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Two Phylogenetic Lines of Coelenterates from the Viewpoint of Symmetry¹⁾

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(With 4 Text-figures)

The morphological features of adult Coelenterates and Echinoderms are often reported that they are radially symmetrical. But it seems to be phylogenetically reasonable to take consideration of developmental processes for the discussion of animal symmetry. For instance, the Echinoderms show pentamerous radial symmetry in the adult but their larvae are generally bilaterally symmetrical. Moreover, the radial symmetry of the adult is obviously secondarily derived: the left larval mesocoel develops and forms the pentamerous circular canals, and subsequently pentaradiate animals are formed. In reference to the developmental processes the Hydrozoa and Scyphozoa are evidently animals of radial symmetry, while the Anthozoa are those of bilateral symmetry.

Firstly the Hydrozoa are radially symmetrical in their polyps and also in medusae. Hydropolyps are furnished with a round mouth and one or two whorls of tentacles, which are arranged radially. A few bilateral forms such as *Branchiocerianthus* and *Proboscidactyla* (=Lar) may be derived from the typical form. Young polyps are generally observed to have four tentacles. But sometimes these tentacles do not appear synchronously; often one opposing pair proceeds the other pair.

It is generally admitted that the most primitive hydromedusa is represented by the anthomedusan genus *Sarsia*. The medusa has four radial canals, four hollow marginal tentacles and a manubrium with a round mouth, encircled by a gonad. In the higher types of other hydromedusan genera, the manubrium becomes four-sided; radial canals and tentacles increase fourfold; and the gonad becomes divided into four (sometimes eight) masses. The increase of tentacles occurs successively at definite points in each tetrant or in each octant, radial symmetry generally being retained.

The sequences of appearance of marginal tentacles will be summarized as follows;

1) Contributions from the Akkeshi Marine Biological Station, No. 122.
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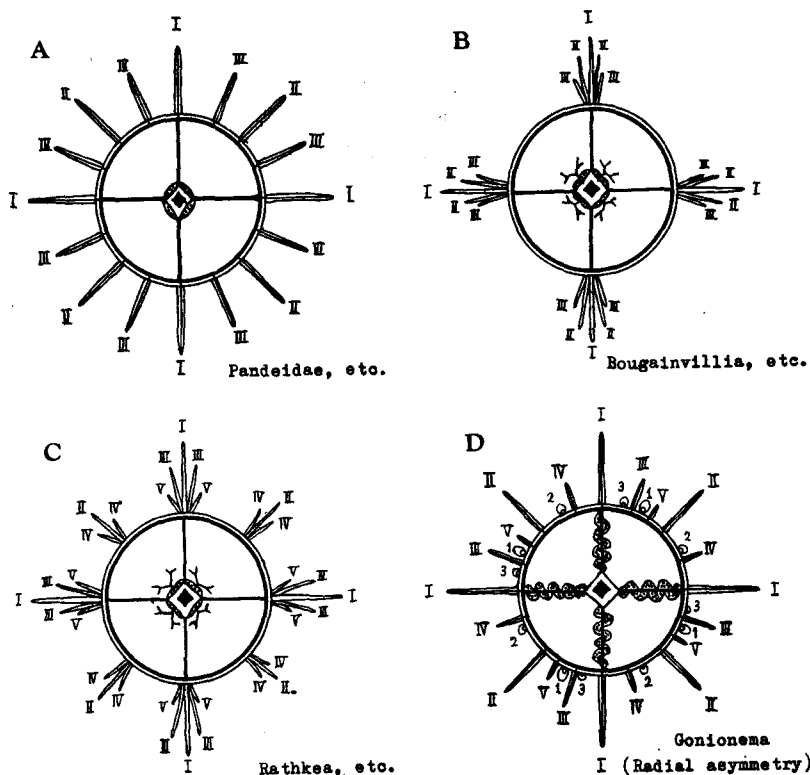


Fig. 1. The sequences of appearance of marginal tentacles in Hydromedusae: A. Most of hydromedusae including Pandeidae; B. Most of Bougainvilliidae; C. *Rathkea*, *Köllikeria* etc.; D. Olindiadae e.g. *Gonionema*. Tentacles arise from growing points which are distributed in radial-symmetrical arrangement.

a. Medusae belonging to the Pandeidae of Anthomedusae, most of Limnomedusae and Leptomedusae are subject to the following sequence in appearance of tentacles. The youngest medusa has a four-sided manubrium, generally four radial canals, and four marginal primary tentacles, one in each perradius. The second set of tentacles arises in each interradius, the third set in each adradius, and the fourth in each eradius, and so on. Therefore, the tentacles are counted 4, 8, 16, 32, and so on. From the arrangement of tentacles, the medusae are always radially symmetrical (Fig. 1, A).

b. Some hydromedusae belonging to the Bougainvilliidae, such as *Bougainvillia* and *Nemopsis*, have four oral tentacles and four clusters of solid marginal tentacles, one in each perradius. There are one or two primary tentacles; and the secondary and tertiary tentacles appear one by one on their both sides.

