape Adare.

able variation according to state of contraction. The manubrium is veryc ontractile in all directions, being sometimes very flat and open (fig.1), sometimes barrel-shaped (fig. 4) or prismatic (fig. 3), sometimes cross-shaped in transverse section (figs. 2 and 8), always short, hardly ever longer than broad. In *Octogonade* the mouth has eight short lips; in all other species there are four perradial lips, usually short and simple. The length and shape of the lips are, however, much dependent on the state of contraction; when the upper part of the stomach is laterally contracted, the lips appear long and pointed, when the stomach is expanded, the lips become short and insignificant. In *Mitrocoma discoidea* and in *Halistaura cellularia* the lips must be described as comparatively long and slender; in *Tiaropsis multicirrata* they are long and broad. In the latter species the mouth rim is complexly folded and finely lobated, in other species it is more or less folded or crenulated, with a narrow everted edge. The walls of the manubrium are fairly thin; the ectoderm consists of small cubical cells (figs. 5—7); the endoderm cells are narrow and cylindrical, and the endodermal epithelium of the stomach may be transversally folded or wrinkled, whereas it is smooth near the edge of the mouth. The mesosarc is usually very thin (figs. 5 and 7), but in *Halopsis ocellata* (fig. 6) it is fairly thick (only few species have been examined in this respect).

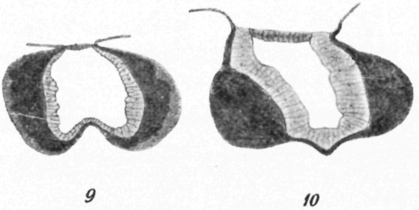


5a *5b* *6a* *6b* *7* *8*

Figs. 5—7. Longitudinal sections of wall of manubrium, 5*a*, 6*a*, 7 near the mouth-rim, 5*b* and 6*b* in proximal part of stomach. — Fig. 5. *Mitrocomella polydiademata*. — Fig. 6. *Halopsis ocellata*. — Fig. 7. *Cosmetira pilosella*. — Fig. 8. Cross-section of stomach of *Cosmetira pilosella*. — In figs. 5—7 the ectoderm is to the left; obs. the thick mesosarc in *Halopsis*. — Figs. 5—6 × 170, fig. 7 × 225, fig. 8 × 70.

Canals. — With two exceptions there are 4 radial canals; in *Octogonade mediterranea* 8 canals arise separately from the stomach; in *Halopsis ocellata* there are about 12—16 canals, arranged in four groups. In the latter species irregularities in number and arrangement of radial canals are frequent (Kramp 1919 pp. 70—71, 1920 pp. 11—12). The radial canals are always narrow, the circular canal usually a little broader, though seldom conspicuously broad (*Mitrocomella frigida*). The endodermal epithelium of the circular canal is usually somewhat thickened on the subumbrella side, particularly so in *Mitrocoma annæ* (see fig. 31 p. 333).

Gonads. — In most, probably in all, *Mitrocomidæ* the gonads are situated on the lateral sides of the radial canals, being longitudinally divided into two bands; this division is, however, not always easily seen except in sections, particularly in female individuals (fig. 11). In some species, belonging to different genera, the gonads occupy almost the entire length of the radial canals, leaving only a short part free at both ends. In *Tiaropsidium roseum* the short, oval gonads are placed somewhat nearer to the stomach than to the circular canal; in *Tiaropsis multicirrata* they are in the middle parts of the radial canals; in all other species the gonads of adult specimens are in the distal parts of the radial canals, their length varying from $^1/_6$ to $^4/_5$ of the canals. In a few species the gonads are oval, swollen, but as a rule they are linear and more or less wavy or sinuous; in *Mitrocomella frigida* and *Tiaropsidium kelseyi* they are curtain-like and hang down from the radial canals in vertical folds. In *Tiaropsidium roseum* the young gonads are found very near the stomach (fig. 2 p. 322); in all other species, in so far as young individuals have been observed, the gonads first appear in the middle part of the radial canals; during the growth of the umbrella the position of the gonads is gradually changed, their distance from the stomach increasing at a quicker rate than their distance from the umbrella margin.



Figs. 9—10. Cross-sections of male gonads. — Fig. 9. *Mitrocomella brownei.* — Fig. 10. *Cosmetira pilosella.* — Fig. 9 × 200, fig. 10 × 150.

I. Apstein (1913) has written an interesting paper on the differentiation of the sexual cells and their position in the gonads of various Leptomedusæ. In the male gonads, the sexual products are always in the ectoderm, outside the mesosarc, and the exterior surface is not covered with a distinct epithelium; the *Mitrocomidæ* present no exception from this rule (figs. 9—10). In the female gonads Apstein found that the egg-cells in some species are differentiated in the ectoderm, in others in the endoderm; in both cases they find their final position enclosed in the mesosarc. The latter may be more or less strongly developed and is sometimes, during the growth of the eggs, pushed inwards among the endoderm cells. My examination of some *Mitrocomidæ* compared with various other Leptomedusæ and with Apstein's statements give the following results: In *Mitrocomella brownei* and *M. polydiademata* (fig. 11) in which the gonads have a very thin mesosarc, the young eggs are in the ectoderm, and the larger eggs, enclosed in the mesosarc, push the latter inwards into the endoderm. Similar conditions are found by Apstein in *Octorchis gegenbauri*, *Eutimium elephas*, *Saphenia* sp., *Helgicirrha schulzi*, *Eutimeta levuca*, and *Eutonina socialis* (= *indicans*), and by me in *Eutonina indicans* and *Phialidium hemisphæricum* (in *Phialidium* sp. Apstein found the young eggs in the endoderm). — In *Halopsis ocellata* (fig. 12) the young egg-cells are likewise in the ectoderm, but the mesosarc is fairly strong and only to a slight degree pushed inwards towards the endoderm; I have found similar conditions in *Chromatonema rubrum*, *Laodicea undulata*, *Ptychogena crocea*, *Melicertum octocostatum*, and *Tima bairdi*. — In *Cosmetira pilosella* (fig. 13), *Mitrocoma discoidea*, and (according to Apstein) in *Mitrocoma annæ* the young eggs are found in the endoderm; the older eggs are enclosed in the mesosarc, bulging inwards among the endoderm cells. The same mode of development is observed by Apstein in *Eucheilota maculata*, *Obelia*, *Phialidium* (see above), and *Phialucium*, and by me in *Mitrocomium cirratum*. — In *Tiaropsis multicirrata* (figs. 14—15) young eggs are found in the endoderm; older eggs are enclosed in the strongly developed

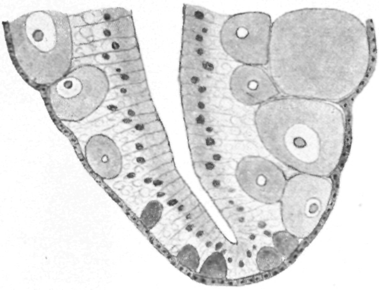
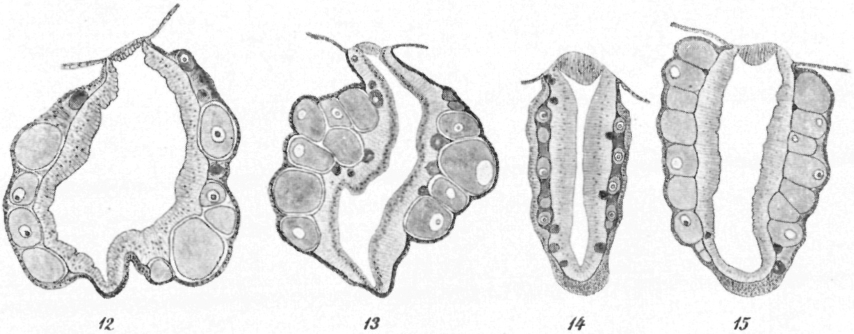


Fig. 11. *Mitrocomella polydiademata*. Cross-section of part of female gonad, × 285.

mesosarc (fig. 14); during their further development the eggs grow outwards, the strong mesosarc retaining an almost straight inner limit, so that the eggs become flattened on their inner side (fig. 15). — From these investigations it seems to be a general rule that the eggs of the Leptomedusæ, after they have passed their first stages of development, become enclosed in the mesosarc (in *Saphenia gracilis*, however, I have found fairly large eggs still resting among the endoderm cells inside a distinct mesosarc). The investigations also show that no great systematical importance can be applied to the differentiation of the young egg-cells taking place in the ectoderm or in the endoderm. I have also examined some few Anthomedusæ; in species of *Codonidæ* and *Margelidæ* the eggs are all in the ectoderm without any connection with the mesosarc; in some *Pandeidæ*, on the other hand, the eggs are enclosed in the mesosarc exactly as in the Leptomedusæ. This is interesting, because the *Pandeidæ* is evidently the group among the Anthomedusæ, from which the Leptomedusæ are derived (see Kramp 1919 p. 6).



Figs. 12—15. Cross-sections of female gonads. — Fig. 12. *Halopsis ocellata*. — Fig 13. *Cosmetira pilosella*. — Fig. 14. Young gonad of *Tiaropsis multicirrata*. — Fig. 15. Mature gonad of same. — Figs. 12—14 × 80, fig. 15 × 65.

Tentacles. — The number of fully developed tentacles in adult specimens varies from 2 to about 450; their length varies from about $^1/_4$ to about $^5/_4$ of the bell diameter, and they are able to coil themselves spirally. The tentacles are always provided with a distinct and well-developed basal bulb of varying shape and size, sometimes broad and swollen and sharply set off from the tentacle proper (fig. 16), sometimes more or less elongated conical or cylindrical (Pl. X figs. 2, 3, 4, 6). There are never found the slightest traces of abaxial basal "spurs", neither ectodermal nor endodermal, as in some species of *Laodiceidæ* and *Eucopidæ*. On the other hand, a short triangular prolongation of the exumbrella may extend some way down the abaxial side of the bulb (fig. 16). An excretory pore is never found. When the tentacle bulb is conspicuously "swollen", it is usually due to a considerable thickening of its ectoderm, especially on the adaxial side (figs. 17 and 18 *a*). The bulb is hollow, with a more or less thickened, folded endoderm. The tentacle proper is hollow in more or less of its proximal part (figs. 18 *b-c*, 19 *a-b*, 20), but in the distal part the central cavity is filled up by the endoderm cells which are placed in several rows, or quite irregularly (figs. 19 *c-e*, fig. 21), never in a single file as in the cirri (see below) or as in the true "solid" tentacles of e. g. *Obelia*. — In most species the nematocysts are arranged in transverse bands forming more or less complete rings on the tentacles (figs. 16, 22, 23, Pl. X figs. 3 and 6), transversely elongated or oval groups on

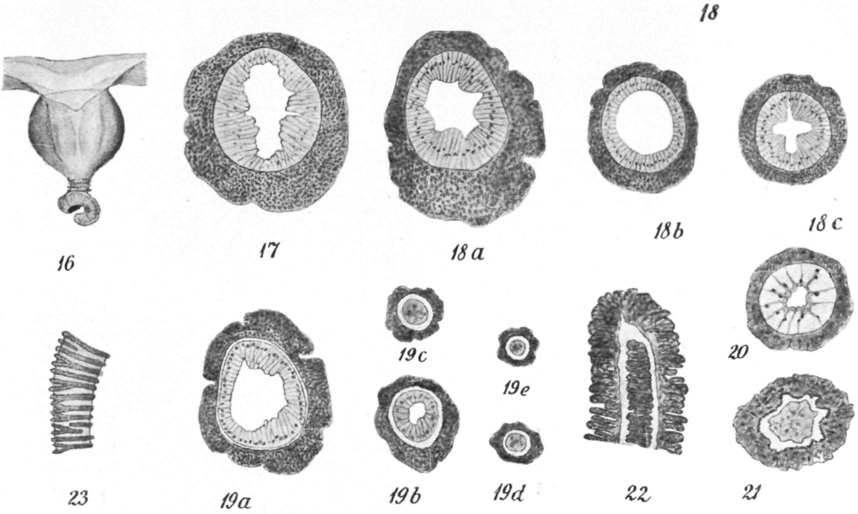


Fig. 16. *Cosmetira pilosella*, front view of tentacle. — Figs. 17—21. Cross-sections of tentacles. — Fig. 17. *Cosmetira pilosella*, tentacle bulb. — Fig. 18 *a-c*. *Mitrocomella polydiademata*. — Fig. 19 *a-e*. *Halopsis ocellata*. — Fig. 20. *Tiaropsis multicirrata*. — Fig. 21. *Mitrocoma annæ*. Obs. the thickened mesosarc in *Halopsis* and *Mitrocoma*. — Fig. 22. Longitudinal section of tentacle of *Mitrocoma discoidea*. — Fig. 23. *Mitrocomella frigida*, part of tentacle with bands of nematocysts, from type specimen. — In figs. 17, 18 *a*, and 19 *a* the abaxial side is uppermost. — Fig. 16 × 55, fig. 17 × 85, figs. 18, 19, 21, and 22 × 135, fig. 20 × 260.

the bulbs (Pl. X figs. 3 and 6); but in some species (*Cosmetirella davisi*, *Tiaropsidium japonicum* and perhaps in more species) the nematocysts are evenly scattered over the surface of the tentacles. In most of the species investigated (*Mitrocomella brownei*, *M. polydiademata*, *Cosmetira pilosella*, *Tiaropsis multicirrata*, see figs. 17, 18, 20) the tentacles have a thin and simple mesosarc; but in *Halopsis ocellata*, *Mitrocoma discoidea*, and *M. annæ* the mesosarc is thickened (figs. 19, 21, 22); in *Mitrocoma* its external surface is, moreover, longitudinally furrowed, giving room for a large number of strong muscle fibres which are, however, equally developed on all sides of the tentacle.

A very peculiar and interesting structure of the tentacles is found in *Tiaropsidium japonicum* n. sp. (fig. 24 and Pl. X fig. 2): The basal part of the bulb has a smooth surface and is almost circular in cross-section; but from the distal part of the bulb outwards along the entire length of the tentacle there are some characteristic longitudinal furrows or grooves, both on the abaxial and on the adaxial side. Sections show that the furrows on the two sides are entirely different in structure. The ectoderm outside the furrows consists of high and very narrow cylindrical cells without conspicuous basal muscle fibres. From the distal part of the bulb outwards along the tentacle there are, on the abaxial side, two narrow but distinct muscle bands (fig. 24 *b*); distalwards these bands are more and more deeply sunk into the mesosarc which, at the same time, increases considerably in thickness (fig. 24 *c-e*); in the depressed area between the two muscle bands the ectodermal epithelium is very thin. On the adaxial side of the tentacle there is one powerful muscular band, changing greatly in appearance from the basal part outwards; in the tentacle bulb it is hardly discernible from outside; in the proximal part of the tentacle proper the muscle forms a broad band, marked out on either side by a prominent ridge (fig. 24 *c-d*). Distalwards the muscle becomes more and more complexly folded and embedded into the thickened mesosarc. The ridges approach each other (fig. 24 *e*) and finally meet, so that the muscular band is concealed at the bottom of a deep and sharp furrow running throughout the length of the tentacle (fig. 24 *f*). Also the endoderm of this tentacle is interesting: in the bulb and in the proximal part of the tentacle proper, two prominent, lateral ridges of the endodermal epithelium divide the central cavity into two (fig. 24 *a-c*), but at a short distance from the bulb the ridges disappear (fig. 24 *d*); distalwards the central cavity of the tentacle is gradually compressed into an irregular and narrow slit owing to the increasing thickness of the mesosarc and the inward migration of the muscular bands (fig. 24 *e-f*). I have never seen any similarly constructed tentacles among the Leptomedusæ, nor do I know of any corresponding structures within the Anthomedusæ.

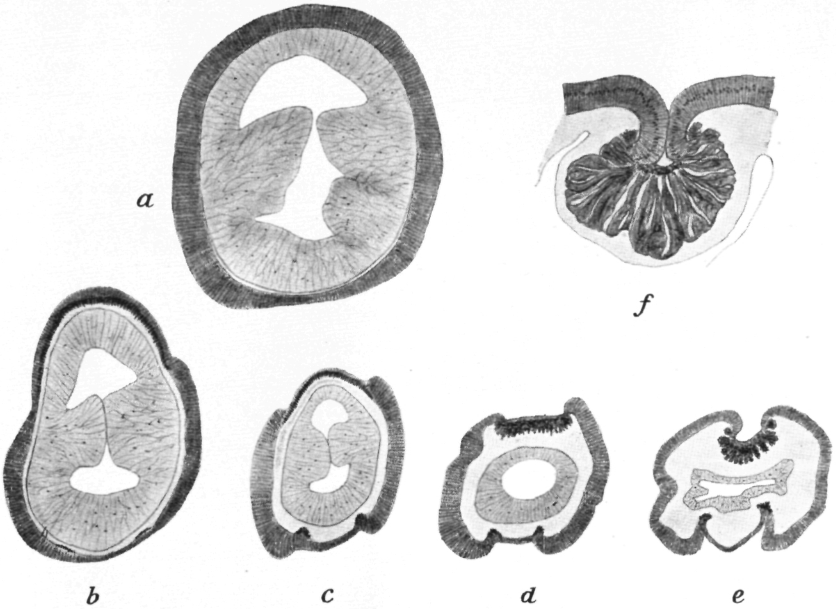


Fig. 24. *Tiaropsidium japonicum*, cross-sections of tentacle; in all figures the adaxial side is turned upwards. Obs. the increasing thickness of the mesosarc from the bulb outwards, and the muscle bands. — Fig. *f* shows the adaxial muscle band in the distal part of the tentacle. — Figs. *a-e* × 75, fig. *f* × 185.

