


Classification and evolution of the burrowing sea anemones (Anthozoa: Actiniaria: Athenaria): a review of the past and current views

Классификация и эволюция закапывающихся актиний (Anthozoa: Actiniaria: Athenaria): обзор прежних и современных представлений

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Abstract. The opinions of systematists about the classification and evolution of burrowing sea anemones have repeatedly changed over the long-term study of Actiniaria. Four stages can be distinguished over the course of the classification history. Each system was characterised by the use of mainly one particular feature. These features were: (1) characters of the external morphology, (2) arrangement of the mesenteries, (3) presence or absence of the basilar muscles and (4) molecular markers. The views on the origin and the evolution of the burrowing sea anemones were also altered more than once, that led to the emergence of several hypotheses. The burrowing sea anemones were considered as a primitive group or, on the contrary, as more advanced descendants of large hexamerous actinians.

Резюме. Представления исследователей о классификации и эволюции закапывающихся актиний неоднократно менялись в течение длительного времени изучения Actiniaria. В процессе формирования классификации можно выделить четыре этапа. Каждый из них характеризовался использованием в основном одного признака, на который опирались авторы при построении своей системы. К этим признакам следует отнести: (1) черты внешнего строения, (2) расположение мезентериев, (3) наличие или отсутствие базиллярных мускулов и (4) молекулярные маркеры. Представления о происхождении и эволюции закапывающихся актиний также неоднократно изменялись, что привело к появлению нескольких гипотез. Закапывающиеся морские анемоны рассматривались в качестве примитивной группы или, наоборот, как более продвинутые потомки крупных гексамерных актиний.

Key words: burrowing anemones, comparative morpho-anatomical analysis, taxonomic characters, classification, evolution, Athenaria

Ключевые слова: закапывающиеся актинии, сравнительный морфо-анатомический анализ, таксономические признаки, классификация, эволюция, Athenaria

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Introduction

The classification of the burrowing sea anemones has a long history dating back more than 150 years. During this time, researchers conducted a

huge amount of work in an attempt to build a natural classification that reflected the evolution of this group. The first researchers (Milne-Edwards & Haime, 1857; Gosse, 1858, 1860) relied mainly on the external features of the burrowing sea

anemones to arrive at a classification. Later it became clear that anatomical characters were more stable and reliable characters (Hertwig, 1882; McMurrich, 1893).

The transition to a classification based on internal features was associated with a detailed study of the successive development of the mesenteries by Hertwig & Hertwig (1879). It became soon clear, however, that relying solely on the arrangement of the mesenteries led to the union of unrelated polyps and to the separation of closely related forms (Beneden, 1897). According to Carlgren (1898, 1900, 1905), the most important feature in classifying the burrowing sea anemones is the absence of the basilar muscles. Over time, his system was improved, developed, and published in the monograph "A survey of the Ptychodactiaria, Corallimorpharia and Actiniaria" (1949). Carlgren's (1949) classification was universally accepted and was used by all researchers until recently. In the second half of the 20th century, however, Carlgren's system was increasingly though not to reflect the phylogeny of Actiniaria, and the burrowing sea anemones were ultimately considered

to represent a polyphyletic group (Hand, 1966; Schmidt, 1972, 1974).

Following the contemporary trend in the natural sciences, many specialists had high hopes of solving the difficult problems of phylogeny and systematics based on molecular genetic studies. Unfortunately, as evident from the new higher-level classification for Actiniaria proposed by Rodríguez et al. (2014), these issues are still far from being resolved. Firstly, that classification yields a combination of completely dissimilar forms. For example, the edwardsians and the endocoelanthans are placed in one order: apart from sequence similarity, however, these sea anemones have no other common features in either structure or biology. Secondly, placing some burrowing sea anemones, which lack acontia, together with the thenarian polyps that possess them, in the superfamily Metridioidea, was explained by loss of the acontia. Thirdly, when using one set of markers, the position of many genera in the scheme reflected a particular phylogenetic relationship, whereas using other markers yielded a quite different result. That cast doubt on the applicability of the method itself.



Fig 1. Early sea anemone division based on characters of their external morphology. **a**, burrowing sea anemones, elongated forms with a rounded aboral end or physis; **b**, large attached sea anemones with a well-developed, flat, adhesive and muscular pedal disc. After Gosse (1860).

1. Development of classification of the burrowing sea anemones

1.1. Classification based on external morphological features

The taxonomists of the mid-19th century relied on external features to construct the classification of sea anemones. They separated the burrowing forms from the remaining representatives based on their elongated body shape and absence of a pedal disc (Fig. 1a, b). Milne-Edwards & Haime (1857) placed these anemones inside of the subfamily Actininae in section “Actinines pivotantes”, defining them as “species whose base is very small and body is very elongated” (Fig. 2). In constructing his system, Gosse (1860) also relied on the presence or absence of a sticky pedal disc. Accordingly, he isolated the worm-like anemones along with the cerianthids from other anemones in the family Ilyanthidae (Gosse, 1858). Verrill (1864) was among the first zoologists to draw attention to internal features of the polyp, indicating the number of mesenteries (“internal lamellae”) in a description of the species. Nonetheless, as diagnostic features for distinguishing genera and families, Verrill mainly used external features: body shape, surface structure, tentacles number, etc. Klunzinger (1877) also used the elongated body and rounded or pointed proximal end of the body without a well-differentiated pedal disc as diagnostic characteristics.

1.2. Transition to the classification based on internal features: the succession of arising mesenteries

The system of all Anthozoa, including the sea anemones, was later based on features of the internal organization of the polyp (McMurrich, 1893). Haime (1854) was the first to point out the importance of anatomical features, but only Hertwig & Hertwig (1879) began to use them in constructing their classification. Having traced the formation of mesenteries in the sea anemones, the zoanthids, and the octocorals, Hertwig & Hertwig (1879) considered that the arrangement of mesenteries and the development of their muscles (but not their number as Ehrenberg (1834) and Haeckel (1866) believed) should be regarded as the most important taxonomic characters.

Hertwig & Hertwig (1879) and many subsequent researchers demonstrated that, in the early stages of development, sea anemones are bilaterally symmetrical animals. This is underlined by the presence of eight primary mesenteries, which are symmetrical with respect to the plane of a flattened pharynx. First, in anemone larvae, two ventro-lateral mesenteries are formed to the right and left of the flattened pharynx, making up the bilateral pair (“couple”) (Fig. 3a). They divide the body cavity into a smaller part located on the conventionally ventral side, and a large portion on the conventionally dorsal side. The next mesenteries