Other medusae belonging to the Bougainvilliidae such as *Rathkea* and *Köllikeria*, have four oral tentacles and eight clusters of solid marginal tentacles, one in each perradius and interradius. The mode of increase of tentacles is similar to the case just mentioned, though they are octomerous in structure. The medusa *Spirocodon* with hollow tentacles follows this mode (Fig. 1, B & C).

c. Some genera belonging to the Limnomedusae such as: *Gonionema*, *Scolionema* and *Eperetmus* and the trachomedusa *Petasiella* are eligible for a group which is named the group of radial asymmetry. In these medusae the secondary tentacles appear close to the statocyst in the interradius at first, but gradually shift away from it with the enlargement of the margin. Tentacles of the third and fourth series also follow the same pattern (Fig. 1, D).

Judging from the mode of appearance of tentacles, the Hydromedusae seem to belong to the group of radial symmetry.

The Scyphozoa are tetramerously symmetrical as polyps and medusae. In the scyphopolyp the mouth is four-sided; enteric cavity is divided into four chambers by four septa; the tentacles are at first four in number and increase gradually to 16 or more by multiples of four. The tentacles arise first at the perradii, secondly at the interradii, thirdly at adradii, etc.

In the Scyphomedusae the tetramerous symmetry is very obvious; they have a four-sided mouth (Cubomedusae, Stauromedusae and ephyrae of higher orders), four oral arms (Semaestomae) or eight oral arms (Rhizostomae), four gonads, each with a cluster of gastral filaments and four radial pockets (Cubomedusae and Stauromedusae) or eight divisions of canal system (Semaestomae and Rhizostomae). Moreover, the sensory organs are generally eight (four in Cubomedusae) and the marginal lappets and tentacles increase in multiples of eight.

From the metamorphosis of them, it is clear that the two classes, Hydrozoa and Scyphozoa, have several growing points which are radially arranged.

It is well known that all members of the Anthozoa are morphologically of biradial symmetry, showing serial grades of bilaterality. The Octocorallia have a special dorsal pair of mesenteries besides three ventral pairs. The Actinaria, Madreporaria, Zoantharia, and Antipatharia are all bilaterally symmetrical, viewed from the arrangement of their mesenteries. Moreover, at their larval stages, so far as is known, they have all three pairs of mesenteries arranged bilaterally. Their presence of one or two siphonoglyphs is also a bilateral feature. The anthozoans here considered are generally known as biradial forms, because they indicate fairly radial feature. Though they are bilateral in form, these anthozoans have many growing points radially arranged of mesenteries and tentacles. In the possession of these growing points, they agree with the Hydrozoa and Scyphozoa. The palaeozoic Tetracorallia were always bilateral in the arrangement of the mesenteries at first but gradually tended to be tetramerous.

Among the Anthozoa the Ceriantharia, in spite of an external appearance of radial symmetry, are typically bilateral animals. Their young pelagic forms have

