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Symmetry of actinians and its significance for the classification of Anthozoa

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Characteristics of body symmetry have long served as a basis of the taxonomy of Coelenterata. The principle of dividing the group by the number of antimers was first proposed by Ehrenberg (1834) for defining the limits of Anthozoa, Octactinia, and Plyactinia [sic]. Later the method was used by Haeckel (1866) for separating Tetracorallia, Octocorallia and Hexacorallia. However, it was later justifiably noted by the brothers Hertwig (Hertwig, O., Hertwig, R. 1879) that for the classification of Anthozoa, more important were not the number of radially-symmetrical organs but their orientation and sequence of insertion.

The symmetry of coral polyps is determined by the number of mesenteries and sclerosepta. The number of tentacles is often strictly equal to the number of mesenteries (Actiniidae of order Actiniaria), although sometimes growth of the tentacles is slightly ahead of or behind that of the mesenteries. The marginal spherules, vesicles, and verrucae present on the body of many actinians (Actinia, Anthopleura, Bunodactis, Cribrinopsis of family Actiniidae) are obviously determined by tentacles. They are located under each tentacle or under the largest tentacles singly or in longitudinal lines. Among representatives of the number of families (Actinodendridae [sic], Thallassianthidae [sic], Aurelianidae, Minyadidae, Homostichanthidae, Stoichactiidae, Phimananthiidae [sic] of order Actiniaria) with each endocoel and exocoel connected to not one but several tentacles. But in each case are observed a correlation between number of tentacles, marginal spherules and vesicles, verrucae and number of mesenteries. So with regard to symmetry of the "soft" corals, first of all attention is directed to the location of the mesenterial pairs and among animals to the presence of calcareous skeleton – to the location of sclerosepta, i.e. to the characteristics most accessible for study in collected specimens.

Contemporary systematics of actinians, the foundation for which was made by Richard Hertwig during study of material of the expedition of the ship "Challenger" (Hertwig, 1882), is based on characteristics of internal organization of the polyp. Thanks to it, anatomy of the species is well known. Within the order Actiniaria to the present time are described groups with strict radial symmetry and also some that have clear symptoms of bilateral symmetry. Among radially symmetrical there are penta-, hexa-, hepta-, octa- and deca-meral representatives. The number of antimers here has wider variation than in all other Anthozoa, therefore the impression is created of great variety of symmetrical forms. For true understanding of that phenomenon we should observe how the sequence of symmetry is determined during development of a polyp. [end page 101]

TRANSFORMATION OF SYMMETRY IN ONTOGENESIS

Edwardsia stage

Independence of the order Actiniaria was essentially founded by the brothers Hertwig (Hertwig, O., Hertwig R., 1879) thanks to description of the development of the mesenterial cycles of Alcyonaria, Ceriantharia, Zoantharia and Actiniaria. It was discovered that actinians have two variants of location of the first 8 mesenteries: the first is the type of Aiptasia diaphana* (Rapp, 1829) and Edwardsia tuberculata Düben et Koren, 1847. On the basis of this Edwardsiidae (in modern terms, a family of the order Actiniaria) were regarded as of the same taxonomic rank as Actiniaria.

*the Hertwigs called it Adamsia diaphana

Among the 8 oldest mesenteries in Aiptasia (Figure 1: 2, 4), 2 pairs of directive mesenteries, adhering to the narrow sides of the flattened actinopharynx, have turned their muscle bundles in opposite directions. The 4 lateral mesenteries are turned with their muscle bundles in pairs head to head with each other. In such a way, a young polyp of Aiptasia already in the 8-mesentery stage has two different planes of symmetry, and consequently, has biradial symmetry.

Without questioning the correctness of the Hertwig brothers' observation about the development of Aiptasia, we have to admit that most actinians, if not all, as Pax (1925) states, pass through the stage traditionally called the Edwardsia stage (Figure 1: 1, 3). Subsequent researchers did not note development of an Aiptasia type. At the Edwardsia stage, a polyp has 8 radially located mesenteries. 4 of them form 2 diametrically-opposite lying pairs of directive mesenteries supporting siphonoglyphs in adult polyps. The mesenteries unified in directive pairs have turned muscle bundles in different directions. 4 other lateral mesenteries have directed their muscle bundles in the way of one of the directive pairs. This pair is customarily called ventral, the one opposite to it dorsal. Thanks to the disposition of the muscle bundles, on one -- the ventral – side of all lateral mesenteries, a polyp in the Edwardsia stage has characteristics of bilateral symmetry and has only one plane of symmetry. It is possible that the brothers Hertwig observed young specimens of Edwardsia because adult polyps of any sufficiently described species of actinians do not stop at the Edwardsia stage and have a greater number of mesenteries.

Halcampula stage

After development of the eight mesenteries attached to the actinopharynx, one more mesenterial rudiment appears near each of the lateral mesenteries on the ventral side. In such forms, grown polyps with 12 primary mesenteries (8 micromesenteries and 4 undeveloped micromesenteries) are found only in Edwardsiidae (Halcampogeton, some species of Edwardsia and other genera). In other actinians, all 12 mesenteries of the first cycle soon equalize in size. The directive pairs as usual bear the muscle bundles on the outer side of the mesenteries. The lateral pairs are made from mesenteries that have their muscle bundles turned toward each other. In this stage (Halcampula stage; Figure 1: 5, 6), characterized by the presence of 6 pairs of primary mesenteries (protomesenteries or protocnemes), the polyp begins to lose its characteristic bilateral symmetry and becomes radially symmetrical. The presence of 2 (more rarely 1) [bottom page 102] siphonoglyphs attached to the directive mesenterial pairs gives to the body of the animal the characteristic biradial symmetry that persists to the end of its life. On the other hand, the presence of the 6 pairs of protomesenteries determines the dominant hexameral symmetry, which is often lost in later development, but serves, as we will see, as the starting type of symmetry for all coral polyps, passing through the Halcampula stage.

The development of metamesenteries

As is known, the increase in number of mesenteries ends at the Halcampula stage only in one species of actinian – Halcampoides purpurea (Studer, 1878) of family Halcampoididae (Figure 1: 6). In all other actinians, after the first cycle of mesenteries forms – 6 pairs of protomesenteries – one or several cycles of metamesenteries develop. Metamesenteries appear at once in pairs; in most families their development originates in the exocoels. Pairs of the second cycle (first metamesenteries) appear in between the pairs of the first cycle, i.e., in the exocoels of the first order. The third cycle develops between pairs of the first and the second cycle in the exocoels of the second order, and so forth. The number of exocoels of the following order is twice as great as that in the previous; the number of mesenterial pairs grows in geometric progression: 6 pairs of first + 6 pairs of second + 12 pairs of third +24 pairs of the fourth cycle … + = $6 \times 2^{n-1}$, where n is the number of mesenterial cycles. During synchronous development of the mesenterial pairs, the hexameral symmetry formed in the Halcampula stage is preserved in the large adult polyps, which have passed through many cycles of mesenterial development. As an example, Hormathia digitata (Müller, 1776) could serve. Among dozens of examined specimens of this species I did not find any case of disrupted symmetry.