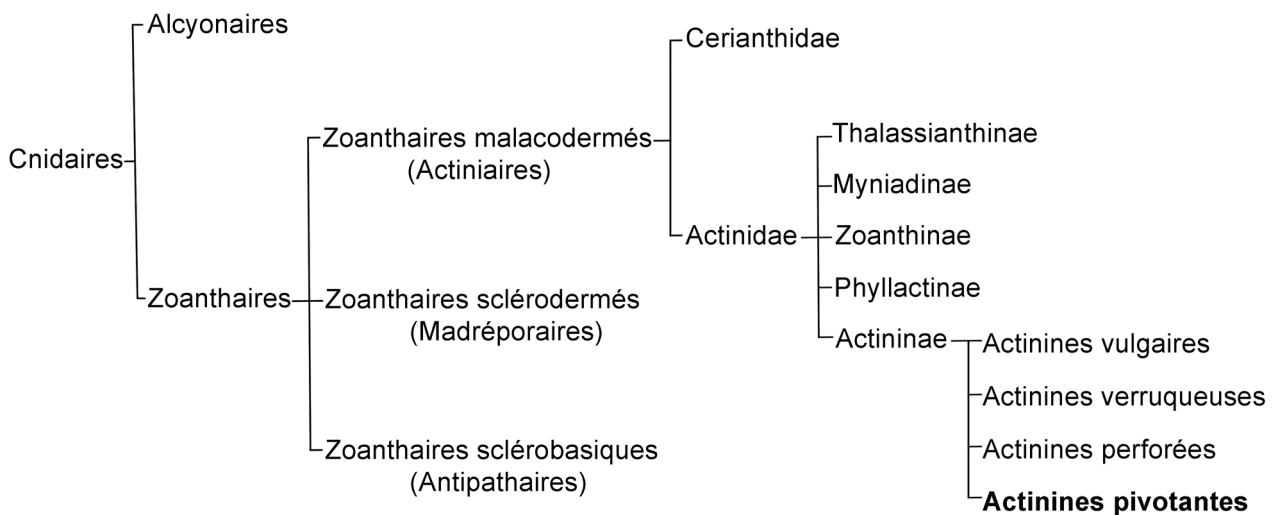
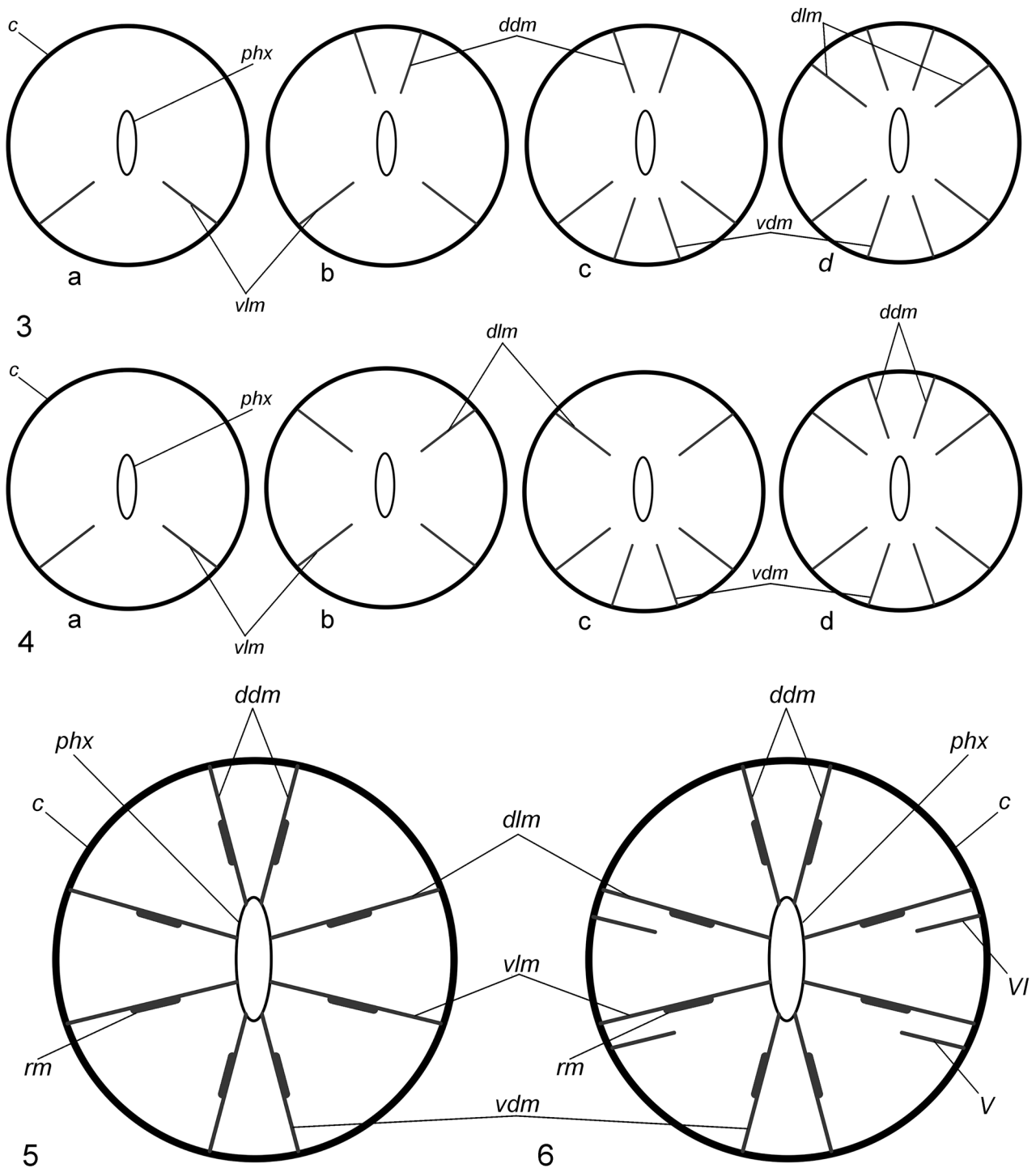
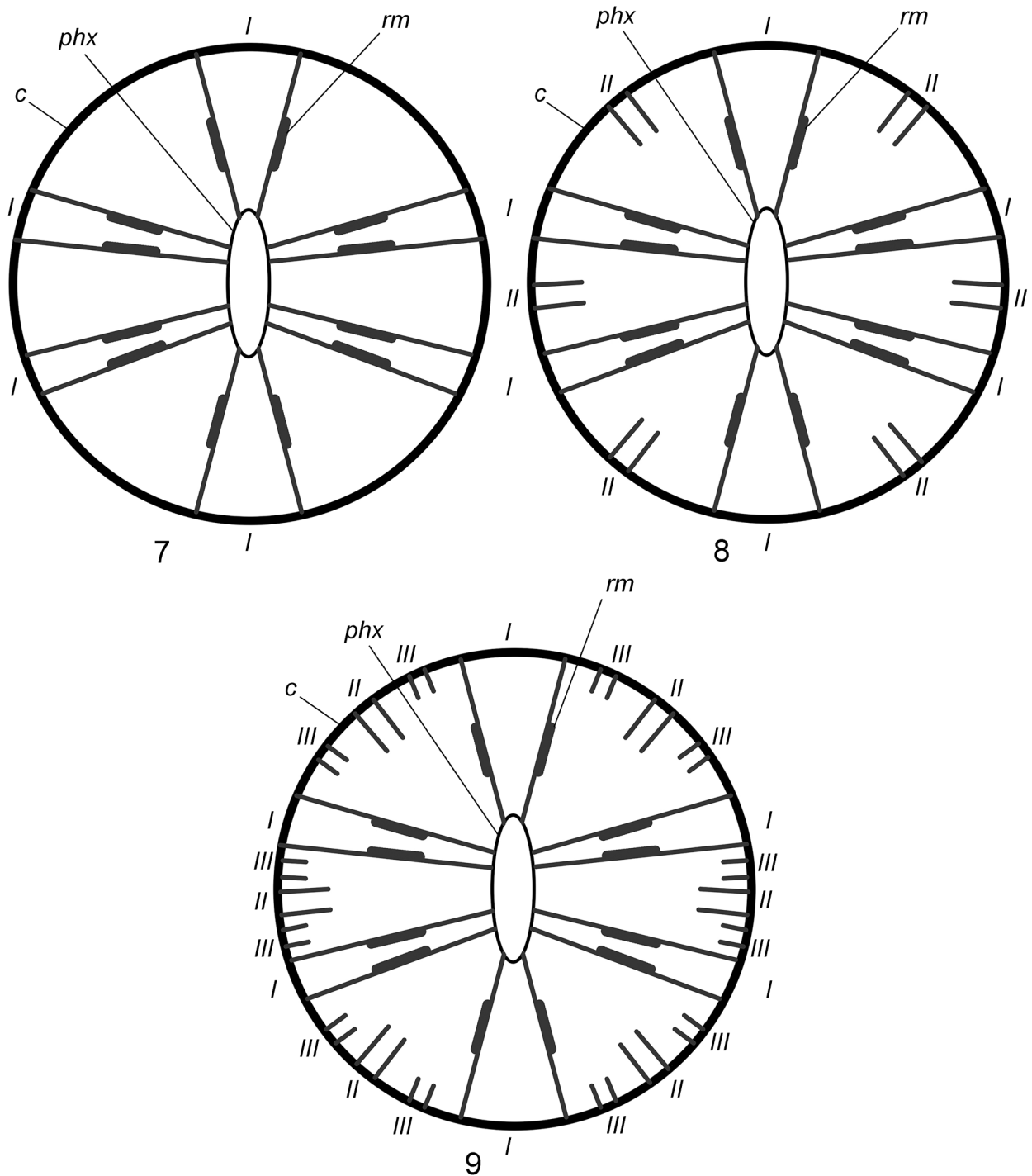


Fig 2. The position of burrowing sea anemones (in bold) in Milne-Edwards & Haime’s (1857) classification of coral polyps.