When I found that my new species *Tiaropsidium japonicum* had such peculiar tentacles, I naturally wanted to know something about the tentacles in other species of the same genus. I therefore sent a short description accompanied by a sketch to Mr. E. T. Browne and to Professor H. B. Torrey. Mr. Browne kindly re-examined his specimen of *Tiaropsidium roseum* which is in rather bad condition with only one tentacle left and he sent me the following description: "The tentacle has contracted into lateral folds, with a plain broad central line running on its abaxial side, down the basal bulb and along the whole length of the tentacle to its tip. On the adaxial side there is only a line, marking the division between the lateral folds of the tentacle. Now, looking at the contracted tentacle there is no well-marked indication of a groove on either side of the tentacle. If one does exist on the adaxial side then it is completely covered over by the lateral folds of the tentacle. On the abaxial side there is a broad open line, which you might look upon as a furrow because owing to the puckering up of the folds it lies in a hollow. When the tentacle is expanded these folds would stretch out and then I doubt if a furrow would exist. I am inclined to look upon the broad line as a muscle band, for it is not drawn up into folds; it has simply contracted straight back. The main point, I think, is that the tentacle does show that the bands of nematocysts are divided longitudinally into two series. These divisions in the tentacle of *T. roseum* would correspond to the furrows in your new species".

Apart from one single specimen, examined by Foerster (1923), the Californian species *Tiaropsidium kelseyi* has not been found since it was described by Torrey (1909), and letters to me from professor Torrey (now at Stanford University, Cal.), professor Ch. A. Kofoid (the Berkeley University, Cal.), and professor T. Wayland Vaughan (the Scripps Institution, La Jolla, Cal.) state that the type specimens are nowhere to be found.

Besides the common tentacles there are, in the genera *Tiaropsidium* and *Octogonade*, some very small, rudimentary tentacles (see Pl. X fig. 2): tiny, conical, more or less pointed protuberances on the bell margin, each with a broad and flattened basal bulb, and containing a prolongation of the cavity of the circular canal. They are quite distinct from young developmental stages of common tentacles, in which the basal bulb grows into a roundish knob of somewhat considerable size, before the tentacle proper makes its appearance as a conical projection on the bulb.

Cirri. — Two entirely different types of marginal cirri occur in the *Mitrocomidæ*. I call them flexile cirri and spiral cirri.

a) Flexile cirri are only found in the genus *Cosmetira*. Hartlaub (1909) has called attention to these cirri which never coil spirally, and he prefers to call them dwarf-tentacles; I do not agree with him in this respect. In contradistinction to the true, spiral cirri of *Mitrocoma* they are "starrere Fäden, deren gleichmässige Kürze auf geringe Kontraktionsfähigkeit schliessen lässt". Hartlaub has, however, only seen these cirri in an almost completely contracted state; as a matter of fact, they have a remarkably great power of extension and contraction (fig. 25). When fully extended they are very long and thin; the retraction is effected exclusively by a considerable foreshortening without any indication of coiling. When fully contracted they are slightly conical, when they are partly contracted, their width may be different in different parts, because the degree of contraction is not necessarily equal in all parts; in fig. 25 four different states of contraction are represented. The cirrus is provided with a large number of nematocysts, arranged in distinct transverse belts except in the basal part, where they are more or less uniformly distributed. When the cirrus is fully contracted, the belts of nematocysts become indistinct. A distinct terminal cluster of nematocysts is not present. The endoderm of these cirri consists of a single row of cylindrical cells (fig. 26), short and disk-like in the contracted state, long and narrow when the cirrus is extended. The younger cirri are on the bell margin, but during the growth of the umbrella the older cirri become more or less removed from the margin, inserted some way up upon the exumbrella, but still connected with the endoderm of the circular canal by a string of endoderm cells (fig. 27), as described by Hartlaub (like the peronia of the Narcomedusæ). — Previous authors have paid *too little attention to the minor structure of the marginal cirri*; it is not easy, therefore, to decide which other species of medusæ possess cirri of the same type as *Cosmetira*. They certainly occur in *Phialopsis diegensis* Torrey among the *Eucopidæ*, probably also in

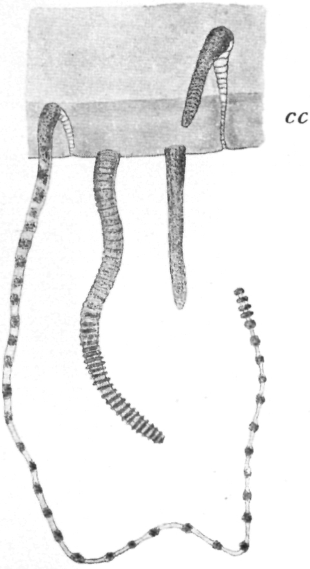
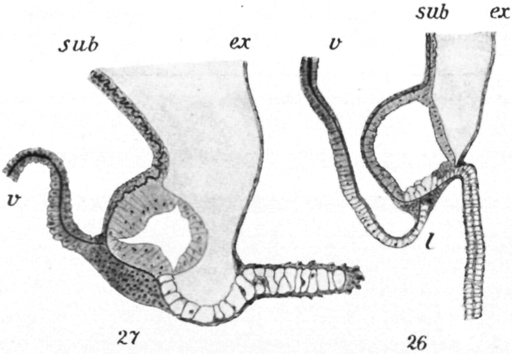


Fig. 25. *Cosmetira pilosella*, four cirri in different states of contraction, showing the bands of nematocysts and the "roots" of the exumbrellar cirri. *cc* circular canal.

Orchistoma pileus (Lesson) among the *Melicertidæ*[1]), whereas it does not seem probable that the "very short" cirri of *Eutima levuca* var. *ocellata* Maas (1905 p. 35) should be fundamentally different from the typical spiral cirri of the other species of that genus.



Figs. 26—27. *Cosmetira pilosella*, radial sections of bell margin. — Fig. 26. Marginal cirrus and lithocyst. — Fig. 27. Basal part of exumbrellar cirrus with its connection with the circular canal. — *ex* exumbrella, *sub* subumbrella, *v* velum, *l* lithocyst. — Fig. 26 × 160, fig. 27 × 210.

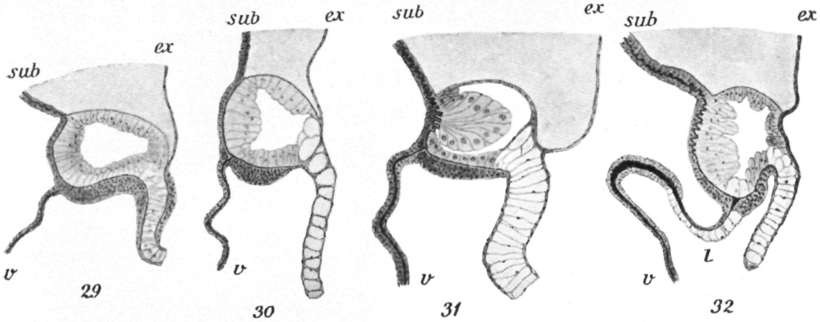
Spiral cirri (figs. 28—32 and Pl. X figs. 3, 4, and 6) occur in the

Fig. 28. *Halopsis ocellata*, marginal cirri in different states of contraction; fig. *e* is a young cirrus.

---

[1]) Hartlaub's comparison between the cirri of *Cosmetira* and *Orchistoma* seems justified by the drawings by Haeckel 1879 Taf. 15 fig. 4, and Mayer 1910 Pl. 25 fig. 2, though in his description Haeckel states that the cirri of *Orchistoma* are spiral. The type specimens of *O. steenstrupii* Haeckel are in Copenhagen, but have been dried up.

genera *Mitrocomella*, *Mitrocoma*, and *Halopsis*. They are long and slender, slightly tapering from the base outwards, and they terminate in a distinct oval cluster of nematocysts, other large nematocysts being irregularly scattered in the ectoderm along the entire length of the cirrus. The endoderm consists of a single row of cylindrical cells, at the base connected with the endoderm of the circular canal (figs. 29—32). Their power of contraction by shortening is much less than in the flexile cirri of *Cosmetira*, but they retract by coiling themselves into a spiral which may be very close and tight. The proximal part of the cirrus does not coil, but is contracted by shortening itself and then attains the appearance of a conical basal bulb (fig. 28 *c-d*) with a fairly thick, smooth ectoderm and, therefore, appears dark in transmitted light, whereas any part of an extended cirrus (fig. 28 *a-b*) is clear and transparent, with a very thin ectoderm, and with the endoderm cells clearly visible even in unstained condition. Sometimes the basal part of the cirrus is contracted, becoming conical, at the same time as more or less of the distal part is fully extended (fig. 28 *b-c*).



Figs. 29—32. Radial sections of bell margin with marginal cirri. — Fig. 29. Young cirrus of *Mitrocomella polydiademata.* — Fig. 30. Older cirrus of same. — Fig. 31. *Mitrocoma annæ,* observe the thickening of the endoderm in the circular canal. — Fig. 32. *Halopsis ocellata,* cirrus and lithocyst, observe the thick mesosarc in the velum. — *ex* exumbrella, *sub* subumbrella, *v* velum, *l* lithocyst. — × 160.

When I described my new species *Trissocoma brownei* n. g., n. sp. (Kramp 1930 pp. 22 ff.) I then believed that two kinds of cirri existed in that species and also in *Mitrocoma* (*Mitrocomella*) *polydiademata:* Spiral cirri with a terminal cluster of nematocysts, with a distinct basal bulb with thickened ectoderm, and with a fair amount of protoplasm in the endoderm cells; and "Rigid" cirri, somewhat shorter, without terminal cluster of nematocysts, with a very thin ectoderm throughout, and with very little protoplasm in the endoderm cells; moreover these "rigid" cirri were placed at a higher level on the bell margin than the "spiral" cirri. In Mr. Browne's collection I, however, found an adult and particularly well preserved specimen of *Mitrocomella polydiademata* (Pl. X fig. 3) in which the cirri were all alike, all of the spiral type with cluster of nematocysts, but with very thin ectoderm and transparent endoderm cells, and all placed at the same height on the umbrella margin. Pl. X fig. 4 represents a somewhat younger stage of development of the same species, transparent "rigid" cirri alternating with opaque "spiral" cirri, exactly as formerly observed in *Trissocoma*. As a matter of fact, the cirri with a basal bulb, fairly thick ectoderm, and with the endoderm cells containing a fair amount of protoplasm (fig. 29) are young ones, not easily broken, and therefore frequently found with the coiled distal part and the terminal cluster of nematocysts, whereas the transparent cirri with no trace of basal bulb, and placed at a higher level than the others, are old ones which have been very long and apt to break by preservation. In *Mitrocomella* as well as in *Mitrocoma annæ* and *Halopsis ocellata* I have seen young cirri in different stages of development: as tiny knobs on the umbrella margin, as small conical protuberances, as somewhat elongated with a terminal swelling and then either dark with a slightly bulbous base and a single coil or indication of a coil (fig. 28 *e*) or more or less straight and transparent, somewhat like Haeckel's fig. 8, Taf. X.

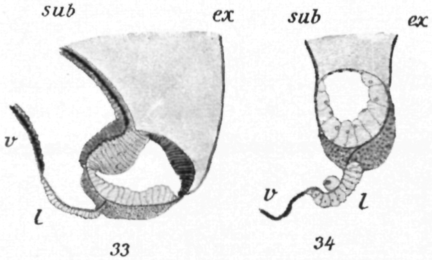
As mentioned above, the older cirri in *Mitrocomella brownei* and *polydiademata* are usually placed at a little distance above the bell margin (Pl. X fig. 4), but they are always directly connected with the endoderm of the circular canal. In *Mitrocomella frigida* (Pl. X fig. 6) the difference in position of the old and the young cirri is considerably more pronounced, which is due to the circular canal being particularly broad in that species.

Spiral cirri of much the same structure as here described are found in several other Leptomedusæ belonging to different families: *Laodicea*, *Eucheilota*, *Mitrocomium*, *Saphenia*, *Eutima*, *Eirene*. Phylogenetically, therefore, they must be considered very ancient structures. Their origin is not easily traced, because nothing similar is found in any of the Anthomedusæ. The hollow marginal clubs (cordyli) of the *Laodiceidæ* are inherited from the lower *Pandeidæ*, such as *Tiaranna*, in which similar structures are found (Kramp 1919 p. 5, 1920 p. 9); they are undoubtedly derived from tentacles. The solid cirri of both types, occurring in various Leptomedusæ, are entirely different from cordyli; nevertheless they are probably also derived from tentacles. Amongst the Hydromedusæ, especially amongst the Anthomedusæ, we know several different kinds of tentacles: hollow and solid, some which coil spirally and others which do not coil, some provided with a distinct terminal cluster of nematocysts and others in which the nematocysts are arranged in various other ways; quite different types of tentacles may be found within one and the same family. Still we may take it for granted that all kinds of tentacles are homologous and derived from the same origin. Apparently, therefore, there is no objection to our assuming that the two kinds of cirri in the Leptomedusæ are likewise homologous, and presumably derived from tentacles. Their origin and further fate, their occurrence in species of quite different families of Leptomedusæ, and their absence in other species of the same families, may be subject to considerable speculation from which, however, I will entirely abstain. Perhaps the structure and distribution of cirri may, in future, contribute to a better understanding of the classification of the Leptomedusæ; for the present we must be content to state that the cirri have a certain systematic importance within such a limited group as the *Mitrocomidæ*. The presence of flexile cirri distinguishes the genus *Cosmetira*, and the three genera with spiral cirri constitute a natural group in contradistinction to all other genera of the family.

Lithocysts. — The minor structure of the open marginal lithocysts of the *Mitrocomidæ* has been described by several authors, first of all by O. & R. Hertwig in *Mitrocoma annæ* (1878 a pp. 81—85, Taf. VII figs. 10, 11, 14, 19); Kühn (1914 p. 395, fig. 92 A and B) has given an excellent schematic figure of an open and a closed lithocyst, from which it appears that the latter is derived from the former. I have cut sections of the lithocysts of several species of *Mitrocomidæ* (figs. 26 p. 332, 32 p. 333, 33—34 p. 336, 35—36 p. 337), and apart from size and the number of concretions I find no great variation. The opening of the vesicle into the subumbrella cavity may be more or less wide, or it may be a narrow slit; this, however, does not seem to be a specific character, but merely due to state of contraction. In sections the lithocysts can always be distinguished by the structure of the external epithelium in which the cells are large and vacuolated.

The number of concretions in the lithocysts increases during the growth of the medusa, the middle one in each vesicle being the older, new ones being developed towards both sides until a maximal number is reached, different in each species. In some species the maximal number is 5 or 7, in others 20 or 30; when the concretions are numerous, they are usually placed in two or three crescentic rows.

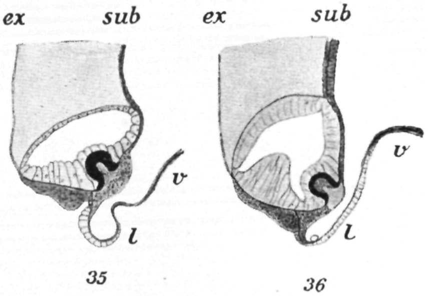
The number of lithocysts varies from 8 to about 160 in the different species. Browne, in his classification of the *Mitrocomidæ* (1910) laid much stress upon the number of lithocysts as generic characters, whereas Vanhöffen (1912a p. 369) finds it "misslich ... die Gattungen nach Zahl der Randkörper zu unterscheiden". As a matter of fact, abnormal individuals with supernumerary lithocysts are rather frequently observed in some species, but, as will be demonstrated below, after the species and genera have been classified into natural groups according to various other characters, the number of lithocysts will prove to be of systematic importance within each of these groups. The discovery of some new species (*Mitrocomella sinuosa* (Foerster), *Mitrocomella brownei* Kramp, and *Tiaropsidium japonicum* n. sp.) makes it necessary to alter some of Browne's generic definitions, but his principle remains the same. It seems to me a feature of importance, whether a species has a certain constant number of lithocysts (8, 12 or 16), or whether the number is variable; in the latter case the number increases during the growth of the medusa, whereas in



Figs. 33—34. Radial sections of bell margin with lithocysts. — Fig. 33. *Mitrocoma discoidea*. — Fig. 34. *Cosmetirella davisi*. — *ex* exumbrella, *sub* subumbrella, *v* velum, *l* lithocyst. — Fig. 33 × 65.

the former case the full number is present even in the youngest stages known.

As far as the *Eucopidæ* are concerned, Mayer (1910) certainly exaggerated the systematic importance of the number of lithocysts. The *Eucopidæ* is undoubtedly a heterogenous group which must be divided into smaller groups or families according to various morphological characters, and within each of these groups the number of lithocysts may prove to have a similar systematic importance as in the *Mitrocomidæ*, being valuable as a generic character and perhaps characteristic of certain groups of genera.



Figs. 35—36. Radial sections of bell margin with lithocysts and ocelli. — Fig. 35. *Tiaropsis multicirrata*. — Fig. 36. *Tiaropsidium japonicum*. — *ex* exumbrella, *sub* subumbrella, *v* velum, *l* lithocyst. — Fig. 35 × 160, fig. 36 × 85.

Ocelli. — Ectodermal, epithelial ocelli are unknown among the *Mitrocomidæ*, but in *Tiaropsis*, *Tiaropsidium*, and *Octogonade* we find the peculiar subepithelial ocelli, first correctly described by Linko (1900 a pp. 154—156, fig. 5, and 1900 b p. 15), a cup-shaped mass of black pigment in the endoderm of the circular canal, the cavity of the cup filled up by subepithelial cells from the ectodermal nerve layer on the adaxial side of the umbrella margin (see figs. 35—36). This type of ocellus is unique among the Hydromedusæ. — Hartlaub (1909) described ocelli at the base of the tentacles in *Cosmetira*, but that was an error, for no ocelli are present.

Colour. — Some species are only known from preserved specimens in which the original colours have changed or disappeared. In some species, observed in living condition, the umbrella has a faint pink or violet hue. Delicate yellow, rosy, or purple colours are usually found in the endoderm of manubrium, gonads, canals, and tentacle bulbs;

in *Cosmetira pilosella* and *Halistaura cellularia* the endoderm of the tentacle bulbs is dark purple or violet. In *Tiaropsis multicirrata* fine black granules are found on the surface of the tentacle bulbs and, to a less degree, of the gonads and the manubrium, whereas the endoderm of the same organs is yellowish.

Ontogeny. — The hydroid polyp is unknown in all species except *Mitrocoma annæ*, from which Metschnikoff (1886 b) reared a small polyp resembling *Cuspidella*. — It is very interesting that polyps like *Cuspidella* and simple forms of *Campanulina* have been reared from several medusæ belonging to quite different families: *Laodicea*, *Dipleurosoma*, *Mitrocoma*, *Eucheilota*, *Eutonina*, *Æquorea*.