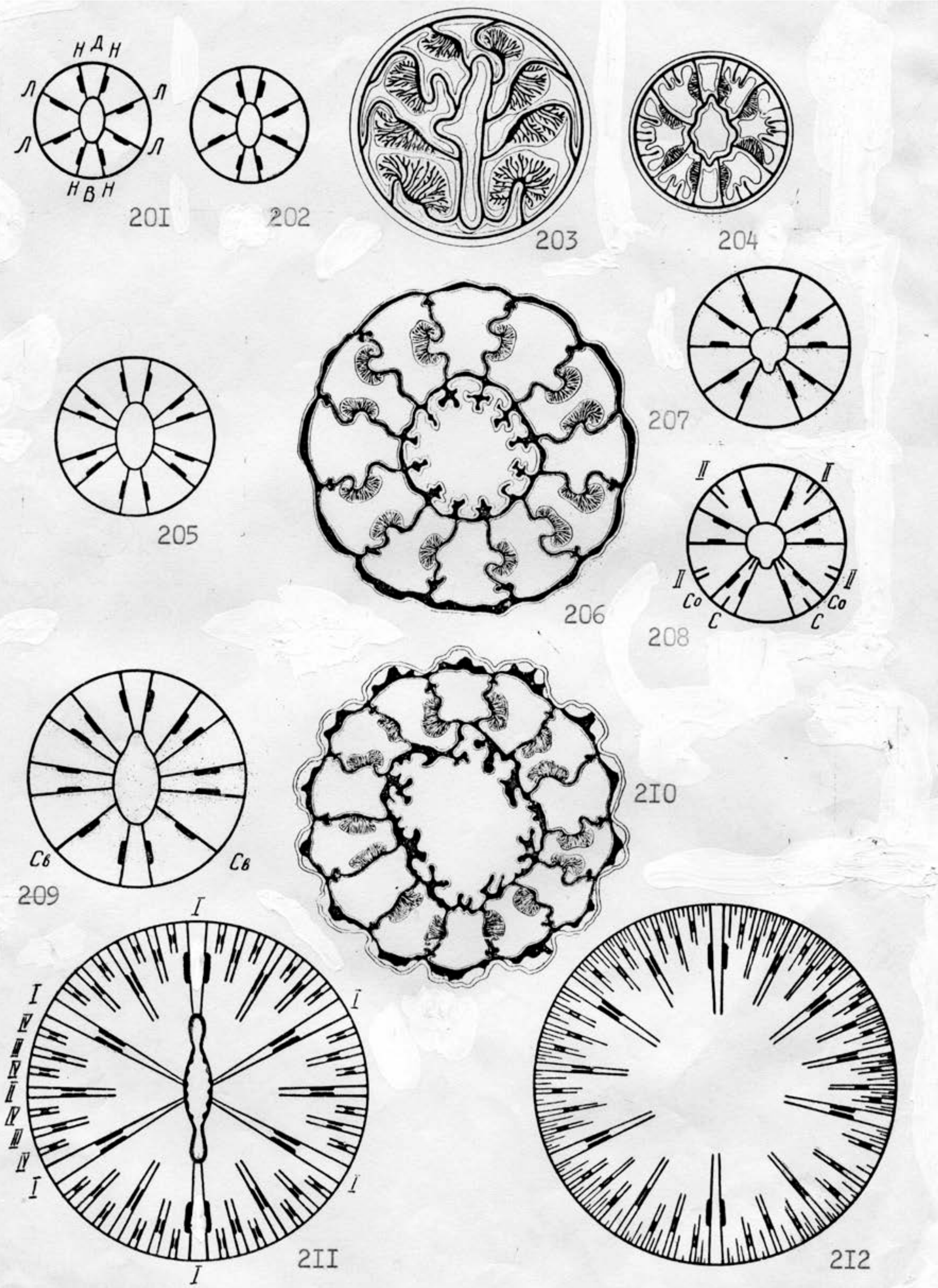


Рис.20I-2I2. Расположение мезентериев у молоди и взрослых пента-, гекса- и гептамерных актиний. (Обозначения см. след.стр.)

ABERRANT FORMS OF SYMMETRY

The Actinostola rule

Mesenteries of the same pair most often are of the same size, but not always. Many representatives of Actinostolidae: Actinostola, Paractinostola, Ophiodiscus, Stomphia, Sicyonis, Parasicyonis, Synsicyonis – differ in location of mesenteries according to the "Actinostola-rule." The essence of this rule is that young mesenterial pairs are made of unevenly developed mesenteries in which the muscle bundles are directed, as in most actinians, to the endocoels, but, of the two mesenteries of a pair, the larger is that which is directed to the side of the mesenterial pair of the previous cycle. A typical example to illustrate the mesenterial arrangement of the Actinostola rule is Actinostola callosa (Verrill, 1882). Although the mesenteries of the young pairs are not equal in size, the pairs are arrayed regularly and radially, and are added in all the exocoels simultaneously.

Penta- and heptametral symmetry

Sharp violation in development of the mesenteries of one of the cycles leads to the appearance in actinians of such unusual – for coral polyps – forms of symmetry as penta- and heptameral. On the lower part of the body of Pentactinia californica Carlgren, 1900 (Halcampoididae) [bottom page 104] are only 10 protomesenteries (Figure 1: *7*). On the dorsal side, opposite the single siphonoglyph, lies a pair of directive mesenteries with muscle bundles turned outward, toward the exocoels. On each side of it are located one pair of mesenteries, the muscle bundles of which are turned, as usual in lateral pairs, toward the endocoels. On the ventral side to the right and left of the siphonoglyph, attached to the actinopharynx are two mesenteries, situated as the two mesenterial pairs. As a result, we have the impression that the lower part of the polyp has 5 mesenterial pairs, among which only one pair is the directive one. However, in the upper part of the body (Figure 1: *8*), besides 10 well developed complete mesenteries appear 4 symmetrically spaced exocoelic mesenterial pairs of the second cycle. Moreover, near the siphonoglyph is the beginning of two more complete mesenteries (C), the buds of which are visible on the wall of the column and actinopharynx. Although their muscle bundles are not yet formed, it is natural to assume that when fully developed, those, together with the complete mesenteries [end page 105] lying laterally to them (Co), form the ventrolateral pairs of the protomesenteries. In such a case, mesenteries located nearer to the siphonoglyphs could not be regarded as any but the ventral pair of directive mesenteries with the normal (for those) orientation of the muscle bundles – outward toward the exocoels. In such a way, the polyp has in developed or embryonic form, all 12 protomesenteries organized into 6 pairs (the first cycle) and the 4 metamesenterial pairs of the second cycle. Noticeable discrepancy of the hexameral symmetry is only the lesser width of the endocoels adjacent to the ventral pair of directives (metamesenteries), and absence in those 2 pairs of the second cycle. However, the slower development of some exocoels and subsequently later appearance in those the young mesenteries is a phenomenon that is not so rare, and that we could observe also in the example of Tealia (Figure 2: *1-6*).

The other representative of Halcampoididae – Scytophorus striatus R. Hertwig, 1882 – has 14 mesenteries, which correspond to 7 pairs, being the cause of the description of heptameral symmetry (page 1: *10*). All mesenteries attached to the actinopharynx are developed equally and are separated by even intervals. On the section (in its upper part) is seen 1 pair of directives turned with their muscle bundles away from each other, the other 12 mesenteries, being paired and turned toward each other, could be taken for six mesenterial pairs. The sequence of appearance of mesenteries in Scytophorus is not known; therefore, we can only infer the presence of the second pair of directive mesenteries. Most Halcampoididae characteristically have 2 pairs of directives (Halcampoides, Figure 1: *6*). Besides, in some of those (for example in Pentactinia) is observed a temporal discrepancy in appearance of the second cycle. If we take into account those circumstances, we could propose quite a simple explanation for the unusual symmetry of Scyophorus. The pair of directive mesenteries has an opposite pair of directive mesenteries also with the muscle bundles turned away from each other. On both sides of it (Figure 1: *9*) lie single mesenteries of the second cycle (CB). They "mask" ["camouflage"] the pair of directive ones. Except for these first odd mesenteries of the second cycle, the distribution of mesenteries of Scytophorus would not differ from the position characteristic for Halcampoides, which has only a hexameral cycle of protomesenteries.