Figs 3–6. The succession of arising mesenteries, schematic transversal section. **3**, the first type; **a**, the first couple (ventro-lateral mesenteries); **b**, the second couple (dorsal directive mesenteries); **c**, the third couple (ventral directive mesenteries); **d**, the fourth couple (dorso-lateral mesenteries); **4**, the second type; **a**, the first couple (ventro-lateral mesenteries); **b**, the second couple (dorso-lateral mesenteries); **c**, the third couple (ventral directive mesenteries); **d**, the fourth couple (dorsal directive mesenteries); **5**, *Edwardsia* stage; **6**, arising of the fifth and sixth couples of lateral mesenteries. *c*, column; *phx*, pharynx; *rm*, retractor muscle; *vlm*, ventro-lateral mesenteries; *dlm*, dorso-lateral mesenteries; *vdm*, ventral directive mesenteries; *ddm*, dorsal directive mesenteries; *V*, fifth couple of lateral mesenteries; *VI*, sixth couple of lateral mesenteries.



Figs 7–9. The succession of arising mesenteries, schematic transversal section. **7**, *Halcampa* stage; **8**, formation of the secondary mesenteries; **9**, formation of the tertiary mesenteries. *c*, column; *phx*, pharynx; *rm*, retractor muscle; *I*, mesentery pairs of the first cycle; *II*, mesentery pairs of the second cycle; *III*, mesentery pairs of the third cycle.

are formed in a similar mode, namely in bilateral pairs. This encompasses a pair of dorsal directive, ventral directive and dorso-lateral mesenteries (Fig. 3b–d). Sometimes the sequence of pair development differs (Fig. 4a–d). The stage of eight primary mesenteries was called the *Edwardsia* stage by McMurrich (1889) (Fig. 5). Among the eight primary mesenteries, the dorsal and ventral mesenteries, which grow to the narrow sides of the flattened pharynx, are termed directive mesenteries. The location of retractor muscles on the mesenteries also determines the bilateral symmetry of the anemone body: in the directives they face outwards, towards the exocoels, whereas in the lateral mesenteries they face towards the ventral pair of directives (Fig. 5) (Haddon, 1889; McMurrich, 1889; Bourne, 1900; Duerden, 1899; Panikkar, 1937; Grebelny, 1982; Berking, 2007; Malakhov, 2016).

After development of the first eight mesenteries, one mesentery appears on the ventral side of each lateral mesentery, with a retractor muscle facing to it. This yields four lateral pairs (“pairs”). These four mesenteries remain rudimentary in some burrowing anemones (Fig. 6) (*Edwardsiidae* Andres, 1881) but reach the size of the primary mesenteries in all others. At this stage (the *Halcampa*, the *Halcampula* or the *Halcampoides* stage) the polyp already has twelve mesenteries, which constitute the first hexamerous cycle and make the animal radially symmetrical (Fig. 7). Subsequently, mesentery formation occurs in ordinary pairs consisting of adjoining mesenteries, with retractor muscles facing each other. The number of mesenterial pairs increases according to the rule: 6+6+12+24+48 ... (Figs 8, 9) (Hertwig, 1882; Haddon, 1889; Bourne, 1900; Pax, 1914; Grebelny, 1982; Malakhov, 2016).

1.3. Classification based on mesentery arrangement

Studying the development of the mesenteries in soft corals and sea anemones, Hertwig & Hertwig (1879) first noted the similarity between certain worm-like anemones, namely the edwardsians, and the octocorals. Both groups feature, there are eight mesenteries, and their arrangement throughout the life of the polyp determines the bilateral symmetry of the body. The authors concluded that

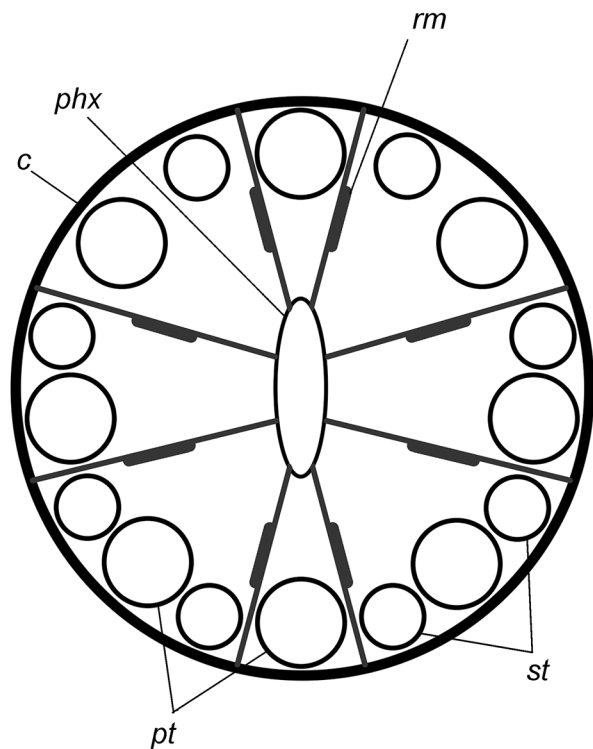


Fig. 10. Early description of a mismatching number of tentacles and mesenteries in *Edwardsia*. *c*, column; *phx*, pharynx; *rm*, retractor muscle; *pt*, primary tentacles; *st*, secondary tentacles. After Andres (1881).

“Edwardsien” were a special group. In their way of life, they resemble the ceriantharians, but their internal organization more closely resembles that of other sea anemones. Nonetheless, the presence of eight mesenteries in *Edwardsia* de Quatrefages, 1842, as well as a mismatching number of tentacles and mesenteries (Fig. 10), led Hertwig & Hertwig (1879) to place the edwardsians in a separate group, unlike the system of Milne-Edwards & Haime (1857) or Gosse (1860).

Like Hertwig & Hertwig (1879), Andres (1881) noted that the edwardsians are a special group. According to Andres, the edwardsiids are octomerous and characterised by a discrepancy between the number of tentacles and endocoels/exocoels. In most anemones, one tentacle corresponds to each endocoel (the space between two mesenteries of the same pair), and one tentacle to each exocoel (the space between different pairs). In *Edwardsia*, each endocoel formed by a pair of directive mesenteries communicates with one tentacle, and each lateral chamber communicates with two or

three tentacles (Fig. 10) (Andres, 1881). Based on these characters, Andres (1883) joined these polyps into the family Edwardsinae Andres, 1883, but other worm-like polyps were combined with large anemones into the family Actininae Andres, 1883, which was subdivided into five subfamilies. Thus, unlike other researchers (Milne-Edwards & Haime, 1857; Gosse, 1860), Andres (1883) began to split the burrowing sea anemones into a larger number of groups rather than putting them in one family (Ilyanthidae). He still relied more on external features, distributing the burrowing sea anemones among different subfamilies: Halcampidae Andres, 1883, Siphonactinidae Andres, 1883 (now Haloclavidae Verrill, 1899), Phellidae Andres, 1883, Ilyanthidae, Heteractidae Andres, 1883, Mesacmaeidae Andres, 1883, whereas the subfamilies Phellidae and Heteractidae included the burrowing forms and sea anemones with a pedal disc (Fig. 11) (Andres, 1883).

Studying the “Challenger” collection, R. Hertwig (1882), based on the number and arrangement of the mesenteries, proposed to divide Actinaria into six tribes: Hexactinia, Paractinia, Monauleae, Edwardsiae, Zoantheae, Ceriantheae. Only three of them, Hexactinia, Paractinia and Edwardsiae, included anemones without a pedal disc. The tribe Edwardsiae was characterised by the presence of only eight mesenteries: two pairs of directive mesenteries and four unpaired mesenteries (Fig. 5). The remaining burrowing anemones were included by Hertwig (1882) in the tribe Hexactinia because they had at least six (usually more) pairs of mesenteries and then increasing in multiples of six (Figs 7–9). The tribe Paractinia included forms in which the number of antimeres did not increase in multiples of six. Based on the shape of the aboral body end, Hertwig (1882, 1888) divided Hexactinia into forms with and without a pedal disc. The polyps, which had no pedal discs, constituted two families, Ilyanthidae and Siphonactinidae. The representatives of the first did not have conchula, in contrast to the second, which did (Hertwig, 1882, 1888).

