THE SYSTEMATIC POSITION OF THE STAUROMEDUSAE

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With 2 Text-figures

The Stauromedusae have hitherto been referred together with the Cubomedusae to the subclass Scyphostomidae in the Scyphomedusae. Recently, however, the life cycle of the cubomedusa, *Tripedalia cystophora* became clear by WERNER, CUTRESS and STUDEBACKER (1971) and it was established that the Cubomedusae only stand in a quite separate position from other orders of Scyphomedusae. On the other hand, WERNER who published several papers on the Scyphozoan polyp, *Stephanoscyphus* (1966–1971) laid stress on the fact that *Stephanoscyphus* can be linked directly with the extinct fossil group of the Conulata and concluded that the Coronatae represent the most basic group of all living Scyphomedusae with the exception of Cubomedusae. Such being the case, the systematic position of the Stauromedusae remains problematical. The present writer is of the opinion that the Stauromedusae are to be entitled to the Ephyridae and are closely related to the Discomedusae, though there occurs no strobilation in the order.

The body of Stauromedusae is composed of two parts; the upper octomerous medusan part and the lower tetramerous scyphistoma portion. No strobilation and no ephyra. Throughout their life history, they lack pelagic life entirely; an egg develops to the solid blastula, which becomes to the planula. The planula is destitute of cilia, therefore it does not swim but only crawls on the substratum. The planula metamorphoses into a scyphistoma of which the upper part becomes medusa-like and the lower portion retains almost the characters of scyphistoma. Therefore, the Stauromedusae are different from other medusae belonging to the Ephyridae in the crawling planula and the lack of free ephyra. Besides, they do not show asexual reproduction, thence they alone are devoid of the alternation of generation in the Ephyridae. The reason why they lack the pelagic life throughout seems to be due to the fact that they are distributed in circumpolar regions as is often seen in other marine invertebrates in the circumboreal habitats. Judging from the facts that the Stauromedusae are generally found attached to sea weed only in shallow subtidal areas in cold waters and include so far only a few degenerated abyssal forms, it may be probable that the group has appeared rather recently and developed after the glacial periods. It seems to be probable that some ancestral forms of Discomedusae have lost the strobilation on account of low temperature and remained in the stage of Stauromedusae.