Here is explained the interpretation of the symmetry of aberrant Halcampoididae given by Carlgren (Carlgren, 1949).

The change in order of symmetry, transition to octa- and decameral symmetries

Reaching the Halcampula stage with normal radial symmetry, all actinians have 6 pairs of protomesenteries. Consequently, development of the hexameral form may be regarded not only as most common, but also as the original form [evolutionarily]. It dominates among most families. Penta- and heptameral symmetries appear, as it was shown, from the hexameral form as a result of asynchronous appearance of mesenteries of one cycle. Much more widespread are octa- and decameral symmetry. They appear also by violating synchrony of development of the subsequent cycle. But further on synchrony establishes itself that leads to the correct, radially symmetrical arrangement of mesenteries of the subsequent cycles, which are not hexameral but octa- and decameral forms.

Examples of regular octameral symmetry in actinians are found among Actinostolidae (Stomphia, Sicyonis), Phymanthidae (some species [end page 106] of Phymanthus), Isophelliidae (Litophellia octoradiata Carlgren, 1938), Aiptasiidae (some species of Bartholomaea), Actiniidae (Bunodactis octoradiata Carlgren, 1899) and Haloclavidae (Metapeachia tropica (Pannikar, 1938). [sic] Decameral symmetry is peculiar to Minyadidae, and among Actiniidae – Tealia and Cribrinopsis. Besides genera are found species that are distinguished by a different order of symmetry: so, Sagartiogeton (Sagartiidae) has species characterized by hexa-, octa-, or decameral situation of the mesenteries. One species is described in which a polyp changes order of symmetry twice: Parantheopsis cruentata (Couthouy in Dana, 1849) (Actiniidae) during development from a hexameral stage with 12 mesenterial pairs to a hexameral stage with 24 pairs passes an octameral stage (Carlgren, 1924). The list could be longer, but these examples show us the quite frequent digression from hexameral symmetry among species of different genera of Actiniaria.

Reorganization of the originally hexameral young polyp Tealia (Actiniidae) to the decameral adult actinian was first shown by Faurot (Faurot, 1895), and afterward by Gemmill (Gemmill, 1919). The same process of reorganization of the hexameral young stock to the definitive decameral state I observed in a different species. Figure 2: *1-6* shows the location of the mesenteries in an adult specimen of Tealia asiatica Averincev, [sic] 1967* (specimen No. 10015) and in 5 young polyps ejected from its gastric region when it was kept in an aquarium. The scheme is laid out in ascending order of number of mesenteries. "The youngest," i.e. the polyp in the earliest stage of ontogenesis (Figure 2: *1*) has 6 pairs of complete protomesenteries. Besides those, in lateral exocoels are 2 mesenterial pairs not yet reaching the actinopharynx and obviously much smaller in size than the protomesenteries. In the exocoels, lying next to the directive pairs, this stage has only small buds of the mesenterial pairs. In the next stage (Figure 2: *2*) to the first 2 large pairs of mesenteries (M) are added two more (Me), lying near one of the siphonoglyphs. Beginning from the opposite siphonoglyph, in the exocoels between 6 pairs of protomesenteries and 6 large pairs of metamesenteries, consecutively begin to form young mesenterial pairs in the fourth polyp (Figure 2: *4*) the full second decameral cycle. In the largest fifth young actinian (Figure 2: *5*) the 4 first pairs of metamesenteries almost attain the size of protomesenteries, 1 of those pairs attaches to the actinopharynx. Finally, the last scheme (Figure 2: *6*) shows the location of mesenteries of the adult, maternal, specimen. The ten largest pairs, forming the first cycle, are equal in size and are separated by regularly alternating mesenterial pairs of the second and third cycles. Decameral symmetry is only affected by the presence of the 2 extra pairs of the third cycle. I have observed similar doubling of some mesenterial pairs of the second and third cycle in several specimens of the also decameral Tealia felina crassicornis (Müller, 1776) from the Okhotsk Sea.

* This species was first placed by V. G. Avernichev in the genus Tealia, but judging by the fertility of the first cycle of mesenteries (based on the appearance of new material from the Okhotsk Sea) he was correct in my opinion in placing it in the genus Cribrinopsis.

In polyps of Stomphia coccinea (Müller, 1776), whereas the first cycle is regular, consisting of 6 most large mesenterial pairs, the second cycle usually includes 10 pairs, having in each of two primary exocoels one pair of the second cycle and in four two each. Such location of the mesenterial pairs obviously violates radial hexameral symmetry. Mesenteries of consecutive cycles are inserted [end page 107] in 16 exocoels between pairs of the first and the second cycle, in even numbers eight; therefore, in the body of an adult actinian of this species most often octameral symmetry is predominant. Seldom are found specimens of Stomphia coccinea that have 12 rather than 10 pairs of mesenteries of the second cycle – 2 pairs in all primary exocoels (Carlgren, 1921: text-fig. 210). Such animals preserve hexameral symmetry because the number of secondary exocoels (18 exocoels), and consequently, the number of mesenterial pairs of the following cycles remains a multiple of six.

As was shown, change in the order of symmetry happens after full formation of the protomesenterial cycle development and is accomplished by insertion in the first or the second mesenterial cycle supplementary mesenterial pairs. The tendency to form additional mesenterial pairs is often evident in the later stages of development, during formation of the third or the later cycles; then in some exocoels appear additional pairs.

All above seen cases of mesenterial insertion in actinians without doubt should be included in the most common hexameral type. The cited deviations could be regarded as irregular variations in the hexameral method of mesenterial cycle development, affected by synchronous appearance of the first, second or later cycles. Symmetry at the beginning is conditioned by the presence of 6 pairs of protomesenteries and formation of metamesenterial pairs in constantly doubling meristematic zones located in the exocoels. But not all polyps at present ascribed to order Actiniaria experience such a method of formation of the mesenterial cycles. Among them are animals with formation of metamesenteries that are fundamentally different; such are Exocoelactiidae, Halcuriidae and Actinernidae.

Symmetry of Exocoelactiidae

An unusual way of growth characterizes actinians of family Exocoelactiidae. However, similarly to the above-mentioned species, they have strict radial symmetry and formation of the mesenterial pairs among them also happens in the exocoels (Figure 4: *1*, *2*).