Danielssen (1890) and McMurrich (1891, 1893), like other zoologists, followed the classification of Hertwig (1882, 1888). Danielssen (1890) appreciated the works of his predecessors (e.g. Gosse, 1858, 1860), but Hertwig’s classification

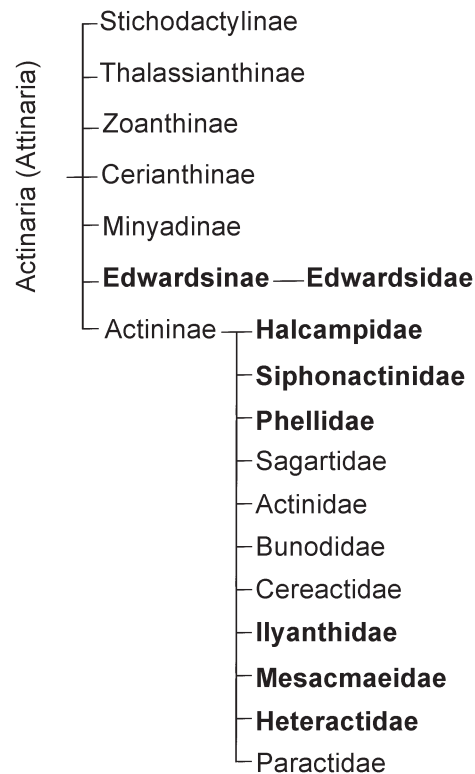


Fig 11. The position of burrowing sea anemones (in bold) in Andres’s (1883) classification of sea anemones sensu lato.

seemed to him more attractive because it relied on a more solid foundation. Nonetheless, external characters should not be ignored because they can be used as valuable auxiliary elements. Danielssen used such a combination of external and internal features in his monograph on the sea anemones collected by the Norwegian North Atlantic Expedition. He described several species of burrowing sea anemones from the North Atlantic and established a new family of Andvakiidae Danielssen, 1890 inside the tribe Hexactinia. He also recognised the new tribe Aegireae Danielssen, 1890, which included the family Aegiridae Danielssen, 1890, in which he placed *Fenja mirabilis* Danielssen, 1890 and *Aegir frigidus* Danielssen, 1890 (both species have now been synonymised with *Halcampoides purpureus* (Studer, 1879).

Faurot (1895) contributed significantly to the development of the taxonomy of burrowing sea anemones. He revealed that *Edwardsia* in fact has more than eight mesenteries (Fig. 6). Faurot discovered that *Edwardsia beautempsii* de Quat-

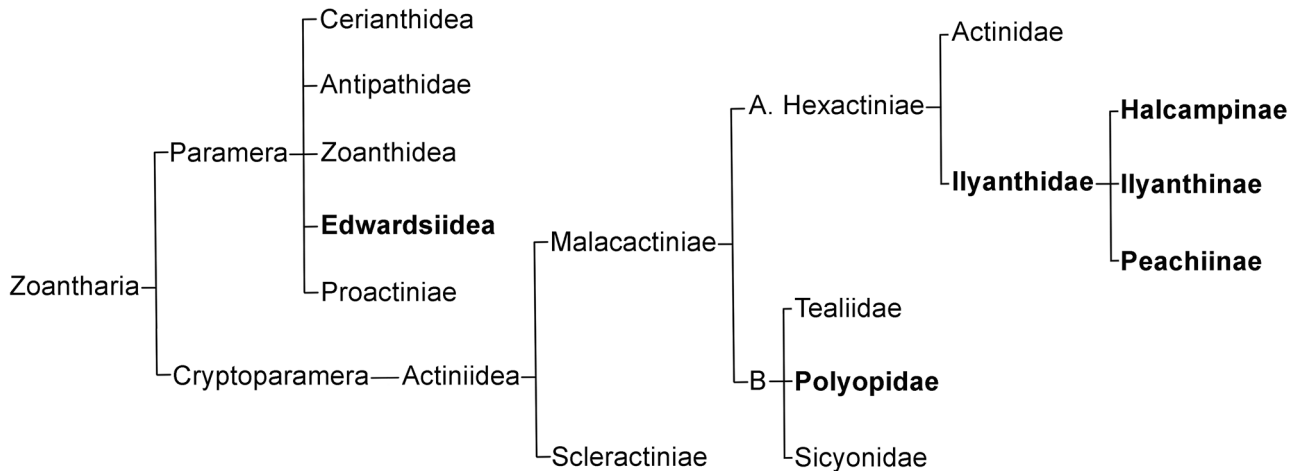


Fig 12. The position of burrowing sea anemones (in bold) in Bourne's (1900) classification of Zoantharia sensu lato.

refages, 1842, in addition to eight macrocnemes (large perfect mesenteries), also developed eight microcnemes (very underdeveloped and which long remained unnoticed by other morphologists). The presence of additional mesenteries explained the presence of sixteen tentacles and made it possible to reject the opinion of early researchers that the number of tentacles in this genus exceeds the number of mesenteries. Although Faurot did not trace the order of appearance of additional mesenteries, he considered it quite probable that they appear in the exocoels, as in all the hexactinians. This discovery of microcnemes in *Edwardsia*, in Faurot's opinion, showed the inconsistency of isolating these anemones in a separate branch (Faurot, 1895).

Beneden (1897) considered Faurot's (1895) discovery of the rudimentary mesenteries to be the most important event for the taxonomy of sea anemones. In recognition of this fact, he considered it impossible to separate the edwardsians from the hexactinians as had been proposed by Hertwig (1882, 1888) because there is no significant difference between the two groups. The adaptation to different habitat conditions should not play a significant role, especially since the remaining burrowing sea anemones are placed in the same tribe as the attached polyps. Based on mesentery development, Beneden's (1897) system placed all sea anemones in the suborder Actiniaria, order Hexactiniaria and subclass Zoanthactiniaria.

Bourne's (1900) classification, like Hertwig's (1882, 1888), separated the edwardsians from all other burrowing anemones into the order Edwardsiidea, which he placed together with the orders Cerianthidea, Antipathidea, Zoanthidea and Proactiniae in the grada Paramera, which united forms with primitive bilateral symmetry. Bourne placed the remaining burrowing sea anemones together with large hexamerous sea anemones in the grada Cryptoparamera. The latter included polyps whose primary bilateral symmetry is substituted by radial development of the second and succeeding cycles of mesenteries. Bourne placed these sea anemones in the order Actiniidea, groups A. Hexactiniae and B. The burrowing forms were placed in the families Ilyanthidae and Polyopidae. As a significant diagnostic feature, Bourne used the presence of a rounded aboral end of the body. Based mainly on the number of mesenteries and tentacles, he distributed them into the subfamilies Halcampinae, Ilyanthinae, Peachiinae in the family Ilyanthidae (Fig. 12) (Bourne, 1900).

Somewhat later, Delage & Hérouard (1901) proposed a curious system. In the suborder Hexactinidae, the authors placed large polyps attached to hard substrates in the tribe Actinina. The burrowing forms were encompassed in the tribes Edwardsina and Halcampina, whose representatives differed in the number of the mesenteries making up the first and the second cycles. The tribe Edwardsina included the families Ed-

wardsinae and Protantheinae. Edwardsinae were defined as forms in which only the first eight mesenteries are well developed, whereas mesenteries of the second cycle are confined to the most distal part. Protantheinae were also characterised by eight well-developed mesenteries, and by micromesenteries that form a more or less complete second cycle developed along entire length of the column. The tribe Halcampina included polyps characterised by the first two complete cycles and sometimes by an incomplete third cycle. Delage & Hérouard referred three families to this tribe. These are Halcampinae, whose polyps are characterised by a first cycle of twelve macromesenteries and whose second cycle is either absent or consists of micromesenteries (genera *Halcompa*, *Halcompoides* Danielssen, 1890, *Peachia* etc.), Monaulinae (genus *Scytophorus* Hertwig, 1882), previously considered by Hertwig (1882) in the rank of tribe, and Holactininae with a single genus *Gyrractis* Boveri, 1893 (Delage & Hérouard, 1901).