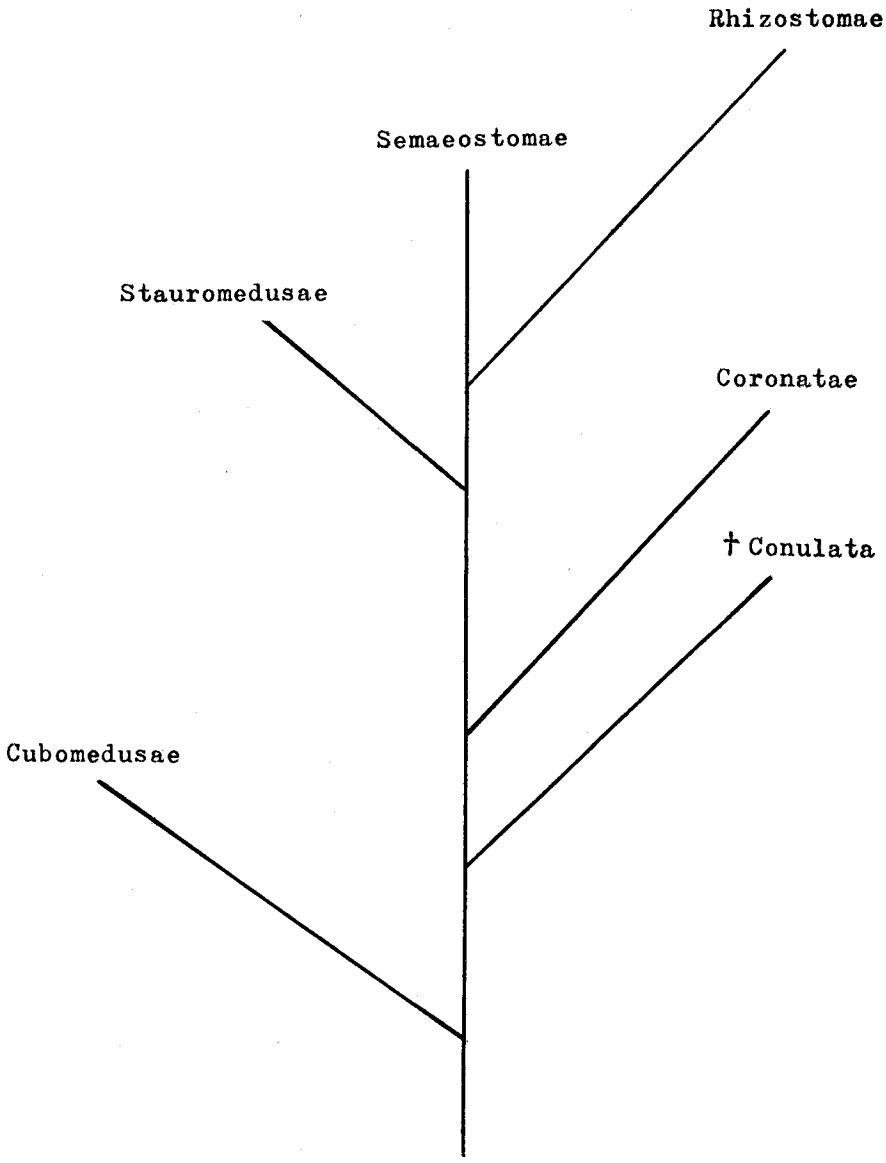

Fig. 1. Phylogeny of Scyphomedusae.

Therefore, the Coronatae, though giving rise to ephyra, are the most primitive in the living Scyphomedusae belonging to the Ephyridae as was pointed out by WERNER (1969) and the Stauromedusae consist of forms of the Ephyridae which have been influenced by special circumstances and have degenerated in structure as well as in life history. They are eligible to a side branch from the main stem including the Semaeostomae and

Rhizostomae in the Discomedusae.

As regards the Stauromedusae, it was customary to use the classification proposed by H. J. CLARK (1863) who divided the order into two families, Cleistocarpidae and Eleutherocarpidae. In 1887 C. VOGT instituted a family Lipkeidae basing on a single young specimen. ANTIPA (1893) denying VOGT's family proposed a new family Capriidae on a single specimen of *Capria sturdzii* which has 10 lappet-like arms without knobbed tentacles but with short tooth-like tentacles arranged in a row. In 1925 KRUMBACH divided the Stauromedusae into the two families of Eleutherocarpidae and Cleistocarpidae, in the former including *Lipkea*, *Capria*, *Stenoscyphus*, *Brochiella*, *Lucernaria*, *Kishinouyea*, *Thaumatoscyphus* and *Haliclystus*, and in the latter *Depastrella*, *Depastrum*, *Craterlophus* and *Halimocyathus*.

In 1929 T. UCHIDA proposed a new classification, with some emendations of the proceeding ones. According to him the Stauromedusae are classified as follows:

1) Family Lipkeidae VOGT, 1887: genus, *Lipkea*.

2) Family Haliclystidae HAECKEL, 1879=Eleutherocarpidae CLARK, 1863 (in part): genera, *Stenoscyphus*, *Haliclystus*, *Lucernaria*, *Lucernariopsis*, *Capria*.

3) Family Cleistocarpidae CLARK, 1863

a) Subfamily Depastrinae n. subfam.: genera, *Depastrum*, *Halimocyathus*, *Thaumatoscyphus*.

b) Subfamily Craterlophinae n. subfam.: genus, *Craterlophus*.

4) Family Kishinouyeidae n. fam.: genera, *Sasakiella*, *Kishinouyea*.

CARLGREN (1935) describing a new stalked medusa, *Depastromorpha africana* n. g. et n. sp., revised the classification as follows:

1) Family Cleistocarpidae

a) Sublamily Depastrinae, including the genera, *Depastrum* (*Depastrella*), *Depastromorpha*.

b) Subfamily Thaumatoscyphinae nov., including the genera, *Thaumatoscyphus* (*Brochiella*), *Halimocyathus*.

c) Subfamily Craterlophinae, including a genus *Craterlophus*.

2) Family Eleutherocarpidae

a) Subfamily Lucernariinae nov., including the genera, *Lucernaria*, *Haliclystus*, *Stenoscyphus*.

b) Subfamily Kishinouyiinae nov., including the genera, *Kishinouyea*, *Sasakiella*, *Lucernariopsis*.

c) Subfamily Lipkeinae, including a genus, *Lipkea* (*Capria*).