Formation of the protomesenteries is not fully traced; it is assumed that there are 6 pairs as usual. Issuing from them, the 12 largest mesenterial pairs that are present in an adult polyp could be interpreted as two hexameral cycles. All subsequent mesenteries are added in the middle of the exocoels between the pairs of the first and second cycle; consequently there are only 12 meristematic zones. Figure 4: *2* shows a narrow sector, including one such zone. In it, synchronously are laid two young mesenterial pairs of each newly appearing cycle. The pairs consist of unequally developed mesenteries, with the larger one always turned with its muscle bundle to the nearest pair of the first or the second cycle. This creates a superficial similarity to the position of mesenteries following the Actinostola rule. But because the number of meristematic zones is fixed, and is equal to 12, the third, fourth and all subsequent cycles include 24 mesenterial pairs each. Increase in the number of mesenterial pairs in Exocoelactis tuberosa (Hertwig, 1882) could be described as: 6 pairs of primary +6 secondary + 24 teriary cycles + 24 + 24+ 24…, and in Actinostola – 6+6+12+24+48…

Symmetry of Halcuriidae and Actinernidae

Halcuriidae and Actinernidae are remarkable in their mesenterial location. Their similarity with other actinians is limited to the presence [end page 108] of 6 large pairs of mesenteries, apparently according with protomesenteries. All consecutive mesenteries develop in 4 lateral endocoels, during which muscle bundles of mesenteries of the second, third and consecutive cycles are divergently directed, i.e. they [end page 109] lie on the outer side of the mesenteries, completing the pair. Both of these particulars sharply delineate Halcuriidae and Actinernidae among all coral polyps characterized by pair-wise addition of mesenteries (Zoantharia, Corallimorpharia, Ptychodactiaria, from typical Actiniaria and Madreporaria).

Carlgrenia desiderata Stephenson, 1918 (Halcuriidae) has 6 pairs of large mesenteries of the first cycle. In the middle between primary mesenteries of each of 4 lateral pairs are formed 2 mesenteries of the second cycle. Their muscle bundles are oriented in unusual fashion: they are directed not toward each other (inside the chamber delineated by the mesenteries of a given pair) as happens in other actinians, but away from each other, i.e. they face toward the nearest mesenteries of the first cycle (Figure 3: *1*). In Synhalcurias elegans (Wasilieff, [sic] 1908), in interstices between mesenteries of the first and second cycles are formed pairs of the third cycle, also with bundles turned outside (Figure 3: *2-3*). As it is not difficult to notice in the figures, some pairs of the last, fourth cycle of Synhalcurias are retarded in development, affecting the symmetry. In the polyp of another related genus – Isactinernus quadrilobatus Carlgren, 1918 – the same scheme of mesenterial layout is more orderly up to the sixth cycle (Figure 3: *4*). [end page 110]

Most representatives of the discussed families, among them Halcurias (Halcuriidae), Synhalcurias and Isactinernus (Actinernidae) have constantly multiplying zones of the mesenterial layout. At the same time, Actinernus has a limited number of zones of development. Actinernus nobilis Verrill, 1879 and other species of that genus have, similar to other Halcuriidae and Actinernidae, 10 pairs of the largest mesenteries (6 pairs of the first and 4 pairs of the second cycle). But because all consecutive mesenterial pairs form in meristematic zones, developing in the middle between the pairs of the first and the second cycles, the number of meristematic zones is limited. The number depends on the number of pairs of the second cycle and, in the presence of four pairs of the second cycle, is equal to eight (Figure 4: 3). Above are described examples in Actiniidae and Actinostolidae of the formation of the supplementary pairs of the further cycles, and in this case unavoidably causes change in the order of symmetry.

Insertion of each extra mesenterial pair into the second cycle leads to an increase in the number of meristematic zones by one: in the case of 4 secondary pairs in Actinonernus [sic] nobilis are observed 8 meristematic zones, in the case of 6-10 (Carlgren, 1918, fig. 10) [sic]. In especially rapidly developing endocoels of the first order are sometimes found up to 4 meristematic zones; this causes perturbation in radial symmetry of the polyp. From this it is clear that location of mesenteries in Actinernus (with a fixed number of meristematic zones) – is only a particular case of a more widespread type (with a constantly increasing number of zones) specific to all other Halcuriidae and Actinernidae.

Figure 4: *4* shows the disposition of mesenteries in one of 8 meristematic zones of Actinernus robustus (Hertwig, 1882). This species has most numerous mesenteries. Pairs of the third – seventh cycles consist of unequally developed mesenteries. The larger of those lies nearer to the middle of the meristematic zone. In the center of the zone are observed 2 small rudiments – those are larger than mesenteries of the 2 pairs of the eighth cycle. 2 other mesenteries of the eighth cycle, retarded in growth, had not appeared yet.

Characteristics of development, determining the symmetry of the coral polyp

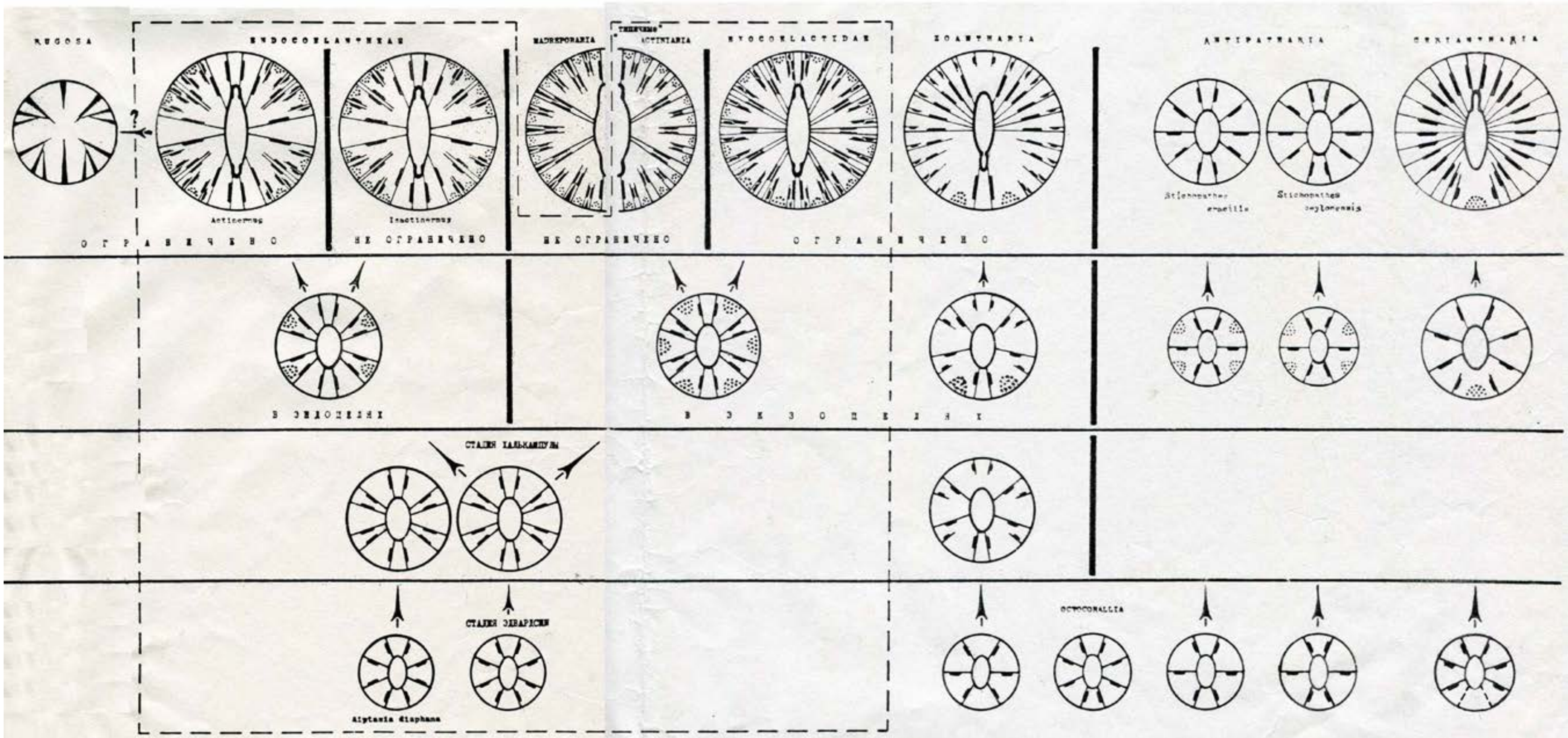
As was shown in the first part, symmetry of the coral polyp during individual development changes. We will try to separate stages in which change of symmetry is affected and establish criteria that influence the symmetry of an adult polyp (Figure 5).