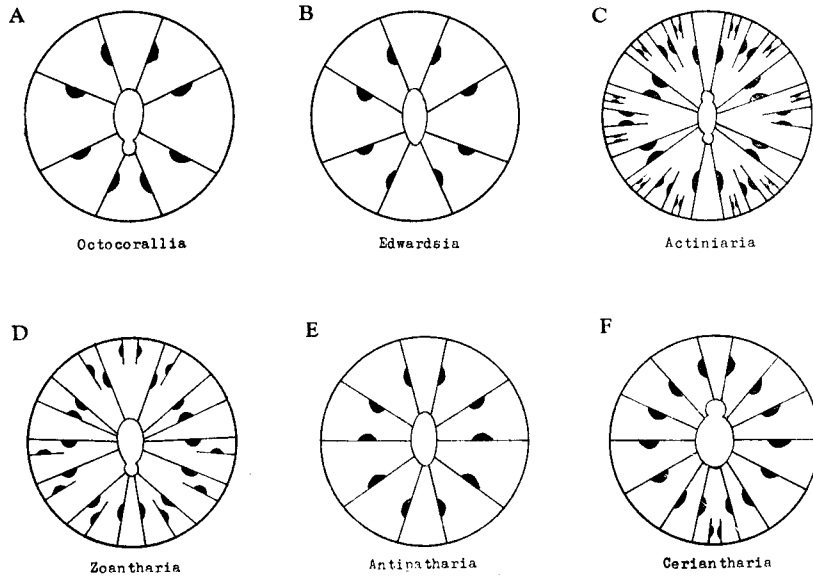


Fig. 2. Several grades of biradial symmetry to bilateral symmetry in the Anthozoa: A. Octocorallia; B. *Edwardsia* (primitive stage of Actiniaria); C. Actiniaria; D. Zoantharia; E. Antipatharia; F. Ceriantharia. From the arrangement of mesenteries all the Anthozoa are bilateral symmetrical, but they become to have the tendency of radial symmetry, since new mesenteries appear from growing points which are arranged radial-symmetrically. The tendency is pronounced in Actiniaria. The Ceriantharia alone have one growing point and show the typical bilateral symmetry.

three pairs of mesenteries at first and new mesenteries appear in pair always at a growing point, resulting in a quadrimesentery. New tentacles always arise in pairs from the growing point corresponding to that of the mesenteries.

As to the interrelationships between the coelenterate classes, the following conclusion may be derived. All the coelenterates have the planula as the first larva just hatched from the egg. It seems highly probable to me that the coelenterates developed from a planuloid ancestor as Hyman (1940) and Hand (1959) have also conjectured. Among the three classes of the coelenterates, the Hydrozoa seem to stand separate from other two classes, Scyphozoa and Anthozoa, in having sexual cells of ectodermal origin and in lacking septa and gastral or mesenterial filaments. The primitive form of the Hydrozoa has been reconstructed as a pelagic actinula-like creatures by Brooks (1886). It was differentiated into sessile polyps as well as into pelagic medusae. The primitive polyp was naked and has probably four marginal tentacles and devoid of septa. These primitive polyps remained solitary and acquired the burrowing habit, showing the alternation of generation. The primitive medusa is rather similar to medusae belonging to the recent genus

Sarsia. The sessile polyps seem to be secondarily organized; some subsequently formed colonies and secreted periderm. The Hydrozoa retained radial symmetry of the primitive form.

The Scyphozoa and Anthozoa have several common characteristics with each other in sexual cells of endoderm origin and in the possession of septa, gastral or mesenterial filaments. But they were probably divided into two groups at the stage of planula: one having the anlage of radial symmetry and the other that of bilateral symmetry. The scyphozoa belong to the former group and the Anthozoa

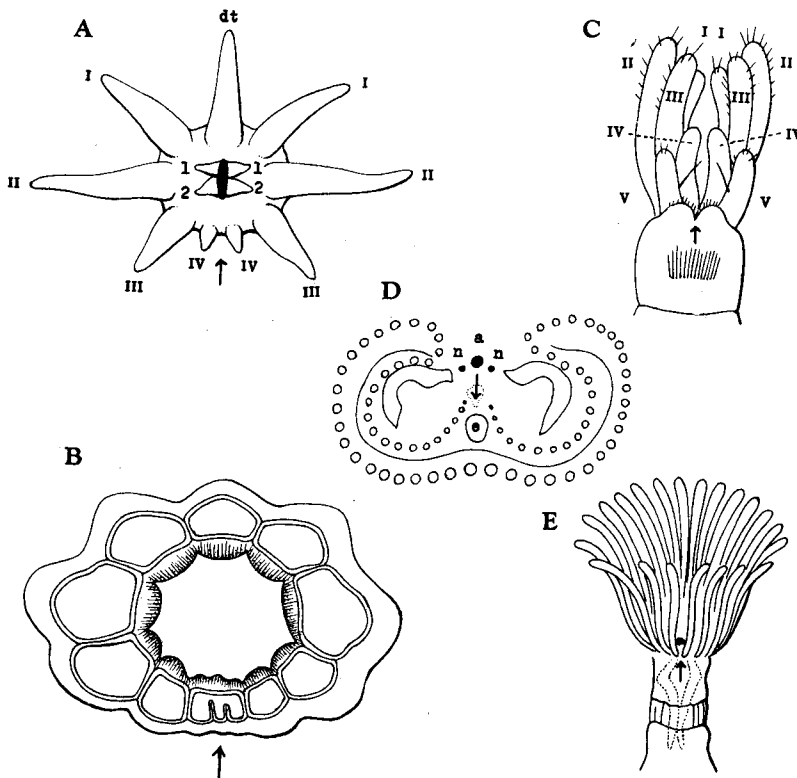


Fig. 3. Bilaterality of Ceriantharia and animals, in which their tentacles are often reported as radially arranged. A. *Arachnactis* (Ceriantharia larva); B. Arrangement of mesenteries of *arachnactis* (A & B were reformed from Nyholm's original, 1943); C. Branchial lobes of a polychaete, *Chone teres*, just metamorphosed (Okuda, 1946); D. Arrangement of tentacles of *Phoronis*; E. Arrangement of a bryozoan *Alcyonidium* (Bronho, 1939). In these animals tentacles of the adult are seemingly arranged in radial symmetry, but they have only one median growing point of tentacles and mesenteries (in Ceriantharia). They are all bilateral in strict sense. I, II, III, IV, V show the series of tentacles due to sequence of appearance. a anus; dt directive tentacle; e epistome; n nephridial pore; ↑ growing point.

to the latter one.