Hickson's (1906) system recognizes two orders: Edwardsiidae and Actiniaria. The order Edwardsiidae encompassed the edwardsians and the protantheans based on the presence of only eight perfect mesenteries. The other burrowing sea anemones were placed along with attached polyps in the order Actiniaria because they had more than eight perfect mesenteries.

Later, Carlgren (1908) divided all coral polyps, Anthozoa, based on the number of primary mesenteries into three subclasses: Hexacorallia, Octocorallia, and Dodecacorallia. The first subclass, Hexacorallia (sensu Carlgren only), was characterised by the presence of six primary mesenteries and later also by a varying number of metamesenteries. Only the ceriantharians and the antipatharians were attributed here. The subclass Octocorallia included polyps with eight bilateral protomesenteries. In the third subclass, Dodecacorallia, he placed polyps with twelve protomesenteries, usually also having a different number of metamesenteries, arranged bilaterally or radially. This subclass encompassed the orders Zoantharia (= Zoanthida), Actiniaria and Madreporaria (= Scleractinia).

Bourne (1916) did not agree with the names of taxa proposed by Carlgren (1908). According to Bourne, the name Hexacorallia was tradition-

ally used for the sea anemones and scleractinians, but not for the antipatharians and ceriantharians. Bourne felt that since the edwardsians did not have six pairs of the first cycle of mesenteries, the names "Hexacorallia" and "Dodecacorallia" did not reflect this. For a subclass that included the edwardsians, the name Zoanthactiniaria proposed by Beneden (1897) would be more appropriate. Even though a detailed study of polyp anatomy and mesentery arrangement clearly indicated that the edwardsians belong to Actiniaria, Bourne continued to consider this group separately from the remaining sea anemones, referring them to the order Edwardsiaria, subclass Zoanthactiniaria. Bourne (1916) united the other sea anemones in the suborder Actiniaria and placed them in the order Dodecactiniaria, subclass Zoanthactiniaria. Thus, he insisted on the independence of the edwardsians based on a detailed study of the sequence of mesenteries and tentacles arising in several edwardsiid species. His observations showed that the succession of appearance of four lateral micromesenteries and tentacles within the genus *Edwardsia* varies. On this basis, he denied any homology of the mesenteries of the fifth and sixth bilateral pairs in *Edwardsia* and other anemones. Moreover, a correspondence of the six primary tentacles to exocoels and the two directive tentacles to endocoels is typical for most anemones, whereas in some *Edwardsia* all eight primary tentacles correspond to the endocoels (Bourne, 1916).

Stephenson (1920, 1921, 1922) in his "On the Classification of Actiniaria" adhered to the Bourne's (1916) system. Stephenson (1921) similarly separated the edwardsians in the order Edwardsiaria, subclass Zoanthactiniaria. He united the remaining forms, as suggested by Bourne (1916), in the suborder Actiniaria, order Dodecactiniaria, subclass Zoanthactiniaria. The further division of the sea anemones by Stephenson was partly consistent with Carlgren's (1898, 1900) system. Stephenson (1922) also separated the tribe Nynantheae within the suborder Actiniaria, but unlike Carlgren (1898, 1900) subdivided this tribe into four subtribes: Athenaria, Endocoelactaria, Mesomyaria, Endomyaria. Some burrowing sea anemones were located in the families Halcampidae and Ilyanthidae in the subtribe Athenaria. One burrowing form, *Andresia*