Bilateral development of mesenteries

The first 6 or 8 protomesenteries of all coral polyps do not form mesenterial pairs, which are composed of two mesenteries side by side, but are laid down as bilateral couples, i.e. bilaterally symmetrical to the plane of the actinopharynx. Thus, orientation of the muscle bundles may be most different. In Octocorallia, all bundles are turned one way – toward one of the directive endocoels. This endocoel is conditionally named ventral. In the same way are also oriented each protomesentery of larval Ceriantharia (having, in the opinion of different authors, 6 or 8 protomesenteries). In Zoantharia, Madreporaria and the great majority of Actiniaria, the ventrally-directed ones are turned head-on toward all other protomesenteries and carry muscle bundles on the other side. In Antipatharia, muscle bundles of both directive pairs can be located on either the outer or the inner side of the mesenteries. In all thus noted cases the arrangement of bundles of 2 or 4 lateral mesenteries make the symmetry of the young [end page 111] polyp bilateral. The sole exception – Aiptasia diaphana. This species of actinian has 4 lateral protomesenteries in pairs with the muscle bundles turned toward each other. For this reason it is not possible to distinguish ventral from dorsal, and the polyp in the 8-protomesentery stage already has biradial symmetry.

At the stage of bilateral addition of mesenteries, determining the symmetry of the polyp serves to orient the first protomesenteries. The characteristics of their addition permits only biradial and bilateral symmetry, of which, as we have seen, both variants are represented in Actiniaria. It would seem that orientation of the first mesenteries should greatly influence the symmetry of an adult polyp, but from the bilaterally symmetrical young of the majority of Actiniaria, passing though the Edwardsia type, grow the same radially symmetrical actinian as from biradially symmetrical Apiptasia.

Polyps of Octocorallia (Stolonifera, Telestacea, Xeniidea, Alcyonacea, Tubiporidea, Helioporidea, Gorgonacea, Pennatulacea), ending their development at the stage of 8 first protomesenteries, preserve the characteristics of bilateral symmetry in the definitive stage. The definitive symmetry of other coral polyps does not depend on the orientation of the first mesenteries and is determined at later stages.



RUGOSA
ENDOCOELANTHEAE
MADREPORARIA
ACTINIARIA
ZOANTHARIA
ANTIPATHARIA
CERIANTHARIA
Actinernus
Isactinernus
Stichopathes gracilis
Stichopathes ceylonensis
ОГРАНИЧЕНО
НЕ ОГРАНИЧЕНО
НЕ ОГРАНИЧЕНО
ОГРАНИЧЕНО
СТАДИЯ ХАЛЬКАМПУЛЫ
СТАДИЯ ЭДВАРСИИ
Aiptasia diaphana
OCTOCORALLIA

Formation of the mesenterial pairs

In later development, the characteristic determining symmetry of the young polyp is the presence or absence of mesenterial pairs: animals forming mesenterial pairs attain strict radial symmetry (which, however, could be lost in secondary development); animals that do not form mesenterial pairs preserve a bilateral essence and location of mesenteries.

In Actiniaria and Madreporaria, near each lateral protomesentery develops one more [protomesentery]. This forms a regular hexameral cycle of protomesenteries. Usually the 4 last protomesenteries grow from the ventral side from the already-existing lateral mesenteries and bear muscle bundles on their dorsal surfaces. Only in Aiptasia diaphana they lie between lateral protomesenteries, being turned with the muscle bundles dorsal-to-dorsal, ventral-to-ventral direction. In the Halcampula stage, after the newly-appearing protomesenteries reach the actinopharynx, the pervious differences in location of mesenteries (by the Edwardsia type and the Adamsia type) completely disappear. The young Zoantharia does not differ from the typical Halcampula in location and orientation of mesenteries, but the dorsal pair of directives appears later, simultaneously with completion of the lateral protomesentery pairs.

Precisely in the stage of formation of mesenterial pairs is established radial symmetry of muscles and all the body, which is very characteristic of large solitary polyps. All further mesenteries – metamesenteries – begin to develop in actinians, madreporarian corals and zoantharians in pairs, consisting of 2 neighboring [adhering to each other – Michel] mesenteries, turning muscle bundles toward each other or in the opposite way.

Ceriantharia and Antipatharia sharply differ from actinian, madpreporarian and zoanthid polyps: the stage of completion of protomesenterial pairs is absent. Their mesenteries at any stage of ontogenesis are arranged only in bilateral pairs. Metamesenteries appear one from each side of the plane of the actinopharynx, the same as the initial [end page 113] protomesenteries, during which the symmetry of the body of the polyp does not change substantially, and throughout life, clear characteristics of bilateral symmetry are preserved.

Occurrence of the primary meristematic zones

In a growing polyp, new mesenteries develop not along the entire perimeter of the body but only in meristematic zones. Symmetry of the mesenterial cycles and precise position of the planes of symmetry depend on the position of the meristematic zones and are determined at the stage when the first meristematic zones begin to appear.

The young polyp at the Halcampula stage is divided by 12 mesenteries into 6 endo- and 6 exocoels. Their number limits the number of primary (first order) meristematic zones, which function either in exo- or endocoels. In the first case could function 6 first meristematic zones corresponding to the number of exocoels of the first order (actinians, madreporarian corals). In the second case, these are formed in only 4 zones, lying in endocoels of each of the lateral protomesenterial pairs* (Halcuriidae and Actinernidae).

Accordingly, a majority of Actiniaria and Madreporaria preserve hexameral symmetry, which appears already in the Halcampula stage, at the time when in bodies of Halcuriidae and Actinernidae during the development of metamesenteries tetrameral symmetry predominates. It is necessary to stress that in both cases that elements of biradial symmetry that appear in the Halcampula stage are preserved (2 pairs of directive mesenteries, splitlike actinopharynx, siphonoglyphs).

*In endocoels of the directive mesenterial pairs, which support siphonoglyphs, meristematic zones, as a rule, do not appear. But Hyman (1940, p. 601, 608) discusses formation of incomplete sclerosepta (and consequently of mesenteries) in ventral and/or ventral and dorsal directive endocoels in Acropora and Porites (Madreporaria). Unfortunately the source of these data is not shown.

Multiplication and stabilization of the meristematic zones

Later, during growth of the polyp, meristematic zones are capable of unlimited growth in number, constantly splitting in two. This is observed as in Isactinernus (Actinernidae) in developing zones in endocoels, so in a majority of actinians and madreporarian corals that have meristematic zones in their exocoels. But unlimited multiplication of zones even in large polyps is not always found. In different groups, independent of one another, appears a tendency for stabilization in number of meristematic zones. Their number decreases, and the surface of those perhaps the most sensitive regions, is decreased.

The presence of few constantly working, in the certain places, zones of mesentery formation, changes the general picture of mesenterial arrangement. The young pairs already stop mixing with the old, but are displaced to the side from the middle of the zone, freeing space for the new to appear (Figure 4: *2*, *4*). Limiting the number of meristematic zones in which appear mesenterial pairs leaves a clear imprint on the organization of the pairs themselves. In each pair, one mesentery is more developed, having a larger muscle bundle. In such a way is established the symmetry of the muscles relative to the meristematic zone instead of symmetry of the muscles of each mesenterial pair relative to its endocoel.