In my opinion, these tiny hydroids, consisting of a small polyp in a delicate chitinous tube with or without a basal constriction, and with the upper part longitudinally folded so as to form a conical operculum, represent a very primitive type of calyptoblastic hydroids. It is my conception that the very first, primitive Leptomedusæ were liberated from such primitive hydroids. From this beginning development proceeded in two different ways: 1) progressive development and high specialization of the hydroid generation at the sacrifice of the medusa generation which in most cases was reduced to a simple sporosac (*Lafoeidæ*, *Haleciidæ*, *Sertulariidæ*, *Plumulariidæ*, *Aglaopheniidæ* etc.), only retained and further developed in few cases (e. g. *Obelia*, *Phialidium*); 2) progressive development and high specialization of the medusa generation, whereas the hydroid generation remained in a state very similar to the original simple and inconspicuous form, practically never observed in nature, but occasionally reared in aquaria from medusæ which now represent quite different families.

V. Geographical Distribution of the Mitrocomidæ.

The *Mitrocomidæ* belong to the coastal waters and are mostly found in the upper water layers; only two species, *Tiaropsidium kelseyi* and *T. japonicum*, have been found at rather considerable depths. Also *Halopsis ocellata* is mainly found in the neighbourhood of the coasts, but it may occasionally be found rather far out in the ocean, though always in the upper strata. Almost all species are inhabitants of the temperate zones, from which *Halopsis ocellata* and *Tiaropsis multicirrata* penetrate into subarctic regions, but are never found under true arctic conditions, whereas *Cosmetirella davisi* which is common at the subantarctic islands, has a smaller growth form near the antarctic continent. *Mitrocomella frigida* is an antarctic species. Three species occur in the Mediterranean and have never been found elsewhere. The only tropical species is *Tiaropsidium roseum* which seems to be widely distributed, though rare, in the tropical seas. Most other species have a fairly narrowly restricted area of distribution. *Halopsis ocellata* and *Mitrocomella polydiademata*, however, occur in boreal waters on both sides of the North Atlantic, the subantarctic *Cosmetirella davisi* and the subarctic *Tiaropsis multicirrata* seem to be circumpolar. Most species occur at the north-western coasts of Europe and the Atlantic and Pacific coasts of North America. — In contradistinction to the species, most of the genera have a wide distribution which indicates that the genera are old. For details, see the adjoining table.

Synopsis of geographical distribution.

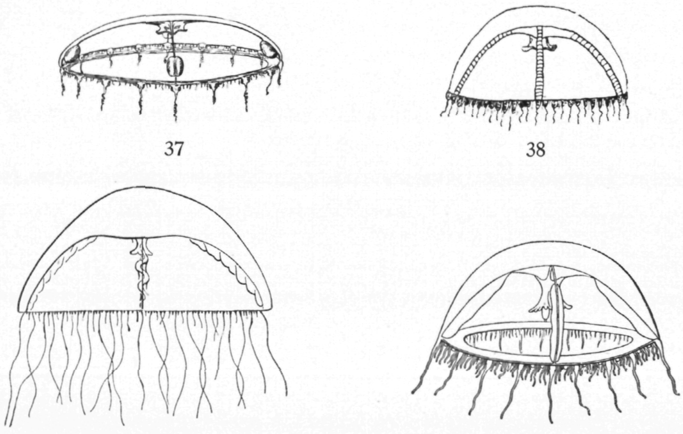
Species	N. W. Europe	Mediterranean	N. America E.	N. America W.	Japan	Tropics	S. Africa	Subantarctic	Antarctic
Mitrocomella brownei	×	..	..	..	..	..	..	..	..
Mitrocomella sinuosa	..	..	..	×	..	..	..	..	..
Mitrocomella cruciata	..	..	×	..	..	..	..	..	..
Mitrocomella fulva	×	..	..	..	..	..	..	..	..
Mitrocomella frigida	..	..	..	..	..	..	..	..	×
Mitrocomella polydiademata	×	..	×	..	..	..	..	..	..
Mitrocoma discoidea	..	..	..	×	..	..	..	..	..
Mitrocoma annæ	..	×	..	..	..	..	..	..	..
Mitrocoma minervæ	..	..	..	..	..	..	×	..	..
Halopsis ocellata	×	..	×	..	..	..	..	..	..
Cosmetira pilosella	×	..	..	..	..	..	..	..	..
Cosmetira megalotis	×	..	..	..	..	..	..	..	..
Cosmetirella davisi	..	..	..	..	..	..	..	×	×
Halistaura cellularia	..	..	..	×	..	..	..	..	..
Tiaropsis multicirrata	×	..	×	×	..	..	..	..	..
Tiaropsidium mediterraneum	..	×	..	..	..	..	..	..	..
Tiaropsidium roseum	..	..	..	..	..	×	..	..	..
Tiaropsidium kelseyi	..	..	..	×	..	..	..	..	..
Tiaropsidium japonicum	..	..	..	..	×	..	..	..	..
Octogonade mediterranea	..	×	..	..	..	..	..	..	..
number of species	7	3	4	5	1	1	1	1	2

VI. Genera and Species of Mitrocomidæ.

Genus *Mitrocomella* Haeckel 1879.

Mitrocomidæ with four radial canals; with 8, 12, or 16 lithocysts without ocelli; with marginal cirri which coil spirally.

Species: *brownei* (Kramp 1930), *sinuosa* (Foerster 1923), *fulva* (Browne 1903), *frigida* (Browne 1910), *polydiademata* (Romanes 1876, genotype). — Doubtful species *cruciata* (A. Agassiz 1865).



37 38 39 40

Figs. 37—40. *Mitrocomella*. — Fig. 37. *M. brownei* Kramp; from Kramp 1930. — Fig. 38. *M. sinuosa* (Foerster); from Foerster 1923. — Fig. 39. *M. cruciata* (A. Agassiz); after A. Agassiz 1865 (from Mayer 1910). — Fig. 40. *M. polydiademata* (Romanes); after Browne 1903 (from Mayer 1910).

This genus is closely related to *Mitrocoma*. The most characteristic difference is that in *Mitrocomella* each species has a limited and, apart from abnormalities, constant number of lithocysts which is the same in all stages of development, whereas in the species of *Mitrocoma* the number is variable and increasing with age.

Most species of *Mitrocomella* are fairly small, 4—22 mm in diameter; only *M. cruciata* is said to be of larger size. The umbrella is usually hemispherical. The stomach is small and the lips simple and slightly folded. The four radial canals are narrow, the circular canal sometimes fairly broad (*M. frigida*). The shape of the gonads is much varying, from short, oval bodies to long sinuous bands. In the female gonads the longitudinal, ventral division is not always distinct (see textfig. 11, p. 325). The tentacles have a well developed basal bulb with an ectodermal thickening all round (fig. 18, p. 327); the tentacle proper has a thin mesosarc, and nematocysts arranged in more or less complete transverse rings (textfig. 23 and Pl. X figs. 3 and 6). The number of tentacles in the adult medusa varies from 16 to about 50 (*sinuosa* and *polydiademata*) or more (*cruciata*). Between the tentacles are a number of long cirri which are able to coil spirally and terminate in an oval cluster of nematocysts. As far as can be made out from the description of *M. cruciata*, that species has only one cirrus between every two tentacles; in the other species there are about 3 to 10 or even more cirri between the tentacles. The number of lithocysts is 8, 12, or 16, the number of concretions in each lithocyst varies from about 4 to nearly 30. The genus has a wide distribution: north-western Europe from the British Channel to northern Norway, both sides of North America, and the Antarctic.

Mitrocomella brownei Kramp.

(Textfigs. 9, 37).

Trissocoma brownei Kramp 1930 p. 23, textfigs. 9—11.

This species was first observed by Browne, in whose collection I saw it several years ago. I found it again among the medusæ from the museum at Brussels and described it as a new species representing a new genus with only eight lithocysts in contradistinction to the related species of *Mitrocoma* (incl. *Mitrocomella*). Its natural place, however, is in the genus *Mitrocomella* as now defined. As mentioned above, I thought I saw two different kinds of marginal cirri, which by closer examination of better preserved material proved to be a mistake. In Browne's collection I found specimens and notes based on living specimens of larger as well as smaller size than the North-Sea specimens previously examined by me, thus giving new information as to the development.

Description: Diameter of adult 4—7 mm. Umbrella watch-glass shaped or hemispherical, gelatinous substance fairly thin. Velum fairly broad, more than length of the tentacle bulbs. Stomach small, short, perradial funnel-shaped parts faintly developed; mouth-rim slightly folded, with four small, simple lips. Radial canals 4, very narrow. Circular canal a little wider than the radial canals. Gonads oval, swollen, distinctly longitudinally divided, near distal ends of radial canals, length $^1/_6$—$^1/_5$ of radial canals. Tentacles; the normal number of fully developed tentacles is 16, but large specimens, 5—7 mm wide, may occasionally be found with 20 or 24. The tentacles are longer than the diameter of the bell; basal bulbs broadly rounded. Cirri 6—8 between the tentacles, 2—3 times as long as the tentacle bulbs. Lihtocysts 8, fairly large, placed near the adradial tentacles on their interradial side, sometimes separated from the adradial tentacle by a cirrus. 5—7 concretions in each lithocyst. Colour of tentacle bulbs bright yellow, gonads faintly pink (in living specimens).

Development. Gonads first appear in the middle part of the radial canals or even somewhat nearer to the stomach, and may just be distinguished when the umbrella is 1.5—2 mm wide; their distance from the stomach gradually increases during the growth of the medusa. The gonads reach their final situation when the specimen is 3.5—4 mm wide, and are then fairly large, much swollen, sometimes fully developed. The youngest individuals observed, 1—1.5 mm, have 4 perradial tentacles, 4 interradial bulbs, and tiny vestiges of a few adradial bulbs just appearing; when the diameter is 2—2.5 mm there are, as a rule, 8 fully developed tentacles. The development of the adradial tentacles proceeds slowly and irregularly; the full number of 16 tentacles is reached when the medusa is 4—5 mm wide. In the smallest specimens (1 mm) there are 16 marginal cirri, when the diameter is 1.5—2 mm the number is 8 × 3—8 × 5, at a diameter of 4 mm the number varies from 16 × 3 to 16 × 7. Each of the 8 lithocysts of the small individuals contains 2 or 3 concretions.

Abnormalities. Among 175 specimens examined, I have found 7 with 9 lithocysts, and one with 11 $(4 + 2 + 3 + 2)$.

Distribution. Port Erin (Isle of Man), Valencia Harbour (Ireland), Scilly Isles, Plymouth, Salcombe Haven, south of Start Point (Browne); south-western North Sea between Zeebrugge and Orford Ness (Kramp).

Seasonal occurrence. Specimens 1—4 mm wide have been found in May, August, and September; specimens up to 7 mm were found at Port Erin in September; at Valencia Harbour the medusa was found in October and November, diam. 3—6.5 mm.

Mitrocomella sinuosa (Foerster).

(Textfig. 38).

Mitrocoma sinuosa Foerster 1923 p. 35, Pl. IV fig. 6.

Description (from Foerster): Diameter 4 mm. Umbrella hemispherical, moderately thick. Velum well developed. Stomach small, "wide and quadratic", mouth large, wide, with four recurved lips. Radial canals 4, narrow. Gonads along distal half of radial canals, not quite reaching the circular canal, "thrown into sinusoidal curves", distinctly longitudinally divided. Tentacles about 50, with thick, conical basal bulbs, fairly short (acc. to fig.). Cirri 3—5 between the tentacles. Lithocysts 12 (4 × 3). Colour of preserved specimen "very pale brown".

Distribution. North of Five Finger Island, Vancouver.

If the only specimen known of this species is not a young medusa with prematurely developed sexual organs, it is well distinguished by its 12 lithocysts and by the large number of tentacles in proportion to size of bell.

Mitrocomella cruciata (A. Agassiz).

(Textfig. 39).

Halopsis cruciata A. Agassiz 1865 p. 102, figs. 151, 152.
Phialis cruciata Haeckel 1879 p. 181.
Halopsis cruciata Metschnikoff 1886 a pp. 241, 260.
Halopsis cruciata Maas 1893 pp. 59, 60.
Mitrocoma cruciata Mayer 1910 p. 289.
Mitrocoma cruciata Bigelow 1914 a p. 14.
non *Mitrocoma cruciata* Bigelow 1915 p. 320, and 1926 p. 348.

This species has never been observed since it was described by Agassiz. Its relationship with *Mitrocoma annæ* and *Halopsis ocellata* was supposed by Metschnikoff (1886 a) and Maas (1893); Mayer (1910) refers it without comment and without evidence to the genus *Mitrocoma*, indicating at the same time that this American medusa with 12 lithocysts might be identical with the Mediterranean *Mitrocoma annæ* in which the number is 60—100, and in this supposition he was followed by Bigelow (1914 a). If the lithocysts are really open, which we do not know, we must refer the species to the genus *Mitrocomella* as here defined, because it has cirri, and because the number of lithocysts is expressly stated to be 12. — In 1915 and in 1926, Bigelow records "*Mitrocoma cruciata*" as a fairly common "boreal neritic species" in the Gulf of Maine, though without giving a new description. Some specimens, kindly sent to me by Prof. Bigelow, however, turn out to be indistinguishable from the European *M. polydiademata* (see below). Agassiz's medusa, thus, still remains a doubtful species. The type specimens are not in existence.

Description (from A. Agassiz): Diameter 40—50 mm. Umbrella hemispherical or somewhat higher, gelatinous substance fairly thick in central part. Velum ?. Stomach very small, with short lips; funnels seem fairly well developed. Radial canals 4, narrow. Gonads "lobed pouches, hanging down in folds", along distal $^1/_2$—$^2/_3$ of radial canals. Tentacles about 100 (according to fig.), essentially as in *Halopsis ocellata*, i. e. long, with conical basal bulbs "tapering very rapidly". Cirri as in *H. ocellata*, i. e. one between the tentacles, long, slender, spiral. Lithocysts 12, with 4—5 concretions. Colour: gonads and bell a light pink.

Occurrence. Massachusetts Bay, Nahant, in June, common (Agassiz).

Mitrocomella fulva Browne.

Mitrocomella fulva Browne 1903 p. 18.

A single specimen was found by Browne near the Eddystone lighthouse in the Channel; it was briefly described (1903) alongside with a Norwegian specimen. Later on (1905 b p. 768—769) Browne has expressed doubt of the identity of the two forms, realizing that the Norwegian specimen belongs to *M. polydiademata*. In Browne's collection I have examined the type specimen from Eddystone. It is distinguished from *M. brownei* by the number of lithocysts being 16, and from *M. polydiademata* by the short, oval gonads. The latter species has never been found in the Channel. It will be correct, therefore, provisionally to keep *M. fulva* as a distinct species and to call attention to it, in case somebody might come across more specimens which might give a clue to the correct identification.

Description: Diameter about 6 mm (preserved in alcohol 4 mm). Umbrella watch-glass shaped. Stomach small, mouth with four short lips. Radial canals 4, narrow. Gonads oval, much swollen, very near the bell margin, $^1/_3$ as long as radial canals. Tentacles about 16 and some small bulbs. Cirri about 4 between tentacles and bulbs. Lithocysts 16, large, with 3—8 concretions. Colour: tentacle bulbs yellowish brown.

Occurrence. Near Eddystone lighthouse, May 28th 1898, 1 specimen.

Mitrocomella frigida (Browne).

(Textfig. 23. Pl. X figs. 5, 6).

Cosmetira frigida Browne 1910 p. 35.
Cosmetira frigida Vanhöffen 1912 a p. 367, textfig. 3.

A reexamination of the original specimens (now in the British Museum) proved that this species belongs to *Mitrocomella*. The specimens are in poor condition, but in the largest individual (diam. 13 mm) the manubrium, two of the gonads, and considerable parts of the bell margin are sufficiently well preserved to enable me to reconstruct the general appearance of the medusa and make a drawing (Pl. X fig. 5) in which only the shape and proportions of the umbrella may be more or less incorrect. The enlarged drawing of the marginal organs (Pl. X fig. 6) is made from another individual.

Browne provisionally placed this species in the genus *Cosmetira*, because the number of lithocysts, which could not be stated exactly, was apparently eight, and because some of the numerous cirri were placed somewhat above the bell margin. He did not then realize the systematic importance of the two different types of marginal cirri which separate the genera *Cosmetira* and *Mitrocomella*. The cirri of *M. frigida* are exactly as in *M. polydiademata*, except that the older ones are less transparent and more distinctly removed from the umbrella margin. This position of the cirri is due to the circular canal being comparatively broad; the cirri are never placed above the circular canal as in *Cosmetira*. The number of lithocysts still remains uncertain. In the largest specimen no lithocysts could be discerned; in two other specimens I could distinguish a few lithocysts, and they are placed eradially, not adradially as would be expected if there were only two in each quadrant, thus indicating that the complete number is 16. In another specimen, 7 mm wide, one of the quadrants has distinctly 4 lithocysts, but this is an abnormal specimen, two of the radial canals reaching the circular canal close together. The structure of the cirri clearly shows that this species does not belong to *Cosmetira;* whether the normal number of lithocysts should turn out to be 8 or 12 or 16, the species finds its natural position within the genus *Mitrocomella*. The curtain-like gonads of the adult specimens are very characteristic of this species.

I believe that the two specimens from the Gauss station, described by Vanhöffen (1912 a) and referred by him to *Cosmetira frigida*, are correctly identified. Vanhöffen was likewise unable to state the exact number of lithocysts.

Description: Diameter of adult 13 mm. Umbrella about hemispherical, with thin walls. Velum about as broad as length of tentacle bulbs. Stomach short and broad, funnels prominent and fairly wide; mouth rim slightly folded, with indications of lips. Radial canals 4, narrow, circular canal fairly broad. Gonads along greater part of radial canals, about $^3/_4$ or more, leaving both ends free; they are band-shaped, curtain-like, and hang down in large vertical folds; in young specimens they are simple and linear. Tentacles about 32 in specimens 9—13 mm wide, at least as long as bell radius, with long, tapering bulbs, slightly laterally compressed. Cirri about 8 between every two tentacles, long, spiral, older cirri situated fairly high up on umbrella margin, but never above the circular canal. Lithocysts, number uncertain, apparently 16, large; number of concretions unknown.