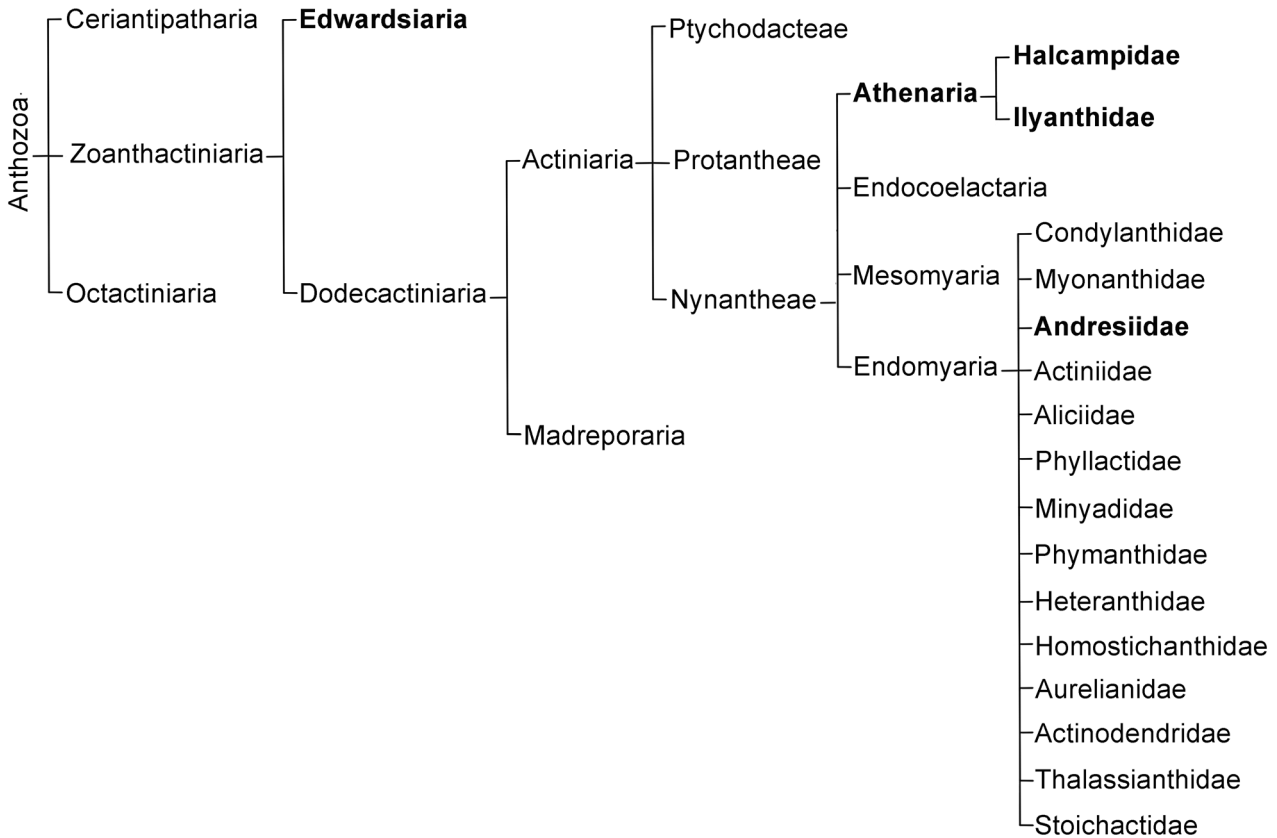


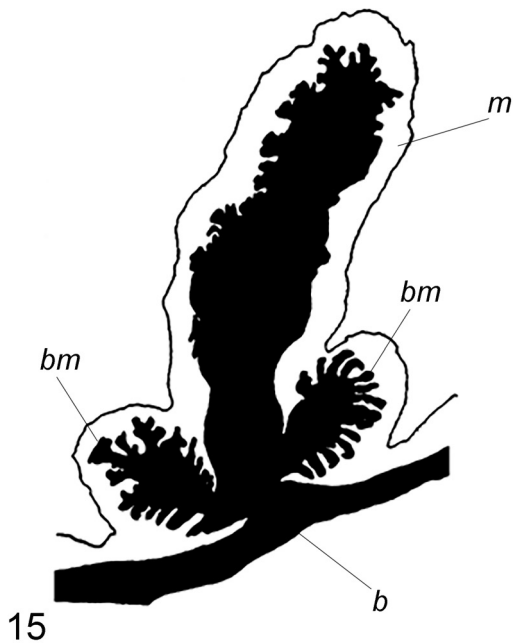
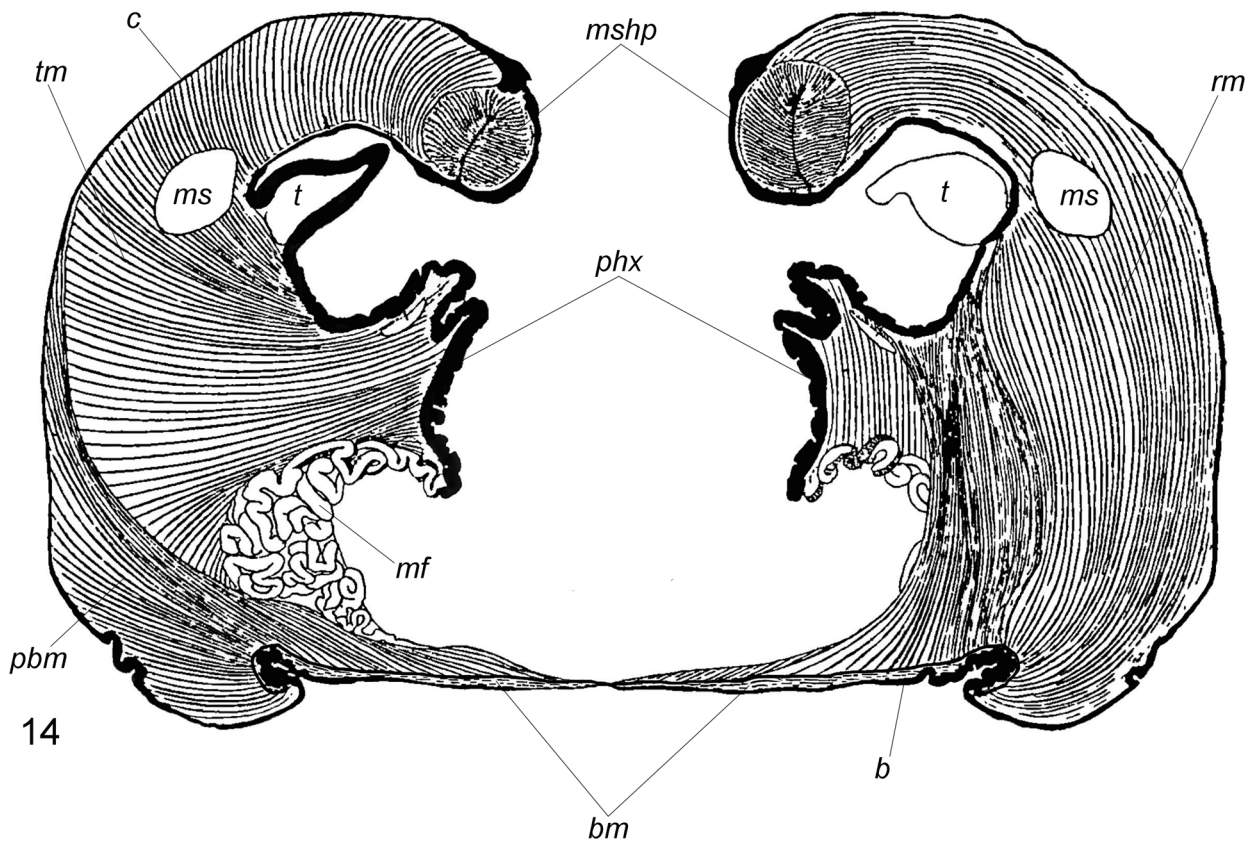
Fig 13. The position of burrowing sea anemones (in bold) in Stephenson’s (1920, 1921, 1922) classification of coral polyps.

partenopea (Andres, 1883), however, was isolated in the family Andresiidae Stephenson, 1922 inside of the subtribe Endomyaria along with polyps that have an endodermal sphincter (Fig. 13).

1.4. Classification based on presence or absence of basilar muscles

The next important step in building an anatomical classification of the sea anemones was the use of a new attribute proposed by Carlgren (1898, 1900), the presence of basilar muscles. The fibers of the basilar muscles pass along the mesentery accretion line to the base on both sides of the mesogloal plate of the mesentery (Figs 14, 15). The basilar muscles constrict edges of a pedal disc to its center and promote crawling. All anemones with basilar muscles and a pedal disc, as a rule, inhabit solid substrates. They were united by Carlgren into a new taxon, Thenaria Carlgren, 1898. At that time the burrowing forms with an

elongated body and a rounded aboral end, but lacking basilar muscles, made up Athenaria Carlgren, 1898 (Fig. 16). That group corresponded to “Actinines pivotantes” and was largely consistent with Ilyanthidae, but did not include the ceriantharians. Carlgren included the edwardsians in Athenaria as a family Edwardsidae. The remaining burrowing sea anemones were distributed among the families Halcampomorphidae Carlgren, 1900, Halcampactidae Carlgren, 1900, Halcampidae, Andvakiidae, and Ilyanthidae. Later, Carlgren (1905) used other names to refer to these groups—Basilaria (for Thenaria) and Abasilaria (for Athenaria)—emphasizing that shape of the proximal end is less important and that the main distinguishing feature is the presence of basilar muscles in the first group and their absence in the second (Figs 14, 16). Both these groups, Thenaria and Athenaria, were united in the tribe Nynantheae Carlgren, 1898 (suborder in Carlgren, 1949).



Figs 14–15. Mesentery musculature of *Thenaria*. **14**, position of different muscles on mesentery, viewed from the exocoelic (left half) and endocoelic (right half) side, vertical section; **15**, position of basilar muscles of mesentery, vertical section. *c*, column; *t*, tentacle; *phx*, pharynx; *mshp*, marginal sphincter; *ms*, marginal stoma; *m*, mesentery; *mf*, mesenterial filament; *b*, base; *rm*, retractor muscle; *tm*, transversal muscle; *pbm*, parieto-basilar muscle; *bm*, basilar muscle. After Carlgren (1905) and Stephenson (1928).