The primitive scyphopolyp seems to be not very different from the recent form. It had possibly four (or eight) tentacles, four septa, and four clusters of gastral filaments. Some scyphopolyps developed into chitinized colonial forms as in the fossil Conulariida and recent *Stephanoscyphus*, but most have remained solitary and did not show much elaboration as sessile polyps. By contrast the Scyphozoa have differentiated in a high degree as medusae, pelagic forms preserving the tetramerous shape of the polyps. The floating habit of the medusa seems to coincide with the radially symmetrical body.

In the Anthozoa their planula seems to have the tendency to be bilaterally symmetrical. In their swimming stage are observed to develop three pairs of mesenteries which are arranged in bilateral symmetry. The most primitive polyp was probably naked, small, and equipped with three pairs of septa, arranged bilaterally. It possibly dwelt in the sandy bottom, inserting its body perpendicularly. The recent Ceriantharians retaining the primitive life-cycle and habits, seem to be well-elaborated forms. Most anthopolyps lost the pelagic life and became sessile, attached to littoral rocks, and secreted a calcareous skeleton like the recent Madreporaria; and some of them, attached to the substratum at a rather great depth, secreted a horny substance in their axis and calcareous material on their surface as seen in the recent Gorgonaria and Antipatharia. The Actiniaria evolved rather well-developed muscles and are now able to move themselves slowly on the substratum to which they are attached. The Pennatulids were probably completely sessile animals at one time, but have regained a limited degree of locomotive ability.

As to the radial arrangement of tentacles, the Ceriantharia agree with the Phoronidea, Bryozoa, Endoprocta and some sedentary Polychaeta (Fig. 3). Though the tentacles of these groups are seemingly radially arranged, new tentacles arise always from a growing point. The fact shows the bilaterality of these animals. It can not be decided whether the biradiality of other anthozoarians is attributable to their original character or due to the adaptation of sessile life. At any rate, the Anthozoa are the bilateral animals.

It is generally known that there are several primitive animals that are found in the sandy bottom of the sea. One can enumerate them as follows: cephalocarid *Hutchinsoniella* in the Crustacea; monoplacophoran *Neopilina* and ammonites in the Mollusca; *Lingula* in the Brachiopoda; *Amphioxus* in the Prochordata; Pogonophora; synaptids in the Holothurian etc. In the coelenterates, sandburrowing coelenterates *Corymorpha*-allies and *Cerianthus* seem to be primitive, though well-developed forms in the Hydrozoa and Anthozoa respectively. They coincide with each other in having pelagic larval forms (actinula or arachnactis) and afterwards sinking to the bottom, where they exhibit burrowing habits in sandy flats. But they are in contrast as to the symmetry: *Corymorpha*-allies have a radially symmetrical stalk, with a dozen longitudinal canals arranged radially

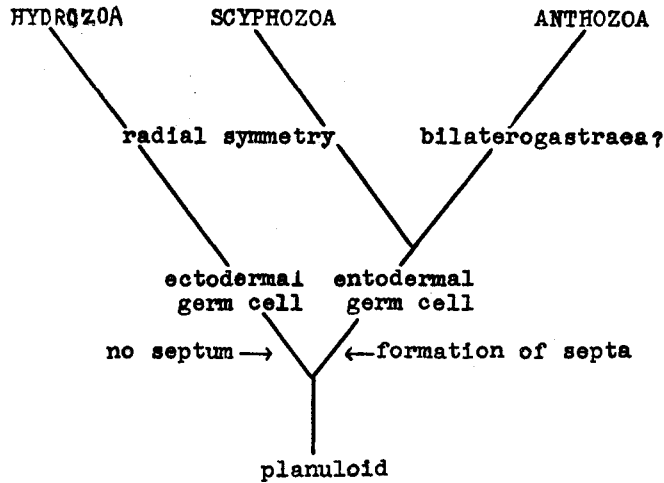


Fig. 4. Phylogenetic tree of Coelenterata.

on the periphery, whereas *Cerianthus* has a bilaterally symmetrical column with many septa that increase pair-wise from a limited ventral region.

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