Distribution. McMurdo Bay, Antarctic (Browne). Gauss station, Antarctic (Vanhöffen).

Mitrocomella polydiademata (Romanes).

(Textfigs. 3, 5, 11, 18, 29, 30, 40. Pl. X figs. 3, 4).

Tiaropsis polydiademata Romanes 1876 a p. 274.
Tiarops polydiademata Romanes 1876 b p. 525.
Tiaropsis polydiademata Romanes 1877 p. 194, Pl. XV fig. 3.
Mitrocomella polydiadema Haeckel 1879 p. 185.
Mitrocomella polydiadema Browne 1895 p. 279.
i. p. *Mitrocomella fulva* Browne 1903 p. 17, Pl. I fig. 3, Pl. III figs. 1, 2.
Mitrocomella polydiademata Hartlaub 1904 p. 104.
Mitrocomella polydiademata Browne 1905 b p. 767.
Mitrocomella polydiademata Evans & Ashworth 1909 p. 303.
Mitrocomella polydiadema Browne 1910 p. 33.
Mitrocoma polydiademata Mayer 1910 p. 290.
Mitrocoma cruciata Bigelow 1915 p. 320.
Mitrocoma polydiademata Kramp 1919 p. 59, Chart VI.
Mitrocoma polydiademata Kramp & Damas 1925 p. 296.

Mitrocoma cruciata Bigelow 1926 p. 348.
Mitrocoma polydiademata Kramp 1927 p. 109.
Mitrocoma polydiademata Kramp 1930 p. 21.

Since the first description of this North-European medusa was published by Romanes, several specimens have been described by Browne (1895, 1903, 1905) and by me (Kramp 1919). In the present paper, therefore, I can only add a few details and some remarks on the development. The most interesting new discovery is that *M. polydiademata* also occurs at the east coast of North America.

Description: Diameter of adult 12—22 mm. Umbrella hemispherical or somewhat higher, gelatinous substance fairly thick. Velum fairly broad. Stomach small, funnels short and broad, mouth rim slightly folded, with four short, simple lips. Radial canals 4, narrow; circular canal narrow. Gonads linear, somewhat sinuous, with 3—4 bends to either side, along distal $^2/_3$—$^4/_5$ of the radial canals, not touching the circular canal; ventral division of female gonad indistinct. Tentacles 36—48, in American specimens up to 64, as long as the diameter of the bell, with long, tapering bulbs. Cirri usually 5—9, sometimes more, between two successive tentacles, spiral, 2—3 times as long as the tentacle bulbs. Lithocysts 16 eradial, each with about 20—30 concretions in two rows or irregularly scattered. Colour: mouth and tentacle bulbs purplish or rosy, gonads yellowish-brown or purplish or rosy (in living specimens).

Development. In specimens 3—4 mm wide, the gonads are already fairly well developed, along distal $^1/_2$—$^2/_3$ of the canals. Even in the youngest specimens observed, the 16 lithocysts are all present. The development of the tentacles, beyond the first 16, proceeds very irregularly, and they are not equidistant; the number of cirri between two successive tentacles is, therefore, very variable, particularly so

diam. mm	tentacles fully developed	cirri between tentacles
3	8—16	3—5
4—5	12—16	4—5
6—7	19—20	3—7
8	16—38	3—9
9	29—36	5—13
11—12	32—43	5—13

in older stages, as will appear from the adjoining table. As to the American specimens, see below.

Distribution. North-western Europe, neritic, northern boreal: Port Erin (Isle of Man), Millport (Firth of Clyde) (Browne); Cromarty Firth (Moray Firth, Romanes), Dunbar (Firth of Forth, Evans & Ashworth); off Firth of Forth and near the coast of Belgium (Kramp); Shetland Islands (Hartlaub and Kramp & Damas), Faeroe Islands (Kramp); Danish waters (Kramp); northern part of the North Sea and along the entire west coast of Norway as far north as Tromsö, about 70° N. (Kramp & Damas). — Gulf of Maine, U. S. A. (Bigelow).

Seasonal occurrence. The records from the coasts of Great Britain and Norway are from March—July; at the coasts of Belgium it was found in July and October, in the Danish waters from May to November. In the Gulf of Maine it has been found from February to July.

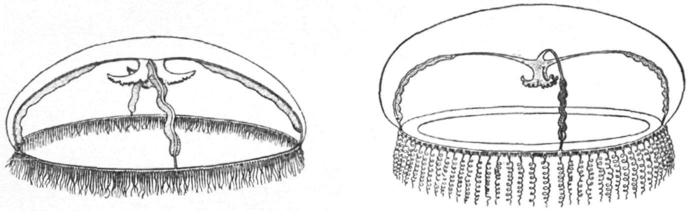
The American specimens. Professor Bigelow, by request, kindly sent me several specimens of "*M. cruciata*" from the Gulf of Maine. They are exactly like European specimens of *M. polydiademata* in all essentials, except that they have some more tentacles on the same size of bell. As the tentacles, accordingly, are somewhat closer together than in European specimens, there is only room for a smaller number of cirri, usually 5, between two successive tentacles, though in several cases I have found about 10, in some large specimens even 12—13 cirri between two tentacles. In specimens 14—21 mm wide, the number of tentacles varies between 48 and 64. The normal number of lithocysts is evidently 16, as most of the specimens in which counting was possible, have 4 in each quadrant. In two specimens one quadrant has only 3 lithocysts, and in about 25 $^0/_0$ of the specimens examined, one or two quadrants have 5 lithocysts. In such case the latter are not equidistant, but two of them are placed near each other, whereas the others are in their normal positions. In one individual I found $4 + 5 + 4 + 6$ lithocysts. The concretions have been dissolved by the formaline. The largest specimen is 21 mm in diameter, and Bigelow states that he has never seen any larger specimens. The differences between the American and the European form seem to me so slight that there is no reason to separate them as two distinct species. It also seems to me very unlikely that the large "*Halopsis cruciata*"

Agassiz should be the final growth-stage of the present form; *cruciata* is 40—50 mm wide, it is expressly stated to have only 12 lithocysts, and each of these only contains 4—5 concretions.

Genus ***Mitrocoma*** Haeckel 1864.

Mitrocomidæ with four radial canals; with numerous lithocysts without ocelli; with marginal cirri which coil spirally.

Species: *discoidea* (Torrey 1909), *annæ* (Haeckel 1864, genotype). — Doubtful species: *minervæ* (Haeckel 1879), *duplex* (Maas 1893).



41 42

Figs. 41—42. *Mitrocoma.* — Fig. 41. *M. discoidea* Torrey; from Torrey 1909. — Fig. 42. *M. annæ* Haeckel; from Mayer 1910.

The genus is distinguished from *Mitrocomella* by the large and variable number of lithocysts. The umbrella is flatter than a hemisphere and of considerable size, 30—45 mm. The stomach is very small, and the lithocysts contain a large number of concretions in two or three rows. The tentacles have a thickened mesosarc (figs. 21 and 22, p. 327), and their nematocysts are arranged in transverse belts. Distribution: Mediterranean and west coast of North America; South Africa?.

Mitrocoma discoidea Torrey.

(Textfigs. 22, 33, 41).

Mitrocoma discoidea Torrey 1909 p. 17, textfig. 4.
Mitrocoma discoidea Foerster 1923 p. 35.

After this species was described by Torrey from the coast of California, some young specimens have been found near Vancouver by Foerster (1923), and from the same locality Dr. Th. Mortensen brought home four large specimens which are now in the Zoological Museum of Copenhagen. Torrey points out that the marginal cirri are readily lost; I have carefully examined the four specimens in our collection, and I found altogether two cirri left which, however, was sufficient to state that they are of the usual spiral type. When all cirri are lost, this species is easily confounded with *Halistaura cellularia* (A. Agassiz). *M. discoidea* is well distinguished from *M. annæ* by smaller number of lithocysts, by larger number of closely packed tentacles, by only one cirrus (in young specimens two) between every two tentacles, and by length of gonads.

Description: Diameter up to 45 mm. Umbrella flatter than a hemisphere, 3—4 times as broad as high, jelly moderately thick. Velum about twice as broad as length of tentacle bulbs. Stomach short and narrow, diam. about $^1/_{10}$ of bell diameter, funnels long and narrow, mouth with four "narrow, ruffled", long and pointed lips. Radial canals 4, narrow, circular canal narrow. Gonads narrow, linear, somewhat sinuous, along almost whole length of radial canals, leaving both ends free. Tentacles 180—240, short, transversally wrinkled, with conical bulbs. Cirri, one between every two tentacles, in younger specimens sometimes 2, spiral. Lithocysts 20—60, with numerous concretions in 2—3 rows. Colour: circular canal yellow-green, tentacle bulbs purple, edges of lips with a single row of delicate purple spots (in living specimens).

Distribution. San Diego, California, in May—July (Torrey); Departure Bay, Vancouver (Foerster); Nanaimo, Vancouver, in June 1915 (new locality).

The specimens examined by me have the following dimensions:

Diam. mm.	30	35	35	40
Number of tentacles, about	160	220	226	?

Mitrocoma annæ Haeckel.

(Textfigs. 21, 31, 42).

Mitrocoma annæ Haeckel 1864 p. 327.

Mitrocoma annæ O. Hertwig 1878 pp. 179 ff., Taf. IX figs. 6, 7, 9, 11.

Mitrocoma annæ O. & R. Hertwig 1878 a pp. 3, 70 ff., 81—86, Taf. VII figs. 10, 11, 14, 18, 19, Taf. X fig. 8.

Mitrocoma annæ O. & R. Hertwig 1878 b pp. 10, 24—25, Taf. I figs. 1, 3, 5.

Mitrocoma annæ Haeckel 1879 p. 189, Taf. X figs. 1—13.
Mitrocoma annæ Metschnikoff 1886 a pp. 240, 260.
Mitrocoma annæ Metschnikoff 1886 b pp. 23—82, Taf. III figs. 20—33, Taf. IV figs. 1—16.
Mitrocoma annæ Zoja 1895 pp. 4, 16, 32, Pl. I figs. 67—76, Pl. II figs. 77—79.
Mitrocoma annæ Mayer 1910 p. 287, textfig. 152.
Mitrocoma annæ Vanhöffen 1912 b p. 21.
?*Mitrocoma duplex* Maas 1893 p. 60.

Mitrocoma annæ has been the subject of thorough investigations by several authors during the last quarter of the 19th century. Haeckel himself had a fancy for this elegant medusa which he had named in memory of his first wife, and he treated it with particular care in his monograph. The brothers Hertwig studied its anatomy and histology, especially the structure of the nervous system, the sense organs, and the gonads; O. Hertwig (1878), Metschnikoff (1886 b), and Zoja (1895) have studied the development and cleavage of the eggs, from which Metschnikoff reared a polyp resembling *Cuspidella*. O. &. R. Hertwig (1878 a) and after them Metschnikoff (1886 a) discussed its systematic position, comparing it with *Halopsis* and *Tiaropsis*.

I have been able to examine some specimens at the British Museum, and also in E. T. Browne's collection, and I have cut sections of the marginal organs and of the male gonads.

Description: Diameter 30—40 mm. Umbrella flatter than a hemisphere, jelly thick. Velum broad, about 3—5 times length of tentacle bulbs. Stomach very small, $^1/_{10}$—$^1/_8$ of diameter of bell, short; funnels small, mouth lips fairly short, pointed, with a somewhat folded rim. Radial canals 4, narrow; circular canal narrow. Gonads linear, sinuous, along distal $^1/_2$—$^3/_4$ of the radial canals, not reaching the circular canal; median division well defined in both sexes. Tentacles 60—100, long, wrinkled, with conical bulbs. Cirri 3—8 between every two tentacles, long, spiral. Lithocysts 60—100, each with about 20 concretions in two rows. Colour; stomach, gonads, canals, and tentacle bulbs amber-yellow or sulphur-yellow.

Development. Vanhöffen (1912 b) describes two young specimens from Gibraltar, 3 mm wide, with 16 tentacles, 96 cirri, and 8 lithocysts; the gonads were in the distal $^1/_3$ of the radial canals.

Abnormalities seem to be rather frequent in this species. In one of the specimens in Browne's collection (now in the Zoological Museum of Copenhagen), 21 mm wide, the mouth opening is divided into two parts by a string from one side of the mouth rim to the opposite side; in one of the specimens in the British Museum the mouth is likewise abnormal, and there are 5 radial canals. *Mitrocoma duplex* Maas from Naples is probably an abnormal specimen of *M. annæ* in which two canals issue from each of the four corners of the stomach.

Distribution. Mediterranean: Nizza (Haeckel), Naples, Messina; Gibraltar (Vanhöffen).

Three of the specimens examined by me show the following dimensions: Diam. 18 mm, about 40 tentacles + about 30 young bulbs, 1 to 3 or 4 cirri between tentacle bulbs; gonads male, along distal $^1/_2$—$^3/_4$ of radial canals, straight, smooth; lips short and very slightly folded. — Diam. 21 mm, 73 tentacles (20 + 19 + 16 + 18), fairly equidistant; 2—5 cirri between the tentacles; gonads male, in distal $^1/_2$ of canals, sinuous, reaching very nearly to the circular canal. — Diam. 35 mm, about 76 tentacles, distances not quite equal, and some very young bulbs; 3—8 cirri between the tentacles; gonads about $^2/_3$ of radial canals, somewhat nearer to bell margin than to stomach, somewhat sinuous, with finely wrinkled surface.

Mitrocoma minervæ Haeckel.

Mitrocoma minervæ Haeckel 1879 p. 189.

Description (from Haeckel): Diameter unknown. Umbrella flattened. Velum ?. Stomach and lips larger than in *M. annæ*. Radial canals 4. Gonads along nearly entire length of radial canals. Tentacles 120—160. Cirri, 1 between the tentacles. Lithocysts 120—160, each with 8—12 concretions in a single row. — Distribution: South Africa.

This is a doubtful species. We do not know for certain, whether the lithocysts are open, the description is deficient, and no figure is given. If the species belongs to *Mitrocoma*, it is distinguished from *M. annæ* by having only one cirrus between the tentacles, and by smaller number of concretions in the lithocysts.

It seems to me doubtful whether the two medusæ mentioned by Vanhöffen (1911 p. 227) from the Nicobares and the island Nias west of Sumatra, really belongs to *M. minervæ* as supposed by him.

They have up to 45 tentacles, 45 lithocysts with 6 concretions, and an indeterminate number of cirri. Vanhöffen says nothing about the lithocysts being open.

Genus ***Halopsis*** A. Agassiz 1863.

Mitrocomidæ with more than eight radial canals; with numerous lithocysts without ocelli; with marginal cirri which coil spirally.

Species: *ocellata* (A. Agassiz 1863, genotype).

The only species of this genus is a large medusa somewhat resembling a *Mitrocoma*, but with 12—16 radial canals, arranged in four groups. The genus was established by A. Agassiz (1863 b and 1865) as belonging to the *Æquoridæ* and comprising two species, *ocellata* with about 16, *cruciata* with 4 radial canals; the latter species must be referred to *Mitrocomella*. Metschnikoff (1886 a) realized the close relationship between *H. ocellata* and *Mitrocoma*, a relationship which was finally proved by Bigelow (1914 b). Haeckel (1879) as well as Mayer (1910) placed *H. ocellata* among the *Æquoridæ*. Further notes on the history of the genus is found in Kramp 1919 p. 67. — Distribution, both sides of the northern Atlantic area.

Halopsis ocellata A. Agassiz.

(Textfigs. 6, 12, 19, 28, 32, 43).

Halopsis ocellata A. Agassiz 1863 b p. 219.
Halopsis ocellata A. Agassiz 1865 p. 99, figs. 143—150.
Halopsis ocellata Haeckel 1879 p. 217.
Halopsis ocellata Fewkes 1888 p. 233, Pl. III fig. 3.
Halopsis ocellata Bigelow 1914 b p. 102.
Halopsis ocellata Kramp 1919 p. 65, Pl. IV figs. 1—5, textfigs. 6—9.
Halopsis ocellata Kramp 1920 p. 10, textfigs. 1—6.
Halopsis ocellata Kramp & Damas 1925 p. 299, textfig. 26.

Bigelow found that the lithocysts are open, thus stating the systematic position. New descriptions, based upon European specimens, are given in some of my previous papers (1919 and 1920), including remarks on variation and abnormalities. In Kramp & Damas (1925) are found some notes on colour and shape of the living medusa accompanied by a figure drawn from life by Damas.

Description: Diameter 60—70 mm. Umbrella about four times as broad as high, jelly moderately thick. Velum fairly narrow, about 3 mm broad. Stomach broad and flat, about $^1/_5$ of the diameter of the bell, circular or star-shaped; funnels well developed; mouth rim folded, with 4 fairly short lips. Radial canals about 12—16 (rarely 11 or 17), in four groups, narrow; circular canal narrow. Gonads linear, sinuous bands along about $^2/_3$ of the radial canals, somewhat nearer to the circular canal than to the stomach; median division distinct in both sexes. Tentacles about 450, fairly long, about $^1/_3$ of bell diameter, with broadly conical bulbs; nematocysts in more or less complete rings. Cirri, 1 between the tentacles, spiral. Lithocysts about 80. Colour, whole medusa rosy (in living specimens).

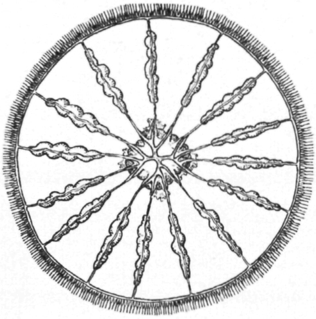


Fig. 43. *Halopsis ocellata* A. Agassiz; after Kramp 1919.

Development. According to Agassiz (1865 p. 100) young specimens "measuring not more than an inch in diameter" (about 25 mm) have only four radial canals. This is not in accordance with my own observations (Kramp & Damas 1925 p. 301); in nine young specimens, 9—18 mm wide, the number of canals varied between 11 and 17, with no correlation to size; the smallest individual, 9 mm, had 14 radial canals. This young specimen had 35 tentacles; the gonads could just be distinguished and were already elongated.