Limiting the number of zones itself, and their constant multiplication, does not prevent radial symmetry of mesenteries and the entire polyp body. [end page 114] In principal, radial symmetry could be preserved if the number of zones decreases to two, but in a large, constantly growing polyp there are more: Exocoelactiidae has 12 zones, Actinernus (Actinernidae) – 8.

Bilateral distribution of the meristematic zones causes bilateral arrangement of the mesenteries. 4 bilaterally arranged zones are present in many Rugosa, originating, according to the hypothesis of Carlgren (Carlgren, 1914, 1918), from forms close to Actinernidae. Their loss of radial symmetry is tied to the side attachment to the substrate (Yakovliev, 1910). Zoanthids have only 2 close meristematic zones, arranged in 2 neighboring exocoels beside the ventral directive pair, but bilaterality of zoanthid polyps probably is not connected to the conditions of habitat (this question will be expounded on below).

Bilateral symmetry of the muscles makes it unusable for the proper contraction of the outer radially-symmetrical body of the polyp independently from its origin. Did it appear as a consequence of forming mesenteries in bilateral pairs, as in cerianthids and antipatharians, or as a result of formation of proper mesenterial pairs in the bilaterally-symmetrical meristematic zones as in zoanthids. Therefore, bilaterally-symmetrical muscles of mesenteries are found only in animals that do not use them very much. Small polyps of predominantly colonial zoanthids do not have thick muscle bundles. In antipatharians, muscle bundles are so underdeveloped that it is not possible to see their origination in all species. Cerianthids, although able to contract strongly lengthwise, use for this function the powerful layer of ectodermal muscles because the mesenterial muscles are rudimentary.

So, in the last stage of development, coral polyps can retain the potential to correct the multiplication of the meristematic zones, the number of which is often limited only by the size of the body, but it is also possible to observe stabilization of the zones of growth. In this case, the presence of this limitation on the number of zones strictly influences not only the number of antimers, but also the character of the distribution of mesenteries in each of the radially-symmetric sectors, which are united in progression around the axis of the body. Therefore, the limited and the unlimited numbers of zones – is the sign evoking above all a clear distinction in the symmetry of adult polyps.

TAXONOMIC CONCLUSIONS

Significance of the number of antimers

Mesenterial pairs

In founding the system of actinians (Actiniaria, syn. Malacodermata), Richard Hertwig (Hertwig, 1882) divided all the then known to him skeletonless coral polyps into six tribes: Hexactiniae, Paractiniae, Monauleae, Edwardsiae, Zoantheae, Ceriantheae. As the basis of taxonomic division, Hertwig used types of symmetry (bilateral, radial) and number of antimers (tentacles, mesenteries).

In Hexactiniae were included polyps with hexamerally arranged mesenteries organized in pairs. The muscle bundles of all pairs pointed toward the endocoels except for the two directive ones in which the orientation of the muscles is opposite.

Paractiniae, i.e. “near to the actinians,” were separated as an independent group because of deviation from the hexameral order of symmetry characteristic of the hexactiniae. The discovery in this group of a representative, Sicyonis crassa Hertwig, 1882, that had octameral symmetry [end page 115] (multiple of four) did cause Hertwig to discuss its similarity to Tetracorallia (=Rugosa). However, now Sicyonis is regarded as a member of family Actinostolidae, many members of which have octameral structure of the mesenteries, which form from hexameral ones. The description of a second species of this tribe – Polyopis striata Hertwig, 1882, -- does not permit us to establish precisely its systematic position, but also it does not contain traits which would block this species as being ascribed to actinians (the hexactiniae of Hertwig).

Hertwig did suppose that the Edwardsiae have only 8 mesenteries and, based on that, he regarded them as octameral, with elements of bilateral symmetry similar in that sense to Alcyonaria. In reality, not only

Edwardsiidae, but all other hexactinians in the Edwardsia stage have octameral organization of mesenteries, which later, without exception, become hexameral.

The reason to separate the tribe Monauleae was due to the existence of its sole representative Scytophorus striatus which had 7 “pairs” of mesenteries. However, comparison with Pentactinia and Halcampoides allowed Carlgren to put Scytophorus into family Halcampoididae, the majority of representatives of which have symmetry typical of hexactiniae.

Two final tribes -- Zoantheae and Ceriantheae – thanks to non-cyclic and, in cerianthids, odd structuring of mesenteries (Hartog, 1977) are removed from Actiniaria and are regarded as independent orders: Zoantharia and Ceriantharia.

Study of not only the geometrical picture of symmetry of an animal, but also methods of formation and ontogenesis of polyps allow us to more completely judge the similarity and differences between the animals. During development of systematics, all groups of actinians were separated only on the basis of the number of radially-symmetrical organs, and were united with the basic core – hexactinians. Therefore, unusual number of antimers could be regarded as certain characteristics of variation from the most widespread type of development pertinent to hexactinians, but it cannot serve as a sure basis for separation of the taxa.

Meristematic zones

Polyps of order Actiniaria (in the contemporary, narrower understanding than that of Hertwig) are characterized by numerous, constantly doubling meristematic zones. The number of zones in a typical hexactinian is limited by the size of the animal, although some influence possibly could be imparted by conditions of the habitat. So, wormlike actinians that dig into the ground, although they have a noticeably long body (5-10 cm), have few mesenteries -- one-two cycles. In contrast to them are species living on hard substrates and in the adult stage growing to large size (sometimes to 1 m), already in the young stage develop 3-4 mesentery cycles, and meristematic zones appear between each two adjacent pairs of mesenteries (Figure 1: *11*). Such limitless increase in number of zones is observed among Halcuriidae and Actinernidae (Figure 3: *3-4*). However, in developing mesenteries in exocoels (Exocoelactiidae) as in endocoels (Actinernidae), it is possible that stabilization of meristematic zones occurs. Exocoelactiidae have 12 persistent zones that do not shift their location. Such a method of growth does not have an analog among the nearest families with exocoelic addition of mesenteries; therefore the symmetry of Excoelactiidae seems unique. Neverthless, comparing them with Halcuriidae and Actinernidae among which we find a number of transitions from unlimited (Isactinernus quadrilobatus – Figure 3: *4*) to stable number [end page 116] of meristematic zones (Actinernus – Figure 4: *3*), we have to admit that location of mesenteries, specific for Exocoelactiidae could easily appear to limit the number of zones in typical hexactinians. Unusual formation of zones (two series diverging from the place of addition consecutively increase in size of mesenteries – Figure 4: *1, 2*) – is the result of a simple decrease in their number. In a similar way appears the single meristematic zone of cerianthids and two side-by-side zones of zoanthids, each of them increasing mesenterial pairs on one side only, are similar to the halves of the meristematic zone of Exocoelactiidae.

In such a way, we see that a tendency to limit zones of growth serves as one cause of the appearance of aberrant forms of symmetry, but the small number of meristematic zones and increased complexity in the structure of the zone itself, discovered in the different groups of coral polyps, should not be understood as taxonomically important features. In full correspondence with this conclusion are representatives of Actinernidae, clearly differing in symmetry but similar in many other features, even at the beginning of this century were unified by Carlgren (1918) in one family.