In the next year, THIEL (1936) nearly adopted UCHIDA's classification as follows:

1) Family Lipkeidae (very uncertain): genus, *Lipkea*.

2) Family Kishinouyeidae: genera, *Kishinouyea*, *Sasakiella*.

3) Family Haliclystidae: genera, *Capria*, *Lucernariopsis*, *Lucernaria*, *Haliclystus*, *Stenoscyphus*.

4) Family Cleistocarpidae: genera, *Depastrum*, *Depastromorpha*, *Brochiella*

(=*Thaumatoscyphus*), *Thaumatoscyphus*, *Halimocyathus*, *Craterlophus*.

As regards the classification of the Stauromedusae, KRAMP (1961) followed CARLGREN (1935) as stated below.

1) Family Eleutherocarpidae

a) Subfamily Lucernariinae, including the genera, *Haliclystus*, *Lucernaria*, *Stephanoscyphus*.

b) Subfamily Kishinouyeinae, including the genera, *Kishinouyea*, *Lucernariopsis*, *Sasakiella*.

c) Subfamily Lipkeinae, including the genus *Lipkea*.

2) Family Cleistocarpidae

a) Subfamily Depastrinae, including the genera, *Depastromorpha*, *Depastrum*.

b) Subfamily Thaumatoscyphinae, including the genera, *Brochiella*, *Halimocyathus*, *Thaumatoscyphus*.

c) Subfamily Craterlophinae, including the genus *Craterlophus*.

With regard to the distribution of the Stauromedusae, the 3 following regions are given: Northern Atlantic, Northern Pacific and Southern Hemisphere. In the Northern Atlantic are recorded the following genera, *Haliclystus*, *Lucernaria*, *Lucernariopsis*, *Lipkea*, *Depastrum*, *Brochiella*, *Thaumatoscyphus*, *Halimocyathus*, and *Craterlophus*. Of these genera, most species of *Lucernaria* are found in this region: seven in the Northern Atlantic and only one in the Antarctic. Three species of *Lipkea* are limitedly distributed in this region. *Halimocyathus* is only found in the area. From the Northern Pacific the following genera are reported: *Haliclystus*, *Stephanoscyphus*, *Kishinouyea*, *Sasakiella*, *Thaumatoscyphus*, and *Craterlophus* (from New Zealand). The three genera, *Stenoscyphus*, *Kishinouyea*, and *Sasakiella* are characteristic of the area. From the Southern Hemisphere, *Haliclystus*, *Lucernaria*, *Lucernariopsis* and *Depastromorpha* are recorded. The 3 former genera are also found in the Northern Atlantic and *Depastromorpha* is closely allied to *Depastrum* found in the Atlantic. It is strikingly noticeable that the family Lipkeidae UCHIDA, 1929 are restricted in distribution in the Northern Atlantic, while the family Kishinouyeidae UCHIDA, 1929 are distributed in the temperate regions of the Northern Pacific. It is also noticeable that the genus *Haliclystus* is commonly found in the three regions above mentioned.

The present author (1929) pointed out that the Lipkeidae are the most primitive group in the Stauromedusae, because he thought at that time that the Stauromedusae have been originated from the scyphistoma directly. THIEL (1936) gives the genealogical tree of the order (p. 165), placing *Lipkea* as the most basic genus. The writer is, however, at present of the opinion that *Lipkea* is a degenerated stalked medusa from the standard form. As stated above, the Stauromedusae have not directly developed from the primitive scyphistoma but possibly represent a side branch from the ancester of Semaeostomae.

Here we confront with the problem which genus of stalked medusae is the most

basic standard type. The author nominates *Haliclystus* as such, because the genus is not only distributed in the three regions, the Northern Atlantic, Northern Pacific and Antarctic, but also it retains a nearly complete form with upper ephyral characters and lower scyphistoma features. The upper part, calyx, is octomerous in symmetry and bears eight anchors, four on the perradial and four on the interradial margin, and eight adradial clusters of knobbed tentacles. The peduncle is tetramerous in symmetry, four-chambered and provided with four interradial muscle strands. The stomach is divided into four radial pockets and has no mesogonial pockets. There are four interradial clusters of gastral filaments and four paired interradial gonads. Instead of pelagic life, the stalked medusa becomes sessile in life, therefore, the sense organs of ephyra have transformed into the anchors. The presence of eight adradial clusters of tentacles is seen in the Cyaneidae in the Semaeostomae. In the development of the stalked medusae, the upper part alone metamorphoses, while the lower part remains unchanged as in the case of strobilation. From the standard form of *Haliclystus*, some parts will differentiate, while some portions will degenerate, and thus other stalked medusae seem to have been derived. For these characters the following ones are enumerated: symmetry, mesogonial pockets, anchors, adradial tentacles, coronal muscles, muscle strands and canals in the stalk.