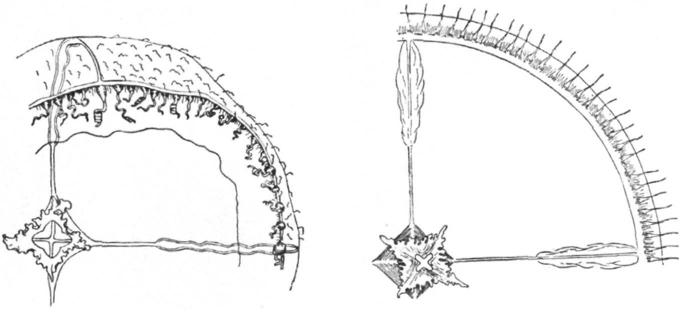
Abnormalities. Abnormal course of the radial canals is frequently observed in this species (Kramp 1919 figs. 9 *a-r*, 1920 figs. 1—6).

Distribution. Gulf of Maine, from Grand Manan to Cape Cod (A. Agassiz, Fewkes, Bigelow). Common off the coasts of north-western Europe from south-west of Ireland to the south coast of Iceland (Kramp), and along the west coast of Norway from Bergen to Tromsö, 69°45′ N. (Kramp & Damas). In 1928 I found several specimens off the west coast of Greenland as far north as the Disko Bay, about 69° N.

Genus ***Cosmetira*** Forbes 1848.

Mitrocomidæ with four radial canals; with eight lithocysts without ocelli; with marginal cirri which do not coil spirally.

Species: *pilosella* (Forbes 1848, genotype), *megalotis* (Maas 1893).



44. 45.

Figs. 44—45. *Cosmetira.* — Fig. 44. *C. pilosella* Forbes; from Hartlaub 1909. — Fig. 45. *C. megalotis* (Maas); after Maas 1893 (from Mayer 1910).

This genus is well distinguished from all other *Mitrocomidæ* by the structure of the cirri some of which are, moreover, placed upon the exumbrella at some distance above the bell margin, connected with the endoderm of the circular canal by a string of endoderm cells. Another characteristic feature, found in both species, is the thin, bulging margin of the umbrella. The nematocysts of the tentacles are arranged in transverse rings, and the tentacles have a thin mesosarc.

Forbes established *Cosmetira* as a subgenus of *Thaumantias*, distinguished from the other species of that genus by the possession of "two kinds of tentacles" (i. e. tentacles and cirri), and comprising only one species, *C. pilosella.* Haeckel (1864 pp. 334—335) applied the generic name of *Cosmetira* to a group of five species: *Cosmetira pilosella* Forbes, *Thaumantias mediterranea* Gegenbaur, *Th. corollata*, Leuckart, *Laodicea calcarata* Agassiz, and *Cosmetira punctata* nov., all of which, except the first, have proved later on to belong to the genus

Laodicea, probably even to one species, *L. undulata* Forbes & Goodsir (see Browne 1896 p. 482, and 1907 pp. 459 ff., Kramp 1919 p. 16 and pp. 21 ff.). In 1879 Haeckel included *Cosmetira pilosella* among his numerous synonyms of "*Laodice cruciata*", causing much confusion which was unravelled by Browne (1896) who provisionally referred *C. pilosella* to the genus *Euchilota*, not then realizing that the lithocysts are open. It was not until 1909, when Hartlaub published a new and thorough description of *Cosmetira pilosella* and demonstrated the true nature of the lithocysts and the cirri, that the systematic position of the genus *Cosmetira* was settled. The definition of the genus, given above, differs from that given by Browne (1910 p. 32) by taking into consideration the structure of the cirri. Besides the species mentioned above (Haeckel), the following species which have been referred to *Cosmetira* must be excluded from that genus: *C. salinarum* du Plessis (= *Laodice salinarum* Haeckel, an altogether uncertain species), and *C. frigida* Browne 1910 (= *Mitrocomella frigida*). — Both species of *Cosmetira* occur at the coasts of north-western Europe.

Cosmetira pilosella Forbes.

(Textfigs. 7, 8, 10, 13, 16, 17, 25, 26, 27, 44).

Thaumantias (Cosmetira) pilosella Forbes 1848 p. 42, Pl. VIII fig. 1.
Cosmetira pilosella Haeckel 1864 p. 335.
i. p. *Laodice cruciata* Haeckel 1879 p. 132.
Euchilota pilosella Browne 1896 p. 484, Pl. XVI figs. 7, 7 a.
Cosmetira pilosella Hartlaub 1909 p. 82, textfigs. 1—4.
Cosmetira pilosella Browne 1910 p. 32.
Cosmetira pilosella Mayer 1910 p. 261.
Cosmetira pilosella Kramp 1919 p. 61.

In his new description of *Cosmetira pilosella* (1909), Hartlaub made one unfortunate mistake: he thought he saw a distinct black ocellus above the base of the older tentacles, and he regarded this ocellus as proving a relationship to the "*Thaumantiadæ*". As a matter of fact, no such ocellus exists in this species. The most important point in Hartlaub's description is the understanding of the difference between the cirri of *Mitrocoma* and those of *Cosmetira*; unfortunately, in the specimens studied by him, all cirri were completely contracted, so that he did not realize their great power of extension (see above, p. 331).

Description: Diameter about 20 mm. Umbrella higher than a hemisphere, dome-like, gelatinous substance moderately thick in central part, very thin towards the margin which has a characteristic down-hanging, slack appearance. Velum broad. Stomach small, with 4 pointed lips, margin somewhat folded; funnels short and broad. Radial canals 4, narrow; circular canal narrow. Gonads linear, narrow, somewhat sinuous, along about $^3/_4$ of radial canals, somewhat nearer to the margin than to stomach; median division distinct in both sexes. Tentacles about 64, short, with globular bulbs. Cirri about 6 on margin and about 4 on exumbrella between two successive tentacles, may be extended to great length and contracted to short, rigid threads by shortening, never coiled; nematocysts in rings; older cirri on exumbrella, 3 mm or more above the circular canal. Lithocysts 8, with 12 or more concretions sometimes arranged in two rows. Colour: stomach and gonads reddish-purple; tentacle bulbs dark purple (in living specimens).

Development. Browne (1896 p. 486) has observed a very young medusa, 1 mm high and broad, which probably belongs to this species; it has only two, opposite tentacles. Somewhat more advanced stages show that the cirri are originally on the umbrella margin whence they are displaced to the exumbrella by the growth of the umbrella. In May 1914 I collected numerous young specimens in the Channel south of Eddystone. The smallest individuals, 2—4 mm wide, have a thick jelly, about 16 fully developed tentacles and about same number of small bulbs just appearing; about 4 cirri between tentacles and bulbs. Specimens 5—10 mm wide have usually about 32 tentacles fully developed, and 6—10 cirri between the tentacles; some of the cirri are already distinctly removed from the umbrella margin. The young gonads appear in the middle part of the radial canals; they soon attain an elongated shape, extending along the middle $^1/_2$—$^2/_3$ of the canals in specimens more than 3.5 mm in diameter.

Abnormalities. Browne has seen a specimen with only three radial canals.

Distribution. Southern and western coasts of the British Isles in April—October; the Shetland Islands in July; Bergen in November (Kramp & Damas 1925 p. 298); west coast of Jutland and northern part of the Kattegat in September—October (Kramp 1927 p. 110).

Cosmetira megalotis (Maas).

(Textfig. 45).

Halopsis megalotis Maas 1893 p. 57, Taf. VI figs. 3—6.
Cosmetira megalotis Browne 1910 p. 33.
Mitrocoma megalota Mayer 1910 p. 289.
Cosmetira megalotis Kramp 1919 p. 64.

Having examined a few specimens from Moray Firth, east coast of Scotland, I pointed out (1919) the difference between this species and *C. pilosella*. The present species is larger, has more tentacles and much shorter gonads.

Description: Diameter 30—40 mm. Umbrella as in *pilosella*. Velum fairly broad. Stomach small, mouth with four short, pointed, crenulated lips. Radial canals 4, narrow, circular canal narrow. Gonads in distal $^1/_3$—$^1/_2$ part of radial canals. Tentacles about 100, fairly short, with globular bulbs. Cirri between every two tentacles about 8 on bell margin and some placed until 3 mm above margin. Lithocysts 8, number of concretions unknown. Colour in alcohol or formaline dirty yellow.

Distribution. North-west of Scotland in July (Maas); Moray Firth, east coast of Scotland in September (Kramp); near Scilly Isles in August (new locality, Kramp).

Genus ***Cosmetirella*** Browne 1910.

Mitrocomidæ with four radial canals; with eight lithocysts without ocelli; without marginal cirri.

Species: *davisi* (Browne 1902, genotype).

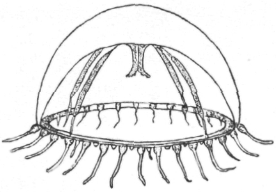
Cosmetirella is distinguished from *Cosmetira* by the absence of cirri and from *Tiaropsis* by the absence of ocelli. The genus was established by Browne (1910 p. 32) for an antarctic medusa *Cosmetirella simplex*, described in the same paper (p. 34). As will be demonstrated below, *Cosmetirella kerguelensis* Vanhöffen (1912 a) is identical with *C. simplex*, and when I examined the type specimens of *Tiaropsis davisi* Browne (1902), I found that this subantarctic medusa belongs to the same genus and species. The genus *Cosmetirella* thus comprises only one species for which we must use the oldest specific name, *C. davisi* (Browne).

Cosmetirella davisi (Browne).

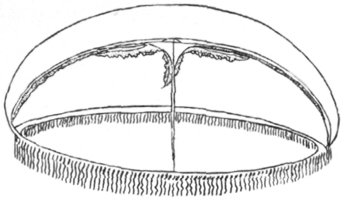
(Textfigs. 4, 34, 46).

Tiaropsis davisii Browne 1902 p. 281.
Cosmetirella simplex Browne 1910 p. 34, Pl. I figs. 6—8.
Phialella falklandica Vanhöffen 1911 p. 223, Taf. XXII fig. 10.
Cosmetirella kerguelensis Vanhöffen 1912 a p. 368.
Cosmetirella simplex Vanhöffen ibid.

Tiaropsis davisi was briefly described by Browne in his "Preliminary Report on Hydromedusæ from the Falkland Islands" (1902). The type specimens are in Browne's collection, where I was able to examine them. I found that no ocelli are present at the base of the lithocysts. A direct comparison with the original specimens of *C. simplex* in the British Museum convinced me of the specific identity of the two forms, and Mr. Browne has agreed with me in uniting them. In the British Museum I also saw a few larger specimens, collected by the "Discovery II" in 1926 and 1927 near South Georgia. These specimens complete the transition from the small *C. simplex* to the larger *C. kerguelensis* Vanhöffen.



46



47

Fig. 46. *Cosmetirella davisi* (Browne); after Browne 1910. — Fig. 47. *Halistaura cellularia* (A. Agassiz); after Murbach & Shearer 1903.

In his report on the "Valdivia" medusæ (1911), Vanhöffen referred some medusæ, found near the Kerguelen Island, to the species *Phialella falklandica* Browne. In his next paper (1912 a) he realized that the Kerguelen specimens had open lithocysts and, therefore, belonged to *Cosmetirella;* owing to their considerable size (19—36 mm) and large number of tentacles (88—144) he considered them representatives of a proper species which he called *C. kerguelensis*. In the same paper Vanhöffen mentions numerous specimens of *C. simplex* from the antarctic sea in the neighbourhood of the Gauss Station; he points out the resemblance between the two species: "*Cosmetirella* *simplex* macht den Eindruck einer verkümmerten *Cosmetirella kerguelensis*, da letztere doppelt so gross wird und bei gleicher Grösse schon weit mehr Tentakel hat" (p. 370). Unfortunately, Vanhöffen gives no precise records of the number of tentacles in his specimens of *C. simplex*, only that specimens 16—18 mm wide have about 64 tentacles (in two specimens with abnormal number of lithocysts, 13—14 mm wide, he has counted 56 and 62 tentacles).

My own studies on the antarctic and subantarctic specimens have given the result that size and number of tentacles make the only points of difference, and even in this respect there is no distinct limit between the two forms. Moreover the development of the tentacles proceeds in an irregular way, as appears from the following table:

Diam. mm	Number of tentacles			
	large	small	total	
7.5	18	10	28	antarctic, abt. 170° E., types of *simplex* Browne.
8	32	7	39	
9	30	8	38	
9	30	18	48	
9	c. 24	c. 32	c. 56	subantarctic, Falkland Islands, types of *davisi* Browne.
9	29	31	60	
11	35	42	77	
12	c. 80	c. 70	c. 150	subantarctic, South Georgia, "Discovery II".
18	c. 112	4	c. 116	
16—18	..	..	c. 64	antarctic, "Gauss", *simplex* Vanhöffen.
19	..	..	88	subantarctic, Kerguelen, *kerguelensis* Vanhöffen.
22	..	..	104	
36	..	..	144	

It will be seen that the relative number of large and small tentacles as well as the total number according to size of specimens are very variable, and also that it is impossible to draw any definite limit which might justify a distinction between two species. I believe that the antarctic *C. simplex* is a smaller growth-form of the subantarctic *C. davisi* (incl. *kerguelensis*). Bottom animals and pelagic holoplanktonic animals often grow to larger size in cold areas than specimens of the same species in temperate seas. Leptomedusæ are, however, seasonal animals; in arctic and antarctic regions their occurrence is limited to a short period, so that some of them quite likely have not sufficient time to reach the same size as specimens in temperate regions.

Vanhöffen (1912 a p. 353) is inclined to think that *Phialidium iridescens* Maas is identical with *Cosmetirella simplex*. As Maas (1906 p. 13) does not mention the lithocysts, I prefer to leave that species as doubtful.

Description: Diameter about 18 mm (antarctic form) or 18—36 mm (subantarctic form). Umbrella hemispherical or somewhat higher, jelly fairly thick, apex evenly rounded. Velum narrow. Stomach small, funnels short and fairly broad; mouth rim somewhat folded, lips narrow and pointed or broad and short according to state of contraction. Radial canals 4, narrow; circular canal narrow. Gonads linear, sinuous, along $^1/_2$—$^2/_3$ of radial canals, somewhat nearer to the margin than to the stomach. Tentacles about 48—64 in antarctic, about 100—150 in full-grown subantarctic specimens; fairly short, with broad basal bulbs with fairly thick ectoderm; nematocysts singly and evenly distributed, not in groups or rings. Lithocysts 8 (abnormal specimens seen with greater number), with several concretions. Colour yellowish to chocolate.

Abnormalities. Browne found a specimen, 7 mm wide, with 13 lithocysts, and Vanhöffen records even higher numbers, 17 and 31 in two specimens 13 and 14 mm in diameter, from which he draws the conclusion that the number of lithocysts may not be used as generic character. It seems to me that, even if we only use the numbers as specific characters, the occurrence of such abnormal individuals involves the same difficulties. We must define the species, or the genera, according to the normal number and structure of the various organs and leave abnormalities for special description; the occurrence of abnormalities has no influence upon the systematic importance of the normal characters. Abnormalities seem to occur especially frequently in certain species, and *Cosmetirella davisi* is one. Among the specimens examined by me, I found two more with supernumerary lithocysts: in one of the types of *C. simplex* (from McMurdo Sound), 9 mm wide, there is a small extra lithocyst close by one in normal position; in a larger specimen, 18 mm wide, from South Georgia, there is one extra lithocyst separated from a perradius by two tentacles and from the neighbouring normal adradial lithocyst by three tentacles. — Vanhöffen found a specimen with a bifurcated radial canal.

Distribution. Antarctic and subantarctic: Falkland Islands, about 52° S. 60° W. (*davisi*, Browne 1902); South Georgia, about 55° S. 38—47° W. ("Discovery II" 1926 and 1927); Kerguelen Island, about 50° S. 70° E. (*kerguelensis*, Vanhöffen 1912 a); Gauss Station, about 66° S. 90° E., also two specimens 58° S. (*simplex*, Vanhöffen 1912 a); South Victoria Land, about 77° S. 165° E., 67° S. 178° E. (*simplex*, Browne 1910).

Genus ***Halistaura*** Bigelow 1913.

Mitrocomidæ with four radial canals; with numerous lithocysts without ocelli; without marginal cirri.

Species: *cellularia* (A. Agassiz 1865, genotype).

Bigelow (1913) found open lithocysts in "*Laodicea cellularia*" Agassiz and therefore referred it to the *Mitrocomidæ* among which it represents a new genus, distinguished from *Cosmetirella* by the large and variable number of lithocysts. Distribution: west coast of North America.

Halistaura cellularia (A. Agassiz).

(Textfig. 47).

Laodicea cellularia A. Agassiz 1865 p. 127, figs. 195, 196.
Thaumantias cellularia Haeckel 1879 p. 129.
Thaumantias cellularia Murbach & Shearer 1903 p. 172, Pl. 17 figs. 2, 2 b.
Thaumantias cellularia Mayer 1910 p. 199.
Halistaura cellularia Bigelow 1913 p. 30.
Halistaura cellularia Foerster 1923 p. 36.

This species was particularly well described and figured by Murbach & Shearer (1903). Bigelow found the lithocysts, but could not count them over the whole margin of any specimen: "... we may assume, tentatively, a total of 12—24". According to Foerster (1923) there are usually 4—5 or 6 in each quadrant, but in one case he found 15.

The species may easily be confounded with *Mitrocoma discoidea*, when the latter has lost its cirri (see above). *H. cellularia* is expressly stated by the authors (also by Bigelow) to have no cirri; there also seems to be a difference in the number of lithocysts which is usually larger in *M. discoidea* than in *H. cellularia.*

Description: Diameter 50—90 mm. Umbrella about hemispherical, thick, especially at the apex. Velum broad (according to fig. by Agassiz). Stomach very small, with 4 long, slender, crenulated lips. Radial canals 4, narrow. Gonads narrow, sinuous, along nearly whole length of radial canals. Tentacles 250—340, long, with swollen, cylindrical bulbs. Lithocysts about 16—24; number of concretions unknown. Colour: umbrella light violet, manubrium and gonads darker, tentacle bulbs still darker violet (in living specimens).

Distribution. West coast of North America: Vancouver and southern Alaska (for details, see Foerster 1923).