Proposed changes in the system of Anthozoa

Symmetry of coral polyps, as was written from the time of Haeckel and the Hertwig brothers, serves as the basis of the classification of that group. The original scheme of Haeckel was based on the impression of the importance of the number of antimers. Class Anthozoa was divided into three subclasses: Tetracorallia (= Rugosa) – four-fold, Hexacorallia – six-fold and Octocorallia – eight-fold corals. Afterward, R. Hertwig, also on the basis of antimers, divided all skeletonless non-colonial corals (Actiniaria in the understanding of Hertwig, i.e. all Hexacorallia except antipatharians and madreporarians) into tribes. Later, without a theoretical appreciation of antimer number, Rugosa were accepted as one order of Hexacorallia, and subclass Tetracorallia was removed from the system. Some tribes of Hertwig were unified and some were regarded as independent orders of Zoantharia and Ceriataria [sic]. The cause of this was accumulation of new data about the variety of symmetry in coral polyps. Considerations presented above about mutual relations of the forms of symmetry allow us to understand some morphological regularity [of natural phenomena] of the development of the group and will serve as an improvement in the systematics of Anthozoa.

The proposed classification of Anthozoa (sm. scheme) does not conform to the generally accepted notion. Usually Ceriantharia and Antipatharia are unified together with Actiniaria, Madreporaria and Zoantharia into subclass Hexacorallia (Hyman, 1940; Pax, 1940; Dogiel, 1975; and others) but as was shown above, there is no basis for such a classification. Disposition of the mesenteries of cerianthids and antipatharians are in principle different from other coral polyps. V. N. Beklemeshev (1952), in his book "System of the Animal Kingdom" first separated them into independent subclasses, which, in my opinion, is the best way to reflect the degree of their phylogenetic relationship with the other coral polyps. Having this point of view, presently living Anthozoa should be divided not in two (Hexacorallia and Octocorallia) as was done by Haeckel but into four subclasses: 1--Hexacorallia, 2—Ceriantharia, 3 – Octocorallia, 4 – Antipatharia.

1. The clearest attribute of Hexacorallia could serve the presence of 6 pairs of protomesenteries determining their radial, primary hexameral system. [end page 117]
2. The main characteristic of Ceriantharia is that their mesenteries are formed like their protomesenteries. The phase of completion of the protomesenterial pairs obviously is absent at the beginning. The polyp in all stages of ontogenesis remains bilaterally-symmetrical.
3. Development of the polyp of Octocorallia ends before the stage of forming metamesenteries paired or odd starts. By number and disposition of mesenteries, adult polyps of octameral corals completely correspond to the polyps of the hexameral while in the edwardsia stage. The only sign that indicates the nearer relation of octocorals to cerianthids than to hexacorals is the orientation of the two ventral mesenteries, which are turned with their muscle bundles toward each other. Such an arrangement of muscles excludes correct radial symmetry of the polyp even in condition that lateral protomesenterial pairs were formed and, obviously, witness about that bilateral symmetry of Octocorallia polyps corresponds to their primary state, and it is not attained as a result of colony formation.
4. The arrangement of mesenteries in Antipatharia allows two explanations of their origin. If odd, bilateral, formation of mesenteries – is a result of decreased dimension and stretching of its body along the colony branch, then antipatharia may be close to the hexameral corals. The basic argument for this theory is the position of the muscle bundles on the dorsal and ventral protomesenteries, permitting (in contrast to the octocorals) acquisition of radial symmetry in case of lateral pair formation. If the bilateral formation of mesenteries corresponds to the primary antipatharian state, they are unconditionally very close to cerianthids. The present method of formation of mesenteries in antipatharians and cerianthids is so similar that their belonging to separate [end 118] subclasses is justified only because there are sharp differences in other characteristics that are not connected directly to body symmetry (colonial state, skeleton and others).

Within subclass Hexacorallia, the most important characteristics determining symmetry of the polyp is the position of the primary meristematic zones, i.e. exocoelic and endocoelic addition of mesenteries. After the appearance of the 6 pairs characteristic of all hexacorallians without exception, metamesenterial pairs in most cases appear in the exocoels. Only in two families – Halcuriidae and Actinernidae – have polyps in which mesenterial pairs start to develop in endocoels. Another unique trait of those animals is probably connected with the unusual position of their meristematic zones, and consists of the muscle bundle of mesenteries in all except the first cycle being turned away from one another. Taking that criterion as a base, Carlgren separated Halcuriidae and Actinernidae into the independent group Endocoelantheae (suborder in the order Actiniaria [Carlgren, 1936, 1949]. In the table showing characteristics of development, determining the symmetry (Figure 5) the dotted lines indicate those forms of polyp symmetry that are observed in groups at present united in order Actiniaria. In the order were included animals with completely different types of mesenterial arrangement – Endocoelantheae and "typical" actinians (Hexactiniae of Hertwig). Neither one of those two types can be accepted as more likely to have originated from the other. It seems that they appeared independently as two variants of the paired formation of metamesenteries, and are characteristic for two separate taxa.

In the works of Carlgren (1914, 1918), especially studies of the anatomy of Endocoelantheae, are noted certain interesting concepts about the possible relationship with ancient corals of the order Rugosa. Schematics of Carlgren (Figure 3: *5*, *6*) how delay in development of mesenteries and sclerosepta on the dorsal side of the polyp leads to formation of the characteristic solitary rugosa type; this obtained by Carlgren by studying the mesenterial disposition in Actinernus. Notwithstanding the reliability of these propositions, it is necessary to stress that symmetry of Rugosa is studied by observing sclerosepta, and of the skeletonless Halcuriidae and Actinernidae the mesenteries. Consequently, the relationship of these groups is questionable until, among modern skeleton-forming corals, is found a group with soft parts similar to those of Halcuriidae and Actinernidae. The principal argument in favor of closeness of rugosans with Endocoelantheae – the really great similarity between symmetry of Actinernidae (with a limited number of meristematic zones) with symmetry of some solitary [single?] {?four-fold?] corals having 4, sometimes 8 (Goniophillum) [sic], bilaterally located meristematic zones (Carlgren, 1918).

However, decrease in number of zones is observed and during endocoels and exocoels founding of mesenteries, therefore appearance of specific for the rugosan picture of disposition of sclerosepta is in principle possible and during formation of metamesenteries in the exocoels, characteristic for modern madreporarian corals.

If Endocoelantheae are not numerous, so polyps with exocoelic addition are a very large group, further division of which goes by the division of skeleton, muscles, coloniality, and so forth. To this group belong first of all "typical" Actiniaria, which were separated by Hertwig into the tribe Hexactiniae. Present notions about formation of mesenterial cycles permits us to unify with the hexactinians also [end page 119] octa-, decanmeral and all other Actiniaria having the exocoelic type of addition of mesenteries. Even Exocoelactiidae with their 12 undivided meristematic zones, it seems could be included among hexactinians because the only difference is there is a limited number of zones.

It is necessary to stress that in the ** [view?] of order of polyp symmetry, Madreporaria do not differ from hexactinians. The soft tissue in both groups develops in a similar way. The madreporarian skeleton strictly follows development of the soft tissue, filling every new endocoel with a new scleroseptum. As far as the character of laying a foundation in studied, in that sense, madreporarians are the same as hexacinians, it is natural to expect that deviations in arrangement of sclerosepta would be similar to those observed in actinians. In fact, in family Stylinidae are found hexa-, octa-, and decameral representatives, as in Actiniidae and Actinostolidae. The cause of change of symmetry undoubtedly lies in insertion in the first cycle of the supplementary mesenterial pairs and laying down between them seclerosepta.