As to the symmetry of the stalked medusae, the calyx is primarily octomerous and the stalk is always tetramerous. *Stephanoscyphus* and some of *Lucernaria* show the tendency to be tetramerous in symmetry, while *Kishinouyea* and *Sasakiella* indicate the strikingly tetramerous symmetry. In this case tetramerous symmetry has been obviously derived from octomerous one. In the Cleistocarpidae are found mesogonial pockets which are formed by differentiation of the claustrum which divides each of the four perradial stomach pouches into an outer space and an inner one. The formation of the mesogonial pockets means a remarkable differentiation of the internal structure. The anchors themselves are degenerated sensory organs in swimming medusae. They are metamorphosed from the perradial and interradial tentacles. Some genera, such as *Lucernaria*, *Lucernariopsis* and *Kishinouyea*, are destitute of the organ, showing an instance of degeneration. In the Cleistocarpidae, the adradial tentacles are disposed to form several rows on the whole margin of the calyx instead of the arrangement in clusters as in the Haliclystidae and Kishinouyeidae. The muscle strands in the stalk are lacking in some stalked medusae, such as *Lucernariopsis*, *Kishinouyea* and *Sasakiella*. This shows another instance of degeneration. The canals of the stalk are generally four, but in the genera mentioned above they are often united to a single crossed form in cross section. In these stalked medusae the stalk is relatively short and not well-developed. These medusae are comparatively liable to be detached from the substratum in living, so far observed in Japanese medusae.

The writer is of the opinion that, so far as the phylogeny concerns, the differentiated features must be valued, while the degenerated characters are less valued. Therefore, the symmetry and the mesogonial pockets are more important than the degeneration

of muscle strands in the stalk. CARLGREN (1935) proposed subfamily Kishinouyeinae, including *Kishinouyea*, *Lucernariopsis* and *Sasakiella*, because these genera lack the muscle strands in the stalk. But *Kishinouyea* and *Sasakiella* are tetramerous, though secondarily, in symmetry, while *Lucernariopsis* retains the original octomerous symmetry. It seems to the author that *Lucernariopsis* is a degenerate form of *Lucernaria* and can not be grouped together with *Kishinouyea* and *Sasakiella*. The two genera just referred to are both distributed only in temperate regions of the Northern Pacific and are found attached to *Sargassum*. LING (1939) recorded *Sasakiella* from Tsingtao (N. 36°, E. 120°), on the coast of Central China, where is the most southern limit of distribution of the Stauromedusae. The two genera seem to be the specialized forms in the shape of tetramerous symmetry and in the limited distribution. Therefore, the Kishinouyeidae must be separated as distinct one from other families.

Then, the writer wants to divide the Stauromedusae into the following four families; Haliclystidae (=Eleutherocarpidae), Lipkeidae, Kishinouyeidae and Cleistocarpidae. The Haliclystidae are the standard family and the Lipkeidae have branched out from the standard form in the primitive state, invaded the deeper portion of the sea and degenerated in structure. The Kishinouyeidae are adapted to rather warmer currents, attached to *Sargassum* and degenerated in the muscle strands in the stalk but differentiated to take the tetramerous symmetry. The Cleistocarpidae