Genus *Tiaropsis* L. Agassiz 1849.

Mitrocomidæ with four radial canals; with 8 lithocysts, each with an ocellus; with only one kind of tentacle; without marginal cirri.

Species: *multicirrata* (M. Sars 1835, genotype).

The relationship between *Tiaropsis* and *Mitrocoma* was already supposed by Metschnikoff (1886 a p. 239—241) who saw that his new species *Tiaropsis* (now *Tiaropsidium*) *mediterranea* had open lithocysts. Agassiz & Mayer (1899 p. 168) found open lithocysts in their new species *Tiaropsis* (now *Tiaropsidium*) *rosea* and, in the same paper (Pl. 7 fig. 23) figured a cross section of the bell margin of *Tiaropsis diademata*, showing the open lithocyst and the endodermal position of the ocellus. A proper description of the ocellus and the lithocyst was given the next year by Linko (1900 a p. 155, *T. diademata*, Pl. fig. 5).

According to the diagnosis above, the genus *Tiaropsis* contains only one species, *multicirrata* Sars (including *diademata* L. Agassiz). Having discussed the matter thoroughly, Mr. Browne and I agree in following Torrey (1909) in separating the species with two different kinds of tentacles (*Tiaropsidium*) from the genus *Tiaropsis*. As further demonstrated below, the species of *Tiaropsidium* and *Octogonade* constitute a progressive developmental series into which *Tiaropsis multicirrata* does not fit. The latter must be regarded as an outsider, derived from the same root, but has developed in another direction. In his diagnosis of *Tiaropsidium*, Torrey includes the lack of a gastric peduncle in contradistinction to *Tiaropsis*. It is true that *Tiaropsis multicirrata* has a stomachal peduncle, but it is broad and flat and sometimes rather inconspicuous, so that no great systematic importance can be applied to it. Besides, the possession of a peduncle is unnecessary for the distinction of the genus and should therefore, not be included in the diagnosis.

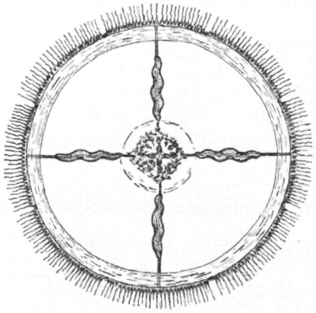


Fig. 48. *Tiaropsis multicirrata* (M. Sars); original.

A further difference between *Tiaropsis* and *Tiaropsidium* may perhaps be found in the structure of the tentacles; in *Tiaropsis* they are quite simple, without longitudinal furrows and thickened mesosarc as found in the large tentacles of some species of *Tiaropsidium*.

Besides the species now referred to *Tiaropsidium*, the following species have to be excluded from the genus *Tiaropsis*: *T. indicans* Romanes (= *Eutonina indicans*), *T. polydiademata* Romanes (= *Mitrocomella polydiademata*), *T. davisi* Browne (= *Cosmetirella davisi*), and the two altogether uncertain species *T. oligoplocama* Romanes and *T. macleayi* von Lendenfeld (see above, p. 320).

Tiaropsis multicirrata (M. Sars).

(Textfigs. 14, 15, 20, 35, 48).

Thaumantias multicirrata M. Sars 1835 p. 26, Pl. 5 figs. 12 a-c.
Thaumantias melanops Forbes 1848 p. 45, Pl. X fig. 3.
Tiaropsis diademata L. Agassiz 1849 p. 289, Pl. 6 figs. 1—18, Pl. 8 fig. 11.

Thaumantias pattersonii Greene 1857 p. 25, Pl. IV figs. 3 a-c.
Tiaropsis diademata L. Agassiz 1862 p. 308, figs. 45—49, Pl. 31 figs. 9—15.
Tiaropsis multicirrhata L. Agassiz ibid. p. 355.
Tiaropsis diademata A. Agassiz 1863 a p. 92, figs. 10—13.
Tiaropsis diademata A. Agassiz 1865 p. 69, figs. 91—93.
Tyaropsis scotica Allman 1871 p. 140, fig. 57.
Tiaropsis scotica Böhm 1878 p. 183, Taf. 2 figs. 15—30.
Thaumantias eschscholtzii Haeckel 1879 p. 129, Taf. VIII fig. 4.
Tiaropsis diademata Linko 1900 a p. 154, Pl. figs. 3—5.
Tiaropsis diademata Mayer 1910 p. 258, Pl. 31 fig. 11, Pl. 32 figs. 8—9.
Tiaropsis multicirrata Mayer ibid. p. 259.
Tiaropsis diademata Bigelow 1913 p. 33.
Tiaropsis multicirrata Kramp 1919 p. 77, Pl. IV figs. 6—10, textfigs. 11—14.

In a previous paper (Kramp 1919) I have demonstrated that the American *Tiaropsis diademata* is identical with the European *T. multicirrata*. In the same paper I communicated the fact that "*Thaumantias eschscholtzii*" Haeckel is nothing but *Tiaropsis multicirrata;* the type specimens from Greenland are in the Zoological Museum of Copenhagen, and their eight ocelli are very conspicuous. As Haeckel's fine drawing has frequently been reprinted in textbooks as a typical representative of *Thaumantias* (even as late as in Kükenthal's Handbuch der Zoologie, Bd. I, 1924) it seems worth while to call attention to the mistake once more.

I am sure that *Thaumantias pattersoni* Greene (1857) and *Tiaropsis scotica* Allman (1871) and Böhm (1878) belong to the present species.

Description: Diameter about 20 mm. Umbrella flatter than a hemisphere (though very variable according to state of contraction), gelatinous substance moderately thick; a broad, flat stomachal peduncle. Velum fairly broad. Stomach fairly small, short; funnels short and broad; mouth with 4 lips, fairly long and broad, margin much folded and crenated. Radial canals 4, narrow; circular canal narrow. Gonads somewhat sinuous, along middle $^1/_2$—$^2/_3$ of the radial canals, from base of stomachal peduncle, not reaching the bell margin; median division distinct in both sexes. Tentacles about 300, fairly short, $^1/_4$—$^1/_3$ of bell diameter, with broad, swollen bulbs. Lithocysts 8, each with about 12 concretions and with a black ocellus at the base. Colour: stomach, gonads, and endoderm of tentacle bulbs dull yellow, tentacle bulbs with black granules in the ectoderm.

Development. The mode and rate of development of the tentacles have been described by A. Agassiz (1863 a p. 92) and by me (Kramp 1919 pp. 79 and 84). In any stage of development the gonads commence at or very near the base of the stomachal peduncle (Kramp 1919 p. 79), but in young specimens the distance from the distal ends of the gonads to the bell margin is proportionately larger than in older individuals.

Distribution. Coastal areas of north-western Europe from the British Channel to the Barents Sea and the north coast of Iceland (for details, see Kramp 1919 pp. 80—81, Kramp & Damas 1925 p. 298, Kramp 1927 p. 111). Common on the east coast of North America from Cape Cod northwards, occasionally found farther south, as far as Woods Hole (see Hargitt 1904 p. 49, Bigelow 1914 a p. 13); it may also occur in vast swarms at the southern part of the west coast of Greenland, where it has been found as far north as in the Disko Bay, about 69° N. Bigelow (1913 p. 33) records this species from Dutch Harbour and Agattu Island in the northern Pacific.

Seasonal occurrence. In the greater part of the area of distribution the occurrence is restricted to the spring, from March to May or June; in the colder regions (Greenland, Iceland, some Norwegian fjords) it occurs somewhat later, until July or August.

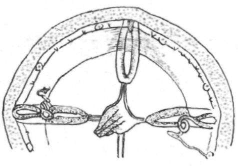
Genus ***Tiaropsidium*** Torrey 1909.

Mitrocomidæ with four radial canals; with 8 or 16 lithocysts, each with an ocellus; with two kinds of tentacles; without marginal cirri.

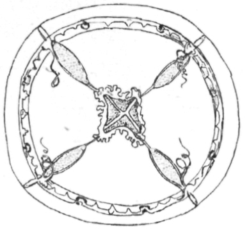
Species: *mediterraneum* (Metschnikoff 1886 a), *roseum* (Maas 1905), *kelseyi* (Torrey 1909, genotype), *japonicum* (nov. sp.). — Doubtful species: *punctatum* (Mayer 1900).

The original definition of this genus (Torrey 1909 p. 18) has to be augmented to include a new species, described below, with 16 marginal lithocysts, but in all other respects so much resembling the species previously known, that the double number of lithocysts does not justify a generic distinction. Browne (1910 p. 33), Mayer (1910 p. 494), and Bigelow (1913 p. 32) did not recognize the genus *Tiaropsidium*, Mayer on account of "the constant difficulty in distinguishing between rudimentary and merely young and undeveloped tentacles".

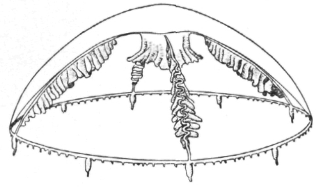
Mr. Browne now agrees with me that the genus is well founded: The number of large tentacles does not exceed 8; the small tentacles (Maas 1905, Taf. VII fig. 46) are so tiny that only in very young specimens they can be mistaken for developmental stages of large tentacles; in at least two, perhaps in all species, the large tentacles are provided with longitudinal furrows containing muscular bands. I consider *Tiaropsidium* more closely allied to *Octogonade* than to *Tiaropsis*.



49



50



51

Figs. 49—51. *Tiaropsidium*. — Fig. 49. *T. mediterraneum* (Metschnikoff); after Metschnikoff 1886. — Fig. 50. *T. roseum* (Maas); after Maas 1905. — Fig. 51. *T. kelseyi* Torrey; from Torrey 1909.

The size of the adult medusæ varies from 15 to 50 mm in diameter. This genus has a wide distribution, preferably in warmer seas: Mediterranean, Mauritius, Malayan Archipelago, Fiji Islands, southern Japan, Pacific coast of North America, and perhaps Florida and the Bahamas.

Tiaropsidium mediterraneum Metschnikoff.

(Textfig. 49).

Tiaropsis mediterranea Metschnikoff 1886 a p. 239, Taf. 22 figs. 6—8.

Ranson (1925 p. 464) records this species from the English Channel; he does not state the size of his two specimens, one of which is said to be adult and is described as follows: "Il a 8 lithocystes adradiaux, 4 tentacules perradiaux et 5 tentacules bien développés dans chaque quadrant. Tout les tentacules ont des bulbes basaux larges". When the non-perradial tentacles are well-developed and have large basal bulbs, the specimens can hardly belong to *Tiaropsidium;* they are most probably young *Tiaropsis multicirrata.*

Description (from Metschnikoff): Diameter 7 mm. Umbrella globular, 5 mm high by 7 mm wide, jelly thick. Stomach short, fairly broad, with 4 short, simple lips. Radial canals 4. Gonads elongated, on distal $^2/_3$ of radial canals. Tentacles two kinds: 2 opposite, perradial, long, almost as long as diameter of bell, and two small perradial bulbs which, however, are distinctly larger than the small rudimentary tentacles, of which there are 5 in each quadrant. Lithocysts 8, each with 20 or more concretions and with a basal ocellus. Colour: gonads, stomach, and tentacle bulbs yellowish-grey.

Distribution. Messina, 1 specimen.

Tiaropsidium roseum Maas.

(Textfigs. 2, 50).

? *Tiaropsis rosea* Agassiz & Mayer 1899 p. 168, Pl. 7 figs. 21—22, young medusa.
Tiaropsis rosea Maas 1905 p. 30, Taf. VII figs. 45—47.
Tiaropsis rosea Browne 1916 p. 186.
? *Tiaropsis punctata* Mayer 1900 p. 49, Pl. 22 figs. 60—63.

It is quite likely that the young medusa described by Agassiz & Mayer (1899) from the Fiji Islands is a young stage of the medusa described later on by Maas (1905) from the Indian Archipelago; it is, however, not fully proved, but as Maas retains the name of *rosea* for his nearly adult and well-described specimen, we may as well keep that name, referring in future to Maas's description for identification. I have seen the Mauritius specimen, described by Browne (1916); the number of tentacles and rudiments as well as the proximal position of the young gonads (see fig. 2) makes it probable that it really belongs to *T. roseum.*

Maas (1905) as well as Mayer (1910) indicate the possibility that *Tiaropsidium roseum* might be identical with *T. mediterraneum;* the latter has, however, only two large tentacles, the two other perradial tentacles being undeveloped in spite of the diameter of the medusa being 7 mm, whereas four tentacles are present in much smaller specimens of *T. roseum;* moreover the distal position of the gonads in *T. mediterraneum* seems to me to contradict the supposed identity of the two species.

"*Tiaropsis punctata*" was described by Mayer (1900 p. 49, Pl. 22 figs. 60—63, 1904 p. 14, Pl. III fig. 21) from the Tortugas, Florida and from the Bahamas. The same was probably described from the Tortugas by Fewkes (1882 p. 277, Pl. 7 figs. 13—14). In 1910 (p. 260) Mayer states that "a study of the medusæ at Tortugas, Florida, inclines me to believe that the tropical Atlantic and Pacific specimens are identical". The Atlantic specimens are all very young, and we have no evidence what they will be like when adult; the young gonads shown in fig. 61 (1900) are proximal and linear (not globular as in Browne's young specimen from Mauritius); this in connection with the long distances from the Bahamas and Tortugas to the Indo-Pacific localities of *Tiaropsidium roseum* make me hesitate to unite the two species until more advanced stages are found which may give evidence of the systematic position of the tropical Atlantic form; the latter must provisionally be regarded as a doubtful species.

Description (partly from Maas): Diameter about 15 mm. Umbrella flattened. Velum narrow (according to fig.). Stomach broad and flat, about $^1/_5$—$^1/_4$ of diameter of bell, mouth rim somewhat crenated, with 4 very short lips. Radial canals 4, narrow; circular canal somewhat broader. Gonads elongated oval, along somewhat more than $^1/_3$ of the radial canals, a little nearer to stomach than to bell margin. Tentacles 4 perradial, fairly long, $^1/_3$—$^1/_2$ of bell diameter, with broad bulbs and with a broad abaxial and a narrow adaxial longitudinal furrow; 7 rudimentary tentacles in each quadrant, each with a broad base and a small pointed tip. Lithocysts 8, with ocelli, each with about 15 concretions. Colour unknown.

Distribution. Suva Harbour, Fiji Islands (Agassiz & Mayer); Damar, Indian Archipelago, surface (Maas); Mauritius (Browne).

Tiaropsidium kelseyi Torrey.

(Textfig. 51).

Tiaropsidium kelseyi Torrey 1909 p. 19, textfig. 5.
Tiaropsidium kelseyi Foerster 1923 p. 37, Pl. IV fig. 7.

Description (from Torrey): Diameter about 50 mm. Umbrella about 3 times as broad as high, somewhat conical, with moderately thick walls. Velum ? Stomach short, wide, fairly broad, about $^1/_6$ of diameter of bell, "*with thin walls and slightly frilled lips*". Radial canals 4, narrow, circular canal narrow. Gonads narrow, curtain-like, much folded, along almost entire length of the radial canals. Tentacles 8, fairly short, with elongated bulbs, all of equal size; about 10 (according to Foerster 16) small rudimentary tentacles in each quadrant. Lithocysts 8, with ocelli, number of concretions unknown. Colour: manubrium, canals, gonads and tentacles a faint yellow.

Distribution. West coast of North America: San Diego and between San Diego and Monterey, California, in fairly deep water (Torrey); Vancouver Island region (Foerster).

Foerster describes some peculiar, hollow "tentacular" processes on the radial canals, irregularly distributed; "the inner layer of the tentacular process is formed from the endoderm of the radial canal while the outer layer is formed from the ectoderm of the subumbrellar wall". As Foerster has only seen one specimen, it seems probable that these processes are some abnormal structures.

Tiaropsidium japonicum n. sp.

(Textfigs. 1, 24, 36. Pl. X figs. 1, 2).

Description: Diameter 18 mm. Umbrella probably watch-glass shaped, thin. Velum narrow. Stomach small, diam. 2.5 mm, $^1/_7$ of bell diameter, flattened, funnels short and broad; mouth rim slightly folded, lips very short. Radial canals 4, narrow; circular canal narrow. Gonads linear, along almost entire length of radial canals, 1 mm or less from circular canal. Tentacles: 8 large tentacles, with large, swollen bulbs, apparently fairly long, nematocysts evenly distributed, not in rings, each tentacle with a broad abaxial and a narrow adaxial furrow containing muscular bands; 6—7 small, pointed rudimentary tentacles between two large tentacles (12—14 in each quadrant). Lithocysts 16, each with a dark-brown basal ocellus; number of concretions unknown. Colour unknown.

Distribution. Japan, 8 miles W. of Misaki, about 600 m. July 9th 1914, collected by Th. Mortensen, two specimens.

As there are two specimens, both alike, the double number of lithocysts (as compared with the other species of the genus) cannot be supposed to be an abnormality. Apart from this character, the species bears so great resemblance to the other species of *Tiaropsidium* that there is no reason to establish a new genus. The peculiar structure of the large tentacles has been described above, p. 328.

Genus *Octogonade* Zoja 1896.

Mitrocomidæ with eight radial canals; with numerous lithocysts, each with an ocellus; with two kinds of tentacles; without marginal cirri.

Species: *mediterranea* (Zoja 1896, genotype).

As the original description of *Octogonade mediterranea* is in a rare Italian periodical, I find it practical to quote it at some length, in English translation.

Zoja's definition of the genus is as follows: "*Octogonade* n. g. Leptomedusa (æquoride?) with 8 simple radial canals, which originate separately from the periphery of the stomach: Stomach almost cylindrical without a peduncle. Mouth with 8 lips. Marginal vesicles with many otoliths" (p. 101).

It will be observed that, apart from the number of radial canals, none of the characters which distinguish this genus from the other *Mitrocomidæ*, and from other medusæ, are mentioned in this diagnosis, though they are taken into consideration further down in the taxonomic discussion, from which I quote the following details:

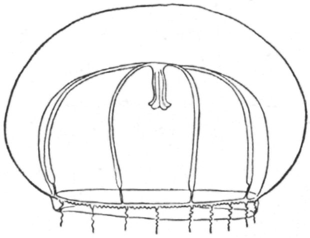


Fig. 52. *Octogonade mediterranea* Zoja; after Zoja 1896 (from Mayer 1910).