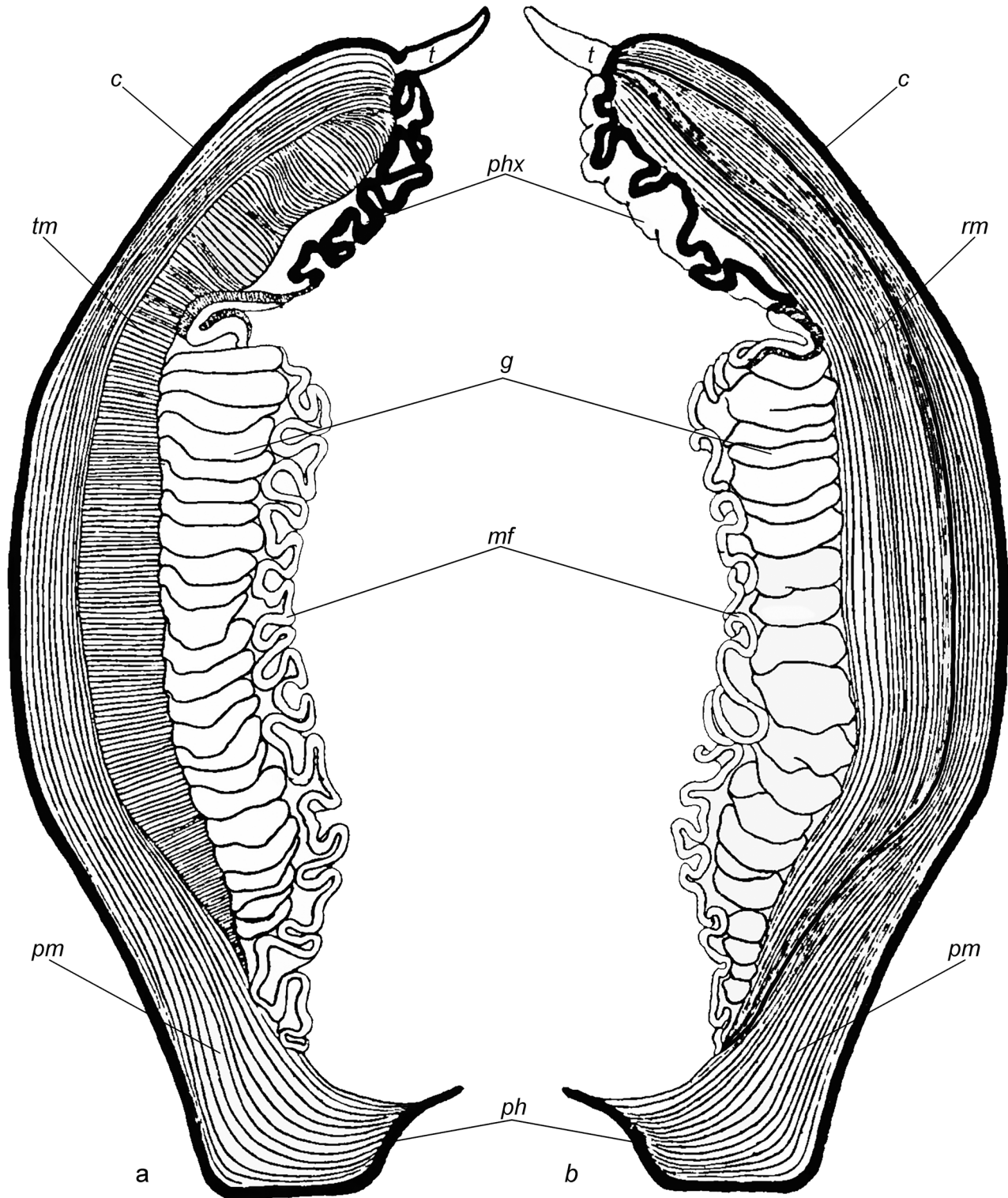


Fig 16. Mesentery musculature of *Athenaria*, vertical section. **a**, viewed from the exocoelic side; **b**, viewed from the endocoelic side. *c*, column; *t*, tentacle; *ph*, physa; *phx*, pharynx; *g*, gonads; *mf*, mesenterial filament; *tm*, transversal muscle; *rm*, retractor muscle; *pm*, parietal muscle. After Carlgren (1905).

McMurrich (1904) did not agree with Carlgren's (1898, 1900) system. He noted that, although Carlgren's classification is based on a stable character, such a division leads to association of unrelated forms and separation of relatives. McMurrich also noted that the relationship between a pedal disc and muscles is so close that it is impossible to modify one without changing the other. Furthermore, from his point of view, it would be more correct to refer not to the absence of a pedal disc, but to its modification into a physa. In this case, the parietal muscles should be considered as homologous with the basilar muscles. Avoiding the system proposed by Carlgren (1898, 1900), McMurrich mainly followed Andres' (1883) classification. Inside the order Actiniaria, he separated the suborder Actininae, which united the burrowing sea anemones and the polyps with a well-developed pedal disc, which were placed by him into different families. McMurrich (1904) considered the edwardsians in the rank of a family and enlarged this family by placing *Cactosoma chilense* (McMurrich, 1904) in it.

In the fundamental work on the anemones collected during the Ingolf Expedition, Carlgren (1921) continued to follow the classification proposed by him in 1898 and 1900. He emphasised that the main feature that distinguished Athenaria (Abasilaria) from Thenaria (Basilaria) was the absence of the basilar muscles in the first group. The earlier researchers (Milne-Edwards & Haime, 1957; Gosse, 1858, 1860; Verrill, 1864; Klunzinger, 1877; Andres, 1883; Hertwig, 1882, 1888) attached great importance to the shape of the proximal end, placing the burrowing sea anemones in a separate group. However, the absence of basilar muscles was a more important feature for combining these polyps because the shape of the proximal end can vary considerably, although many of these sea anemones were undoubtedly characterised by a rounded proximal end (Carlgren, 1921). He considered the presence or absence of a sphincter and its structure, as well as the presence or absence of acontia, as the main features for division of Athenaria into families. Thus, he distinguished the family Edwardsiidae with two subfamilies, Edwardsiinae and Milne-Edwardsiinae, whose representatives lacked a sphincter but differed from each other in

the length of the inner and outer tentacles as well as in the presence or absence of nemathybomes and physa. Furthermore, he established a new family Limnactiniidae Carlgren, 1921, whose polyps lacked either a sphincter and or tentacles. He preserved the family Andvakiidae, characterised by a mesogloal sphincter and acontia. Beyond this, he proposed a new family Halcampactiidae Carlgren, 1921 with acontia but without a sphincter. The family Halcampidae joined forms with a simple or double mesogloal sphincter, but without acontia. Halcampoididae Appellöf, 1896 included polyps without a sphincter or with a very weak endodermal one. Carlgren (1921) also retained the family Ilyanthidae because its representatives exhibited an endodermal sphincter.

Afterwards, as a result of many years of discussion between Carlgren and Stephenson, Carlgren (1949) published the system that has become widespread and still serves as the basis of the Actiniaria classification. In this system, Carlgren distinguished within the infraorder Athenaria nine families, namely Edwardsiidae, Halcampoididae, Haloclavidae, Andresiidae, Halcampidae, Haliactinidae, Octineonidae and Andvakiidae. As before (1921), when classifying the burrowing sea anemones, Carlgren re-

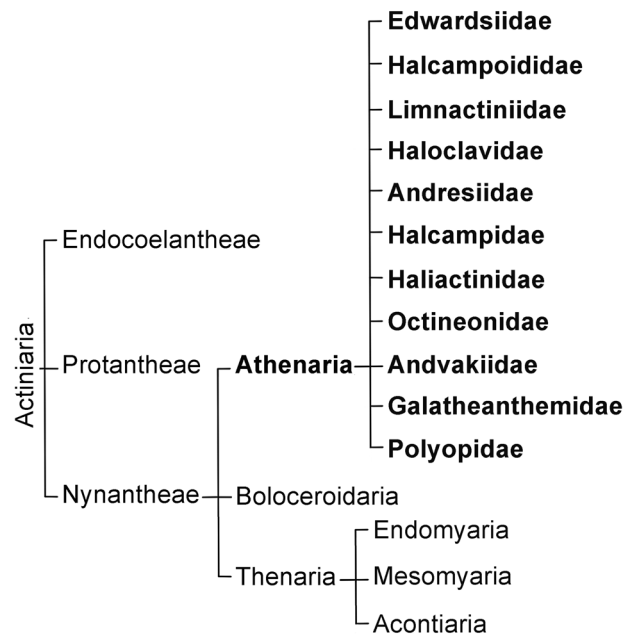


Fig 17. The position of burrowing sea anemones (in bold) in Carlgren's (1949) classification of Actiniaria with some modifications by Fautin (2013).

lied mainly on characters such as presence or absence of a sphincter and acontia. Later, Carlgren (1956) added another family, Galatheanthemidae, whose polyps were characterised by a very strong mesogloal sphincter and a strong cuticle, forming a tube. Carlgren's (1949) system was adopted for a long time by a number of researchers (e.g. Hand & Bushnell, 1967; Manuel, 1977; Fautin, 1988; Sanamyan & Sanamyan, 1998; Gonzalez-Muñoz et al., 2012) and, with minor modifications, was available on the "Hexacorallians of the World" website (Fautin, 2013) (Fig. 17).

1.5. Classification based on molecular markers

Adopting a system based on molecular markers was suggested by Rodríguez et al. (2014). They proposed a completely new classification, in which Actiniaria is divided into two suborders, Anenthemonae and Entthemonae. The representatives of Carlgren's (1949) Athenaria were distributed within the composition of both suborders and settled on very distant branches. The suborder Anenthemonae united the superfamily Edwardsioidea Andres, 1881 with one family of the burrowing sea anemones Edwardsiidae and the superfamily Actinernoidea Stephenson, 1922. This suborder, according to Rodríguez et al., includes the actinarians with a unique arrangement of mesenteries that differs from the most typical hexamerous arrangement with mesenterial pairs arising in exocoels. The remaining burrowing sea anemones are placed in the suborder Entthemonae and distributed among the three superfamilies Actinostoloidea Carlgren, 1932, Metridioidea Carlgren, 1893, and Actinioidea Rafinesque, 1815 (Rodríguez et al., 2014; Gusmão et al., 2019). Members of Entthemonae, according to Rodríguez et al. (2014), have mostly hexamerous cycles with pairs of mesenteries arising in the exocoels.