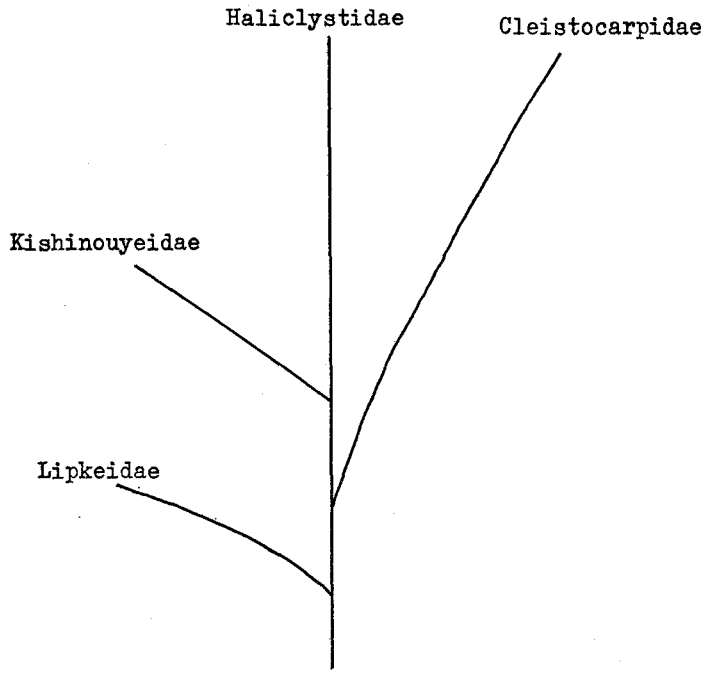

Fig. 2. Interrelationships in the Stauromedusae.

are a well-differentiated group with mesogonial pockets, sometimes adradial tentacles encircling the bell margin and the well-developed stalk. The writer agrees with CARLGREN's system (1935) in dividing the family into the following three subfamilies; Depastrinae, Thaumatoscyphinae and Craterlophinae. Of these subfamilies the Thaumatoscyphinae are the most standard one, the Depastrinae are modified in the calyx and the Craterlophinae are degenerated in the stalk.

LITERATURE

BERRILL, M. 1961. The biology of three new England Stauromedusae, with a description of a new species. Canadian Jour. Zool., vol. 40, pp. 1249–1262.

———— 1963. Comparative functional morphology of the Stauromedusae. *ibid.*, vol. 41, pp. 741–752.

CARLGREN, O. 1930. Die Lucernariden. Further Zool. Res. Swedish Antarc. Exped. 1901–1903. pp. 1–18.

———— 1933. Zur Kenntnis der Lucernariiden, *Lepkea*, *Capria* und *Brochiella*. Lunds Univer. Årss. N.F. Avd. 2, Bd. 29, No. 3, pp. 1–19.

———— 1935. Ueber eine neue Südafrikanische Lucernariidae, *Depastromorpha africana* n. gen. n. sp., nebst Bemerkungen über den Bau und die Systematik dieser Tiergruppe. Kungl. Svenska Vetens. Handl. 3 ser., Bd. 15, No. 1, pp. 1–24.

KRAMP, P. L. 1961. Synopsis of the medusae of the world. Jour. Mar. Biol. Ass. Un. Kingd., vol. 40, pp. 1–469.

LING, S. W. 1939. Studies on Chinese Stauromedusae. II. Further studies on some Stauromedusae from China. Lingnan Sci. J., vol. 18, pp. 281–291, and vol. 18, pp. 495–504.

THIEL, M. E. 1936. Bronns Klassen und Ordnungen des Tierreichs. Bd. 2. Scyphomedusae, pp. 1–172.

UCHIDA, T. 1929. Studies on the Stauromedusae and Cubomedusae, with special reference to their metamorphosis. Jap. Jour. Zool., vol. 2, pp. 103–193, pls. 3–5.

———— 1969. The interrelationships of Scyphozoan classes. Bull. Mar. Biol. Stat. Asamushi, Tohoku Univ., vol. 13, pp. 247–250.

WERNER, B. 1966. *Stephanoscyphus* (Scyphozoa, Coronatae) und seine direkte Abstammung von den fossilen Conulata. Helgoländer wiss. Meeresunters., Bd. 13, pp. 317–347.

———— 1969. Neue Beitrage zur Evolution der Scyphozoa und Cnidaria. Simp. Intern. Zoofilog., pp. 223–244.

———— 1971. Ein neuer, bisher unbekannter Entwicklungsmodus bei einem Scyphopolypen. Experientia, vol. 27, pp. 351–353.

———— 1971. *Stephanoscyphus planulophorus* n. spec., ein neuer Scyphopolyp mit einem neuen Entwicklungsmodus. Helgoländer wiss. Meeresunters., Bd. 22, pp. 120–140.

————, C. E. CUTRESS & J. P. STUDEBAKER, 1971. Life cycle of *Tripedalia cystophora* CONANT (Cubomedusae). Nature, vol. 232, pp. 582–583.