For another important sign about the relation between madreporarian corals and actinians we could refer to the fine structure of their tissues. Van Praet (Van Praet, 1977) on the basis of electron microscopic study of Haplangia durotrix (Madreporaria) established that histological structure of tentacles, cnidoglandular tract, mesenterial filaments and endoderm indicate the connection between actinians and scleractinians (i.e. madreporarian corals).

Close to hexactinians are also Corallimorpharia and Ptychodactiaria separated by Carlgren (Carlgren, 1941, 1949).as independent orders. The basis for their separation from Actiniaria was the peculiar structure of the upper part of the mesenterial filaments of ptychodactiarians, the presence of acrospheres on the tentacles of corallimorpharians, the absence of a cnidoglandular tract on filaments and basilar muscles in polyps of both orders, and very weak development of all musculature [in both orders]. The disposition of mesenteries, however, differs only by recurrent deviation from proper radial symmetry. New data about cnidomes – the system of the *** capsules – of corallimorpharians also indicates their closeness to the large madreporarian polyps Balanophyllia (Dendrophyliidae), Caryophyllia (Caryophylliidae) and others (Schmidt, 1972). Schmidt finds that the cnidom of Corynactis viridis (Allman, 1846) of family Corallimorphidae is perfectly similar to the cnidom of the madreporarians he studied, differing in only a few specific holotrichs characteristic only of corallimorpharians. Gelatinous polyps, corallimorpharians are comparable in size to individuals of the large madreporarian corals, often having at the top of the inflexible tentacles acrospheres (bulbous swellings with numerous nematocysts). Corallimorphus antarcticus Carlgren et Stephenson, 1929 (Corallimorphidae) has a thick, springy mesoglea and apparently represents the same living form as a skeleton-forming solitary coral. Support is provided by mesoglea instead of by sclerosepta. Corallimorpharians tightly attach themselves to rocks and very likely absolutely do not move. The absence of a sphincter does not permit those animals to hide their oral discs. Thus, in many traits of their internal organization, corallimorpharians can be seen by us as peculiar "skeletonless madreporarian corals" that lost their calcareous skeleton or from the beginning solved the problem of bodily support not with calcareous plates but with the help of springy mesoglea. We should note that deep-water Halcuriidae and Actinernidae also lack a sphincter and protect their tentacles by folding them in pyramids into which [end page 120] the oral disc is divided. It is not impossible that this characteristic also as weakly developed mesenterial muscles and powerful mesoglea indicate something about the origin of Endocoelantheae from skeleton-forming corals.

It is most difficult to find a good place in the system of coralline polyps for the order Zoantharia. In characteristics of symmetry of the body and by the way of growth, zoanthids are nearest to the polyps of subclass Ceriantharia. The metamesenteries of cerianthids are formed in a single meristematic zone, zoanthids in two. But each of the two mirror-image zones of zoanthids, similar to half f the single zone of cerianthids, forms a series of new mesenteries left and right from the plane of the actinopharynx. So far, as all large metamesenteries of zoanthids are directed as the mesenteries of cerianthids with muscle bundles to the same side, the similarity is impressive. However, all mesenteries of zoanthids are organized in pairs: near each large mesentery – macromesentery – lies an underdeveloped mesentery – micromesentery. The presence of mesenterial pairs ("true pairs" – pairs [in English], and not “bilateral pairs” – couples [in English]) indicates that zoanthids belong to subclass Hexacorallia, and similarity to cerianthids is engendered only by the small number of meristematic zones. Unequal development of mesenteries in pairs, as was shown above (Actinernus, Exocoelactis), is connected to the localization of the formation of mesenteries in constantly active, indivisible meristematic zones. In zoanthids, the zones are located in exocoels and they cannot be fewer than two. Created by the actinopharynx, the plane of symmetry cuts through the directive endocoels, and the single zone unavoidably will be arranged asymmetrically. So the bilateral symmetry of zoanthids could be regarded either as primary, a fundamental feature of the group, or as a result of decreasing the number of meristematic zones of hexactinians from an unlimited number to two. In favor of the first assumption, apparently, is the structure of the embryo in the halcampula stage: at the stage when the polyps of other hexameral corals, completing formation of the first hexameral cycle of mesenteries, become gradually symmetrical, zoanthid polyps in this and the following stages remain bilateral (a dorsal pair of directives and 4 of the total of 8 lateral protomesenteries stay undeveloped). Deviation from radial symmetry could result from the influence of living conditions as was observed among rugosans (in the case of lateral attachment to the substratum), but in such a case the disposition of the muscles cannot be indifferent and the muscle bundles of all macromesenteries (on micromesenteries muscles are rudimentary) should be turned in either a ventral or a dorsal direction. Besides, the muscle system in zoanthids is generally not well developed, and its influence on the arrangement of the attachment of polyps or their behavioral reaction is doubtful. If the influence of extraneous factors is absent, and bilateral disposition of macromesenteries appeared as a consequence of the peculiarities of the development of mesenterial pairs and having a small number of meristematic zones, then orientation of the muscle cylinders could be random: in Actinernus we observe macromesenteries turned toward the middle of the meristematic zone, and in Exocoelactis – to the edges. Among zoanthids “macrometamesenteries” are directed with muscle bundles toward each other (Figure 5). This fact, in my opinion, proves that bilateral symmetry of zoanthids – is not the consequence of the conditions of habitat but a result of the mechanism of polyp development during the decrease to the minimum number of meristematic zones. If this is so, then the presence of 12 (Exocoelactis), 8 (Actinernus, Goniophyllum), 4 (solitary rugosans) and 2 zones (zoanthids) [end page 121] – are steps in a single process, the process of orderly/regulated stabilization of growth zones. Consequently, the presence in zoanthids of only 2 zones does not bar them from being regarded as hexactinians, having as the base of their symmetry unlimited multiplication of hexamerally arranged meristematic zones.

Therefore, hexactinians, i.e. primarily hexameral coralline polyps, having 6 pairs of protomesenteries and forming in exocoels metamesenterial pairs consisting of mesenteries with muscle bundles turned toward each other, represent a group of much higher rank than Hertwig assumed. To them must be assigned all six-sided corals, with the exception of Endocoelantheae (and probably also rugosans – Rugosa) which comprise a taxon equal in rank to hexactinians. In order to assign a higher rank to the several groups – actinians (especially), madreporarian corals and zoanthids – two strong subdivisions of the subclass Hexacorallia can be expediently viewed as superorders Endocoelanthida with the natural order Endocoelantharia, and Hexactiniida with five orders: Actiniaria, Madreporaria, Zoantharia, Corallimorpharia, Ptychodactiaria.

SCHEME OF CLASSIFICATION OF ANTHOZOA (page 118)

Mesenteries are Arranged in Pairs	6 pairs of protomesenteries, afterwards Metamesenteries Start to develop	SUBCLASS HEXACORALLIA	formation of metamesenteries in exocoels superorder Hexactiniidae order Actiniaria Madreporaria Zoantharia Ptychodactiaria Corallimorpharia Formation of metamesenteries In endocoels Superorder Endocoelanthida Order Endocoelantharia
Mesenteries are Not arranged In true pairs	there are 6 or 8 protomesenteries; metamesenteries Start to develop After them	Colonial. Development of polyps is suppressed. Formation of metamesenteries is not localized in one zone SUBCLASS ANTIPATHARIA Solitary large polyps, each with A single zone of mesentery Formation SUBCLASS CERIANTHARIA	
	There are 8 Protomesenteries; Metamesenteries Are absent	SUBCLASS OCTOCORALLIA	