(p. 103): "Particularly characteristic are the marginal vesicles.

They are much like those known in *Mitrocoma annæ*, and although I cannot ascertain it, they are probably, like those, open at the base. ... A character which distinguishes it from that of *Mitrocoma* is, however, found in the ocellus, a large black pigment spot above the thickened base of each otocyst. As in other cases the ocellus consists of epithelial cells filled with pigment granules; no lens is observed there". — (p. 104): The marginal vesicles of *Octogonade* "are absolutely identical with those of *Tiaropsis*".

As, moreover, the lithocysts contain numerous concretions (12—20), there can hardly be any doubt but that their structure is really like that of *Tiaropsis*, even if the basal opening was not actually observed. A further proof of the relationship to *Tiaropsidium* is the arrangement of the tentacles; there are 16 large tentacles, and "the whole of the margin between the tentacles is ... occupied by numerous conical protuberances, into which enter diverticles from the marginal canal. ... They may be called rudiments of tentacles" (p. 103).

We need not lay much stress upon the following remark (p. 102, repeated p. 104): "... the gonads which are long, cylindrical and not fully developed (poco sviluppate) are not longitudinally divided into two". In the figure of *Tiaropsidium roseum* (Maas 1905, Taf. VII fig. 45) no longitudinal division of the gonads is seen, and in several species I have found that the division of the female gonad is difficult to see except in sections (see above, p. 324).

One of the figures gives an aboral view of the stomach showing eight equally developed peripheral funnels at the bases of the eight radial canals, and, in the middle, a figure like an 8-rayed star, probably indicating that there are as many radiating grooves along which the stomach is attached to the subumbrella.

For these several reasons I do not hesitate to place *Octogonade* among the *Mitrocomidæ*, close by *Tiaropsidium*, from which it is distinguished by its double number of radial canals and by the large and variable number of lithocysts.

Zoja calls attention to the resemblance between *Octogonade* and the family *Lafoeidæ* Metschnikoff, but the eight radial canals seem to place it among the *Æquoridæ*. Mayer (1910 p. 321) has no doubt in referring it to that family together with *Octocanna* and *Halopsis ocellata*, both of which have long ago been removed from the *Æquoridæ*.

Octogonade mediterranea Zoja.

(Textfig. 52).

Octogonade mediterranea Zoja 1896 p. 101—106, 6 figs.

Description (from Zoja): Diameter 60—70 mm. Umbrella globular, a little broader than high, with thick walls. Velum fairly broad (according to fig.). Stomach small, tubular, octagonal, with 8 small but distinct lips; funnels short and broad. Radial canals 8, arising independently, narrow. Gonads linear, cylindrical, along almost entire length of the radial canals, leaving a short part free at both ends. Tentacles 16, long, a little longer than diameter of bell; numerous small rudimentary tentacles (about 150 according to fig.) containing diverticula from the circular canal. Lithocysts 50—60, each with a basal ocellus and with 12—20 concretions. Colour unknown.

Distribution. Messina, February and March 1894.

Zoja does not state his number of specimens, but he has certainly seen more than one, so that the possession of 8 radial canals is not an abnormality, as may be supposed in the case of *Mitrocoma duplex* Maas from Naples.

The original description of the species is as follows, in English translation: "The disk is strongly convex, not much broader than high; the octagonal stomach is small (corto), about $^1/_6$ of the diameter. The mouth ends in 8 small but distinct lips. The gonads are cylindrical, along the 8 radial canals, leaving free the proximal and distal ends. The tentacles, in a number of 16, are longer than the diameter of the disk; 8 of these are situated at the ends of the radial canals. The marginal vesicles are numerous (3—4 in each tentacular interspace (spazio intertentaculare); in all 50 to 60); each of them has numerous otoliths (12—20) and a large black ocellus. Dimensions: Diameter of disk 6—7 cm; height 5. Ontogeny unknown".

VII. Taxonomic Discussion.

The 9 genera of *Mitrocomidæ* can be classified into four natural groups, and within each of these groups we can arrange the genera and species into more or less progressive developmental series. The interrelationship of the four groups will be discussed later on.

Group I. *Mitrocomella — Mitrocoma — Halopsis.*

	Diam. mm	Tentacles	Cirri betw. tents.	Litho-cysts	Con-cre-tions	Distribution
Mitrocomella brownei .	4—7	c. 16	6—8	8	5—7	N. W. Europe
— sinuosa	4	c. 50	3—5	12	?	N. America Pacific
— cruciata........	40—50	c. 100	1	12	4—5	N. America Atlant.
— fulva	6	16	c. 4	16	3—8	N. W. Europe
— frigida.........	13	32	c. 8	?16	?	Antarctic
— polydiademata..	12—22	c. 48	5—9	16	20—30	N. Atlant. Europe and America
Mitrocoma discoidea ..	45	180—240	1	20—60	∞	N. America Pacific
— annæ..........	30—40	60—100	3—8	60—100	c. 20	Mediterranean
— minervæ	?	120—160	1	120—160	8—12	S. Africa
Halopsis ocellata¹)	50—65	c. 450	1	c. 80	∞	N. Atlant. Europe and America

¹) about 12—16 radial canals.

The possession of marginal cirri which coil spirally, unite these genera into a natural group. In the above synopsis the species are arranged into a series according to number of lithocysts. Setting aside for the present the somewhat doubtful species *cruciata*, it will be seen that, on the whole, an increase in number of lithocysts is followed by increase in size, number of tentacles, and number of concretions in the lithocysts. There can hardly be any doubt but that the large medusæ with numerous tentacles and with numerous concretions in the lithocysts (*Mitrocoma* and *Halopsis*) mark a higher state of development than the small and more simply built species of *Mitrocomella;* at any rate, *Halopsis* is unquestionably at the top of the developmental series. This seems to indicate that a large and undetermined number of lithocysts is a token of high specialization, whereas a small and constant number is a primitive character. It will also be observed that, on the whole, the more primitive forms have a comparatively large number of marginal cirri, whereas the number is reduced in most of the highest developed forms. This seems to indicate that the possession of spiral cirri is a primitive character. This is in accordance with their occurrence in species belonging to different families of Leptomedusæ.

The two American species of *Mitrocomella* do not quite fit into the developmental series as given in the synopsis; *sinuosa* is a small medusa with many tentacles, and according to the old description by A. Agassiz, *cruciata* is a large medusa with few lithocysts, each with few concretions.

Group II. *Cosmetira.*

	Diam. mm	Tentacles	Cirri betw. tents.		Lithocysts	Distribution
			marginal	exumbrellar		
C. pilosella	20	c. 64	c. 6	c. 4	8	N. W. Europe
C. megalotis	30—40	c. 100	c. 8	c. 4	8	N. W. Europe

This group only contains one genus with two species. The group is characterized by the possession of cirri which do not coil spirally; similar cirri are known in one or two of the *Eucopidæ*. In spite of the considerable size of the medusæ and the fairly large number of tentacles, the number of lithocysts has remained 8. The exumbral position of some of the cirri is characteristic of this genus.

Group III. *Cosmetirella — Halistaura.*

	Diam. mm	Tentacles	Lithocysts	Distribution
C. davisi	18—36	120—150	8	Antarctic and subantarctic
H. cellularia....	50—90	250—340	16—24	N. America Pacific

Cosmetirella and *Halistaura* form a third group of genera among the *Mitrocomidæ*, characterized by absence of cirri as well as of ocelli. Only two species are known. *Halistaura cellularia* is a large medusa with numerous tentacles and a variable number of lithocysts as in the highest specialized species of the other groups; *Cosmetirella davisi* is much smaller, yet in comparison with other *Mitrocomidæ*, a fair-sized medusa with many tentacles. If I am right, that a constant number of lithocysts is a primitive character, *Cosmetirella* has "retained" the primitive number of 8 of these organs in spite of its having reached a fairly high state of development in size and in number of tentacles. In this connection it is, however, interesting to point out that abnormal specimens with supernumerary lithocysts are particularly frequently observed in this species which may, perhaps, be supposed to be in the act of developing into a form with undetermined and variable number of lithocysts, like *Halistaura*.

Group IV. *Tiaropsis* — *Tiaropsidium* — *Octogonade*.

The peculiar invaginated, cup-shaped ocelli with endodermal pigment, situated at the base of the lithocysts, combine these three genera into a natural group and distinguish them not only from the other *Mitrocomidæ*, but from all other Hydromedusæ as well.

The development of the tentacles: few large tentacles and a number of rudimentary tentacles, combine *Tiaropsidium* and *Octogonade* into a subdivision in contradistinction to *Tiaropsis*.

	Diam. mm	Tentacles		Concretions	Lithocysts	Radial canals	Distribution
		large	rudim. pr. quadr.				
Tiaropsis multicirrata ...	c. 20	c. 300	0	c. 12	8	4	N. Atlant. & Pacific
Tiaropsidium mediterraneum........	7	2+2	5	c. 20	8	4	Mediterranean
— roseum..........	15	4	7	c. 15	8	4	Tropics, Indo-Pacif.
— kelseyi	50	8	18—32	?	8	4	N. America Pacific
— japonicum	18	8	12	?	16	4	Japan
Octogonade mediterranea	70	16	c. 40	12—20	50—60	8	Mediterranean

The synopsis shows that the species of *Tiaropsidium* and *Octogonade* constitute a natural, progressive developmental series, approximately increasing in size alongside with increasing number of tentacles, rudimentary tentacles, and lithocysts. *T. japonicum* has been surpassed by *T. kelseyi* in size and in number of rudimentary tentacles, but its larger number of lithocysts gives it a higher position in the developmental series, which terminates in the large medusa *Octogonade* which is a double *Tiaropsidium* as far as tentacles and radial canals are concerned, and in which the number of lithocysts is not merely very large, but also variable. *Octogonade* is unquestionably at the top of the series, and this supports the view, expressed above under the discussion of the taxonomy of *Mitrocomella*, *Mitrocoma*, and *Halopsis*, that an undetermined number of lithocysts is a token of high specialization, whereas a small and constant number is a primitive character.

Tiaropsis has developed into another direction: its tentacles have greatly increased in number without being specialized into two kinds, but the number of lithocysts has remained eight.

Synopsis of the Genera.

Group	Genera	Radial canals	Cirri	Lithocysts	Ocelli	Tentacles
I	Mitrocomella ..	4	spiral	8—16	0	all alike
	Mitrocoma	4	spiral	20—160	0	all alike
	Halopsis......	> 8	spiral	c. 80	0	all alike
II	Cosmetira.....	4	flexile	8	0	all alike
III	Cosmetirella...	4	0	8	0	all alike
	Halistaura	4	0	16—24	0	all alike
IV	Tiaropsis......	4	0	8	+	all alike
	Tiaropsidium ..	4	0	8—16	+	two kinds
	Octogonade ...	8	0	50—60	+	two kinds

Within each of the four groups mentioned above, the genera and species may be arranged into a progressive developmental series, but the four groups cannot be arranged in a corresponding manner. In each group some species have retained certain characters which are supposed to be primitive, whereas other species of the same group must be designated as highly developed. It is possible that the possession of spiral cirri in group I is a primitive character which, however, is retained even in such a highly specialized form as *Halopsis ocellata*. It is also possible that group III is derived from group I, having lost the cirri, but if so its origin, probably, dates far back. The origin of group II (*Cosmetira*) is quite uncertain, because the flexile cirri are so rare among the Leptomedusæ that their systematic importance cannot be stated. The complicated ocelli, unique among Hydromedusæ, which characterize group IV, assign a high systematic position to that group; this highly specialized organ, alike in all investigated species, must be an ancient structure. Thus everything points towards the conclusion that the four groups of genera of *Mitrocomidæ* are all very old and have diverged from the common origin in very ancient time, and this view is supported by the wide geographical distribution of each group (except group II). As to the interrelationship of the groups, I am inclined to think that the most primitive members of group I are not very far from the original type of the family, from which group IV diverged earlier than group III, whereas I dare not say anything about the origin of group II. Apart from the special characters, the lower members of all groups are so much alike, that their common origin seems to me beyond doubt; in other words: the Leptomedusæ with open lithocysts form a natural and well-defined systematic group, the family *Mitrocomidæ*.

List of Literature.

1863a. Agassiz, A. On the mode of development of the marginal tentacles of the free Medusæ of some Hydroids. — Proc. Boston Soc. nat. Hist. Vol. 9.

1863b. — (Halopsis ocellata). In: ibid. Vol. 9.

1865. — North American Acalephæ. — Catal. Mus. Comp. Zool. Harvard Coll. No. II.

1899. Agassiz, A. & Mayer, A. G. Acalephs from the Fiji Islands. — Bull. Mus. Comp. Zool. Harvard Coll. Vol. 32. No. 9.

1849. Agassiz, L. Contrib. Nat. History of the Acalephæ of North America. Part I. — Mem. Amer. Acad. of Arts and Sciences. New Ser. Vol. IV.

1862. — Contributions to the natural history of the United States. 2nd. Monogr. Vol. IV.

1871. Allman, G. J. A Monograph of the Gymnoblastic or Tubularian Hydroids.

1913. Apstein, I. Beiträge zur Kenntnis der Leptomedusen. — Zool. Jahrb., Abt. Anatomie u. Ontogenie. Bd. 36.

1901—25. Bedot, M. Matériaux pour servir à l'histoire des Hydroïdes. Période 1—7. — Revue Suisse de Zoologie. Tome 9, 13, 18, 20, 24, 26, 32.

1909. Bigelow, H. B. The Medusae. Rep. Sci. Res. Exped. to the Eastern Tropical Pacific . . . by the "Albatross". — Mem. Mus. Comp. Zool. Harvard Coll. Vol. 37.

1913. — Medusae and Siphonophorae collected by the . . . "Albatross" in the north-western Pacific, 1906. — Proc. U. S. Nat. Mus. Vol. 44.

1914a. — List of Medusae craspedotae etc. Fauna of New England, 12. — Occasional Papers Boston Soc. Nat. Hist. VII.

1914b. — Explorations in the Gulf of Maine, July and August 1912, by the . . . "Grampus". — Bull. Mus. Comp. Zool. Harvard Coll. Vol. 58. No. 2.

1915. — Exploration of the Coast Water between Nova Scotia and Chesapeake Bay, July and August 1913, by the . . . "Grampus". — Ibid. Vol. 59. No. 4.

1918. — Some Medusae and Siphonophorae from the Western Atlantic. — Ibid. Vol. 62. No. 8.

1926. — Plankton of the Offshore Waters of the Gulf of Maine. — Bull. Bureau of Fisheries, Washington. Vol. 40. Part II.

1878. Böhm, R. Helgolander Leptomedusen. — Jenaische Zeitschr. f. Naturwiss. Bd. XII (N. F. Bd. I).

1924. Broch, Hj. Hydroida. In: W. Kükenthal, Handbuch der Zoologie, Bd. I.

1895. Browne, E. T. Report on the Medusæ of the L. M. B. C. District. — Proc. & Trans. Liverpool Biol. Soc. Vol. IX.

1896. — On British Hydroids and Medusæ. — Proc. Zool. Soc. London, 1896.

1897. — On British Medusæ. — Proc. Zool. Soc. London, 1897.

1902. — A Preliminary Report on Hydromedusæ from the Falkland Islands. — Ann. Mag. Nat. Hist. Ser. 7. Vol. IX.

1903. — Report on some Medusae from Norway and Spitzbergen. — Bergens Mus. Aarbog 1903.

1905a. — Report on the Medusæ. — Ceylon Pearl Oyster Fisheries. Supplement. Rep. No. 27.

1905b. — A Report on the Medusæ found in the Firth of Clyde (1901—1902). — Proc. Royal Soc. Edinburgh. Session 1904—05. Vol. 25, Part 9.

1905c. — Hydromedusae, with a Revision of the Williadae and Petasidae. — The Fauna and Geography of the Maldive and Laccadive Archipelagoes. Vol. II. Part 3.

1907. — A Revision of the Medusæ belonging to the Family Laodiceidæ. — Ann. Mag. Nat. Hist. Ser. 7. Vol. XX.

1910. — Medusæ. — National Antarctic Exped., Nat. Hist. Vol. V.

1916. — Medusæ from the Indian Ocean. — Trans. Linn. Soc. London. Vol. XVII. Part 2. Zool.

1889—92. Chun, C. Coelenterata. In: Bronn, Klassen und Ordnungen des Thier-Reichs, Bd. II, Abth. 2, Lief. 1—8.

1877. Claus, C. Studien über Polypen und Quallen der Adria. — Denkschr. d. math. naturwiss. Classe d. K. Akad. d. Wissensch. Wien. Bd. 38.

1878. Eimer, T. Die Medusen physiologisch und morphologisch auf ihr Nervensystem untersucht. — Tübingen.

1829. Eschscholtz, Fr. System der Acalephen. — Berlin.

1909. Evans, W. & Ashworth, I. H. Some Medusæ and Ctenophores from the Firth of Forth. — Proc. Royal Phys. Soc. Edinburgh. Vol. 17.

1882. Fewkes, J. W. Notes on Acalephs from the Tortugas. — Bull. Mus. Comp. Zool. Harvard Coll. Vol. 9. No. 7.

1888. — On certain Medusæ from New England. — Ibid. Vol. 13. No. 7.

1923. Foerster, R. E. The Hydromedusæ of the West Coast of North America, with special reference to those of the Vancouver Island Region. — Contrib. Canad. Biol. (N. S.). Vol. 1.

1848. Forbes, E. A Monograph of the British Naked-eyed Medusæ.

1856. Gegenbaur, C. Versuch eines Systemes der Medusen . . . — Zeitschr. f. wiss. Zoologie. Bd. VIII. Heft 2.

1887. Goette, A. Abhandlungen zur Entwickelungsgeschichte der Thiere. 4. Entwickelungsgeschichte der Aurelia aurita und Cotylorhiza tuberculata. — Hamburg und Leipzig.

1857. Greene, I. R. On the Acalephæ of the Dublin Coast. — Nat. Hist. Review. Vol. 4. Proc. of Soc. London.

1864. Haeckel, E. Beschreibung neuer craspedoter Medusen aus dem Golfe von Nizza. — Jenaische Zeitschr. f. Naturwiss. Bd. I.

1879. — Das System der Medusen.

1904. Hargitt, Ch. W. The Medusæ of the Woods Hole Region. — Bull. Bureau of Fisheries, Washington. Vol. 24.

1904. Hartlaub, Cl. Bericht über eine zoologische Studienreise nach Frankreich, Grossbritannien und Norwegen, ausgeführt im Frühjahre 1902. — Wissensch. Meeresunters., Abt. Helgoland. N. F. Bd. V.

1909. — Ueber Thaumantias pilosella Forbes und die neue Lafoëidengattung Cosmetira. — Zoolog. Anzeiger. Bd. 34.

1907-17. — Craspedote Medusen, I. Teil, 1—4. Lief. — Nordisches Plankton Bd. XII.

1878. Hertwig, O. Beiträge zur Kenntniss der Bildung, Befruchtung und Theilung des thierischen Eies. 3. Theil, II. Abschnitt. — Morpholog. Jahrb. Bd. IV.

1878a. Hertwig, O. & R. Das Nervensystem und die Sinnesorgane der Medusen, monographisch dargestellt.

1878b. — Der Organismus der Medusen und seine Stellung zur Keimblättertheorie. — Denkschr. d. med. naturwiss. Gesellsch., Jena. Bd. II. Heft 1.

1879. — Die Aktinien. — Jena.

1919. Kramp, P. L. Medusæ. Part I, Leptomedusæ. — The Danish Ingolf Exped. Vol. V. Part 8.

1920. — Anthomedusae and Leptomedusae. — Rep. Sci. Res. "Michael Sars" N. Atlant. Deep Sea Exped. 1910. Vol. III. Part 2. Zool.

1924. — Medusæ. — Rep. Danish Oceanograph. Exped. 1908—1910 to the Mediterranean and adjacent Seas. Vol. II. H. I.

1926. — Medusæ. Part II, Anthomedusæ. — The Danish Ingolf Exped. Vol. V. Part 10.

1927. — The Hydromedusæ of the Danish Waters. — Mém. de l'Acad. des Sciences et des Lettres de Danemark. Sect. Sci. Sér. 8. T. XII. No. 1.

1928. — Hydromedusæ I. Anthomedusæ. — Papers from Dr. Th. Mortensen's Pacific Exped. XLIII. — Vidensk. Meddel. Dansk Naturhist. Foren. Bd. 85.

1930. — Hydromedusae collected in the south-western part of the North Sea . . . in 1903—1914. — Mém. du Musée R. d'Hist. Nat. de Belgique. Mém. No. 45.

1925. Kramp, P. & Damas, D. Les Méduses de la Norvège. I. — Vidensk. Meddel. Dansk Naturhist. Foren. Bd. 80.

1910. Kühn, A. Entwicklungsgeschichte und Verwandtschaftsbeziehungen der Hydrozoen. — Zoolog. Jahrb., Abt. Anatomie u. Ontogenie. Bd. 30 Heft 1.

1914. — In: Bronn, Klassen und Ordnungen des Thier-Reichs. Bd. II, Abth. 2, Coelenterata.

1884. Lendenfeld, R. v. The Australian Hydromedusæ. — Proc. Linn. Soc. New South Wales. Vol. 9.

1900a. Linko, A. Observations sur les Méduses de la Mer Blanche. — Trav. Soc. Imp. Natural. St. Pétersbourg. Vol. 29, Fasc. 4.

1900b. — Ueber den Bau der Augen bei den Hydromedusen. — Mém. Acad. Imp. Sci. St. Pétersbourg. Sér. 8. Vol. 10. No. 3.

1904. — Zoologische Studien im Barents-Meere. Hydromedusen. — Zoolog. Anzeiger. Bd. 28.

1893. Maas, O. Die craspedoten Medusen der Plankton-Expedition. — Ergebn. d. Plankton-Exped. Bd. II, K. c.

1904. — Bemerkungen zum System der Medusen. Revision der Cannotiden Haeckels. — Sitzber. d. math.-phys. Kl. d. Kgl. Bayer. Akad. d. Wissensch. Bd. 34. Heft 3.

1905. — Die craspedoten Medusen der Siboga-Expedition. — Siboga-Expeditie. Monogr. X.

1906. — Medusen. — Résultats du Voyage Belgica, Rapp. Sci., Zool.

1900. Mayer, A. G. Some Medusæ from the Tortugas, Florida. — Bull. Mus. Comp. Zool. Harvard Coll. Vol. 37. No. 2.

1904. — Medusæ of the Bahamas. — Mem. Nat. Sci. Mus., Brooklyn Inst. Arts., Sci. Vol. I. No. 1.

1910. — Medusæ of the World. Vol. I—III.

1886a. Metschnikoff, E. Medusologische Mittheilungen. — Arb. Zool. Inst. Wien. T. 6.

1886b. — Embryologische Studien an Medusen. — Wien.

1903. Murbach, L. & Shearer, C. On Medusae from the Coast of British Columbia and Alaska. — Proc. Zool. Soc. London, 1903.

1925. Ranson, G. Sur quelques Méduses des Côtes de la Manche. — Bull. Mus. d'hist. nat. Paris, 1925. No. 6.

1876a. Romanes, G. J. Preliminary Observations on the Locomotor System of Medusæ. — Philos. Trans. Royal Soc. London for 1876. Vol. 166.

1876b. — An Account of some new Species, Varieties, and Monstrous Forms of Medusæ. — Journ. Linn. Soc. London. Vol. XII.

1877. — do., Plates. — Ibid. Vol. XIII.

1835. Sars, M. Beskrivelser og Iagttagelser over nogle mærkelige eller nye i Havet ved den Bergenske Kyst levende Dyr. — Bergen.

1909. Torrey, H. B. The Leptomedusae of the San Diego Region. — Univ. of California Publ. in Zool. Vol. 6. No. 2.

1927. Uchida, T. Studies on Japanese Hydromedusae. 1. Anthomedusae. — Journ. Faculty of Sci., Tokyo. Sect. IV Zool. Vol. I. Part 3.

1891. Vanhöffen, E. Versuch einer natürlichen Gruppierung der Anthomedusen. — Zoolog. Anzeiger. No. 379.

1911. — Die Anthomedusen und Leptomedusen der Deutschen Tiefsee-Expedition 1898—99. — Wiss. Ergebn. d. Deutschen Tiefsee-Exped. ("Valdivia") 1898—1899. Bd. 19. Heft 5.

1912a. Vanhöffen, E. Die craspedoten Medusen der Deutschen Südpolar-Expedition. — Deutsche Südpol.-Exp. 1901—03. Bd. XIII. Zool. V.

1912b. — Die craspedoten Medusen des "Vettor Pisani". — Zoologica. Heft 67.

1895. Zoja, R. Sullo sviluppo dei blastomeri isolati dalle uova di alcune Meduse (e di altri organismi). — Arch. f. Entwickl. Mech. Bd. 2.

1896. — Una nuova Medusa (Octogonade mediterranea n. g. n. sp.). — Boll. scient., Anno 17. No. 3—4. 1 Pl. Pavia.

Alphabetical List of Genera and Species of Mitrocomidæ.

(Principal references in darker type, references to figures in *italics*.)

Explanation of Plate X.

Fig. 1. *Tiaropsidium japonicum* n. sp., type specimen. — × $3^1/_2$.

- 2. *Tiaropsidium japonicum* n. sp., part of bell margin, with one large, perradial tentacle, three rudimentary tentacles, and a lithocyst with ocellus.

- 3. *Mitrocomella polydiademata* (Romanes), part of bell margin of adult and well-preserved specimen from Millport, Scotland, all marginal cirri fully developed.

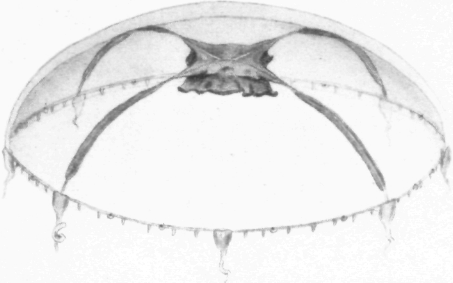
- 4. *Mitrocomella polydiademata* (Romanes), part of bell margin of specimen from Port Erin, with four fully developed cirri, all broken, and with five young cirri in different stages of development.

- 5. *Mitrocomella frigida* (Browne), type specimen, reconstructed. — × 5.

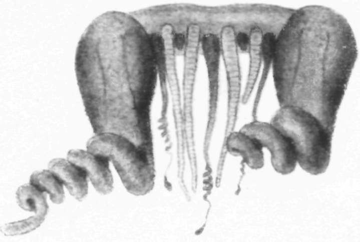
- 6. *Mitrocomella frigida* (Browne), part of bell margin with cirri in different stages of development.

cc circular canal, *rc* radial canal, *v* velum.

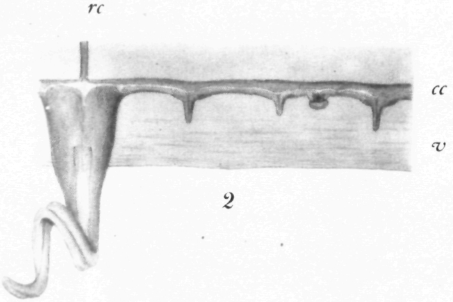
25.—11.—1931.



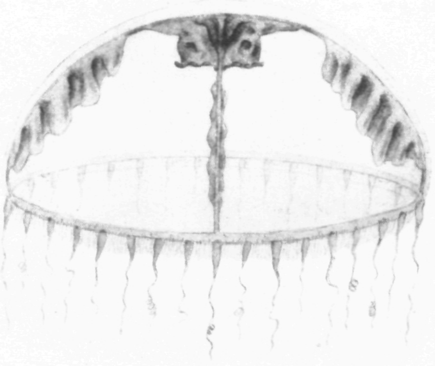
1



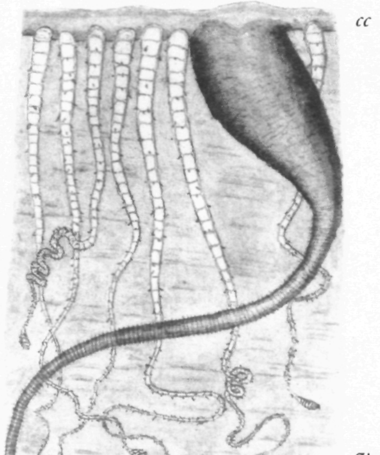
4



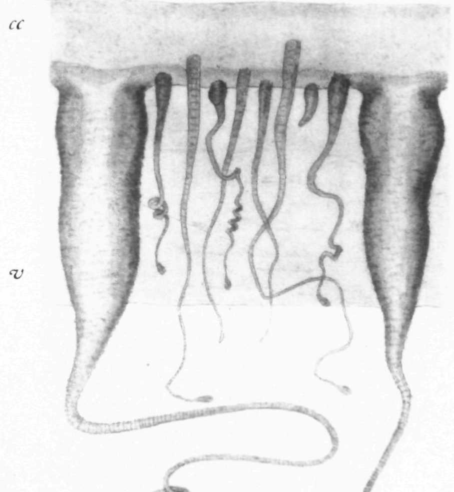
2



5



3



6

P. L. KRAMP DEL.

FOTOTYPI, PACHT & CRONES EFTF.

Dansk Résumé.

Overalt indenfor Zoologien maa Morfologi og Systematik danne Grundlaget for Biologi og Økologi. Fra et biologisk Synspunkt er Meduserne meget interessante Dyr, og de er velegnede som Indikatorer for Havstrømme; men for alle biologiske Formaal er det nødvendigt at kunne bestemme Arterne med Sikkerhed, og derfor maa Dyrene først beskrives og klassificeres. Medusernes Systematik er vanskelig, og for at udrede den maa man foretage komparativ-morfologiske Studier af saa mange Arter som muligt. I Indledningen (Kap. I) er Principperne for Leptolinernes (Antho- og Leptomedusernes) Systematik diskuterede, tildels med Henvisning til Forfatterens tidligere Arbejder, mens Afhandlingens Hovedindhold er en systematisk Revision af Familien *Mitrocomidæ:* Leptomeduser med aabne Randblærer.

Familien er opstillet af Metschnikoff (1886a) under Navnet *Lafoeidæ*, forandret til *Mitrocomidæ* af Torrey (1909); Familiens Historie er kort gennemgaaet i Kap. II. Efter en kritisk Gennemgang er en Del Arter udskudt af Familien (Kap. III), og derefter er Mitrocomidernes komparative Morfologi gennemgaaet saa detailleret som det foreliggende Materiale og Oplysningerne i Litteraturen har gjort det muligt (Kap. IV). Hvert Organsystem er beskrevet for sig, mest efter egne Iagttagelser, og i flere Tilfælde sammenlignet med tilsvarende Organer hos andre Leptomeduser. — I Kap. V er givet en Oversigt over Mitrocomidernes geografiske Udbredelse; de fleste tilhører Kystfarvandene i de tempererede Egne. Arterne har gennemgaaende en ringe Udbredelse, hvorimod de fleste Slægter er vidt udbredte.

Kap. VI giver nye Diagnoser af Slægterne og Beskrivelser af Arterne med Bemærkninger om deres Historie, Nomenklatur, Udvikling, Abnormiteter og Forekomst. Familien omfatter 9 Slægter med 18 sikre og 2 usikre Arter. Jeg har selv haft Lejlighed til at undersøge 13 Arter, dels i Zoologisk Museum i København, dels i British Museum og i Mr. E. T. Browne's Samling i Berkhamstead i England, hvor jeg opholdt mig i Efteraaret 1930.

Diagnoser af Slægterne.

Mitrocomella: 4 Radiærkanaler; 8, 12 eller 16 Randblærer uden Oceller; Randcirrer, der kan rulle sig spiralformet sammen (Spiralcirrer).

Mitrocoma: 4 Radiærkanaler; talrige Randblærer uden Oceller; Spiralcirrer.

Halopsis: mere end 8 Radiærkanaler; talrige Randblærer uden Oceller; Spiralcirrer.

Cosmetira: 4 Radiærkanaler; 8 Randblærer uden Oceller; Randcirrer, der ikke kan rulle sig spiralformet sammen.

Cosmetirella: 4 Radiærkanaler; 8 Randblærer uden Oceller; ingen Randcirrer.

Halistaura: 4 Radiærkanaler; talrige Randblærer uden Oceller; ingen Randcirrer.

Tiaropsis: 4 Radiærkanaler; 8 Randblærer, hver med en Ocel; kun een Slags Tentakler; ingen Randcirrer.

Tiaropsidium: 4 Radiærkanaler; 8 eller 16 Randblærer, hver med en Ocel; to Slags Tentakler; ingen Randcirrer.

Octogonade: 8 Radiærkanaler; talrige Randblærer, hver med en Ocel; to Slags Tentakler; ingen Randcirrer.

Arternes Kendetegn fremgaar af Tabellerne i Kap. VII, der tillige er et Forsøg paa at gruppere Slægter og Arter paa naturlig Maade. Slægterne kan samles i følgende fire Grupper:

I. *Mitrocomella*, *Mitrocoma* og *Halopsis*, med Spiralcirrer, der er forsynede med et distalt Nældebatteri. Cirrer af ganske samme Bygning findes hos mange andre Leptomeduser.

II. *Cosmetira*, med Randcirrer, der er stærkt kontraktile, men ikke kan rulle sig spiralformet sammen, og hvis Nældekapsler ikke er samlede i et distalt Batteri. Lignende Cirrer kendes foreløbig kun hos ganske enkelte andre Leptomeduser, og deres systematiske Betydning kan derfor ikke fastslaas.

III. *Cosmetirella* og *Halistaura*, uden Randcirrer og uden Oceller.

IV. *Tiaropsis*, *Tiaropsidium* og *Octogonade*, uden Randcirrer, med en Ocel ved Grunden af hver Randblære. Disse Oceller har en ejendommelig Bygning, der ikke kendes hos andre Hydromeduser.

Indenfor hver Gruppe kan Slægter og Arter ordnes i en nogenlunde fremadskridende Udviklingsrække. En tilsvarende Ordning af de fire Grupper kan derimod ikke foretages; Grupperne maa paa et tidligt Tidspunkt have udskilt sig fra hverandre og udviklet sig i hver sin Retning. Familiens systematiske Stilling indenfor Leptomedusernes Orden er vanskelig at bestemme, fordi de fleste andre Familier er daarligt definerede og mangelfuldt undersøgte i morfologisk Henseende.

Theses.

1. Den kønnede Generations Udviklingsgrad kan ikke benyttes som Slægtskarakter hos Hydroiderne; derimod kan Gonoforernes Bygning undertiden have systematisk Betydning.
2. Naar abnorm Udvikling af et Organ hos en Meduse forrykker Symmetrien, søges denne ofte genoprettet ved abnorm Udvikling af andre tilsvarende Organer.
3. Flere Arter af littorale Hydroider overvintrer uden Hydranther.
4. Pæleormen *Teredo megotara* er alternerende Hermafrodit.
5. Pælekrebsen, *Limnoria lignorum*, forplanter sig paa alle Tider af Aaret uden Afbrydelse om Vinteren.
6. C. G. J. Petersen har ved sine kvantitative Undersøgelser bidraget til en mere korrekt Forestilling om Dyrenes Fordeling paa Havbunden, men hans Inddeling af Bunddyrene i „Samfund“ er forfejlet.
7. Det er ikke paa Forhaand indlysende, at almindelige Dyr er særlig egnede til at karakterisere et „Samfund“ eller et faunistisk Omraade; thi netop visse almindelige Dyr er i Besiddelse af saa stor Tilpasningsevne, at de kan leve under meget forskellige Forhold, ledsagede af ganske forskellige Dyr de forskellige Steder.
8. Paa en given Lokalitet paa Havbunden reguleres Mængdeforholdet mellem Arterne vel tildels ved Næringskonkurrence og Tilstedeværelse af Rovdyr, men Faunaens kvalitative Sammensætning bestemmes ved de fysiske Faktorer.
9. Betegnelsen „Enaarige Dyr“ bør kun benyttes om saadanne, hvis Livscyklus af indre, fysiologiske og for Arten karakteristiske Aarsager ikke kan fortsættes udover et Aar.