1.6. Four steps in the development of the burrowing sea anemone classification

My review of the establishment of the classification of burrowing sea anemones underlines the result of laborious work devoted to the study of the morphology and anatomy of these animals. Based on the views and assumptions of researchers, four steps in the formation of the classification

can be distinguished. Each stage is characterised by a key feature that underlies the system.

The first period of classification dates back to the mid-19th century and is associated with Milne-Edwards & Haime (1857), Gosse (1858, 1860), and Klunzinger (1877). This period is characterised by allocating the burrowing sea anemones into a separate group, mainly based on their elongated body shape and rounded aboral end (Fig. 1a, b). By attaching such great importance to external features, the researchers combined unrelated forms; for example, Gosse (1860) placed the burrowing sea anemones together with the ceriantharians.

The second stage is associated with the onset of anatomical studies by the German zoologists R. Hertwig and O. Hertwig. The discovery of eight perfect mesenteries (Fig. 5) in members of the family Edwardsiidae led them to be separated from all the other burrowing sea anemones. In turn, the latter were combined with large attached polyps (Hertwig & Hertwig, 1879). Some researchers (e.g. Bourne, 1916; Stephenson, 1920, 1921, 1922) supported this separation of the burrowing forms until the 1920s, even though the uniformity of the mesenterial development in the both edwardsians and all the other hexamerous sea anemones was already shown in the late 19th century (see Faurot, 1895).

The use of the basilar muscles by Carlgren (1898, 1900, 1905, 1949) in creating the system of anemones opens its third stage. Carlgren (1898, 1900, 1949) established the infraorder Athenaria, which combined the burrowing forms without basilar muscles (Fig. 16), and the infraorder Thenaria, whose representatives had such muscles (Figs 14, 15). However, subsequent detailed analysis of morpho-anatomical characters and the description of new species led some specialists (e.g. Schmidt, 1972, 1974) to assume a polyphyly of Athenaria and to reject the absence of basilar muscles as a key feature for isolating all the burrowing sea anemones in a single group.

At present, animal systems based on molecular markers are very popular and considered to be comprehensive. In the classification of the burrowing sea anemones, the use of molecular methods opened the next, fourth stage. However, recent changes in the anemone classification show

that they cannot be considered as exhaustive or successful. This is clearly evident in the new higher-level classification for Actiniaria proposed by Rodríguez et al. (2014). These researchers subdivided the order Actiniaria into the suborder Anenthemonae and the suborder Enthemonae. Rodríguez et al. (2014) noted that their findings highlight the inadequacy of the previous classification of the order Actiniaria. Nonetheless, from the perspective of morphology, anatomy, processes of development, behaviour, and lifestyle, a new system based on molecular markers must also be considered insufficient. Rodríguez et al. (2014) remark that their findings based on the DNA sequence data correspond neatly with several morphological trends observed in the order Actiniaria. For example, they proposed uniting the edwardsian and endocoelanthean sea anemones in the suborder Anenthemonae because these actinarians have a unique mesentery arrangement that differs from the most typical hexamerous arrangement with pairs of mesenteries arising in exocoels. Such a characteristic of the suborder is highly doubtful. In the endocoelanthean sea anemones, when the first twelve mesenteries (six couples) are developed, all the subsequent pairs appear in the lateral endocoels with longitudinal muscles oriented as in directives. Of course, this is a unique arrangement not found in any other group. Nonetheless, the edwardsians do not share this uniqueness with the endocoelanthean sea anemones. As early as 1895, Faurot showed that the edwardsians have the same mesentery organization as numerous hexamerous sea anemones. The edwardsians also have six pairs of mesenteries that constitute the first cycle; the mesenteries of the next cycles also appear in pairs in exocoels. The differences are that the edwardsians have only eight perfect macrocnemes; lateral mesenteries (microcnemes) that make up them pairs are not fully developed. Microcnemes arise only in the most distal part of the column (see Fig. 4 in Sanamyan et al., 2015). Moreover, eight *Edwardsia* mesenteries are also found in other representatives of Carlgren's Athenaria. For example, the arrangement of mesenteries in *Octineon suecicum* Carlgren, 1940 (Octineonidae Fowler, 1894) and *Limnactinia* Carlgren, 1921 (Limnactiniidae Carlgren, 1921) resembles that of the edwardsians (see Sanamyan et al., 2018; Carlgren, 1921, 1927,

respectively). Stephenson (1935) also noted that *Halcampa* could have only eight macrocnemes in the first mesenterial cycle. Moreover, eight *Edwardsia* mesenteries were found in Condylanthidae Stephenson, 1922, in representatives of the genus *Segonzactis* Riemann-Zürneck, 1979 (see Riemann-Zürneck, 1979; Dimitris & Chariton, 2002). Thus, the differences in the developmental processes of mesenteries in edwardsiids and endocoelanthids, as well as the discovery of eight *Edwardsia* mesenteries in representatives of other families, make it impossible to combine these sea anemones into the suborder Anenthemonae. Finally, the edwardsiids differ considerably from the endocoelanthids in other features of anatomy, morphology, behaviour and lifestyle.

The remaining burrowing forms (apart from Edwardsiidae) were placed by Rodríguez et al. (2014) and by Gusmão et al. (2019) in the suborder Enthemonae along with the sea anemones of the remaining Carlgren's groups and distributed among three superfamilies: Actinostoloidea, Metridioidea, and Actinioidea. This new division of the burrowing sea anemones confirms the assumptions of previous researchers about the polyphyly of Athenaria (e.g. Hand, 1966; Schmidt, 1974). The system proposed by Rodríguez et al. (2014), however, joins completely dissimilar sea anemones into one group, and their dissimilarity goes beyond morpho-anatomical characters. Although the burrowing forms have several common structures with the remaining actinarians, they are characterised by features inherent only to them. This leads to indistinctness and diffusiveness of the superfamily diagnoses.

Accordingly, the methods of classification based on molecular markers clearly require significant improvement. Importantly, different markers give different results, as is clearly evident from the position of the mysterious *Relicanthus daphneae* (Daly, 2006). Rodríguez et al. (2014) selected two nuclear and three mitochondrial genes with multiple analytical methods, which did not allow finding a precise position for *Relicanthus* in the Actiniaria system. As the result, the authors had to rank this animal as *incerti ordinis*. In a subsequent publication based on numerous complete nucleotide sequences of mitochondrial DNA, however, the taxonomic status of *Relicanthus daphneae* was

changed: it was returned to the order Actiniaria in the rank of the suborder Helenmonae Daly et Rodríguez, 2019 (Xiao et al., 2019).

The use of the molecular markers to clarify the systematic position of some burrowing sea anemones has also led to unexpected changes. For example, *Haloclava* Verrill, 1899 in the newly presented scheme (see Fig. 2 in Rodríguez et al., 2014) was placed within the clade Actinioidea, but one species *Haloclava producta* (Stimpson, 1856) and another *Haloclava* sp. were moved apart. Later, however, *H. producta* took a position close to representatives of the clade Metridioidea (Xiao et al., 2019). Another genus, *Halcampoides*, was originally (Rodríguez et al., 2014) placed inside the clade Metridioidea, but later (Xiao et al., 2019) became very distant from representatives of that clade.

Thus, at present, I consider that abandoning the traditional classification of Actiniaria (Carlgrén, 1949; Fautin, 2013) built on morpho-anatomical characters and founding it based on molecular markers is premature.

2. Views on the evolution of the burrowing sea anemones

2.1. The burrowing sea anemones are a primitive group, from which all other anemones originate

Based on the study of mesentery development in different anthozoan groups, researchers (Hertwig & Hertwig, 1879; Hertwig, 1882; Boveri, 1890) assumed that the edwardsians are closest to the ancestral forms and that all other anemones originate from them. In the earlier stages of ontogenesis, all sea anemones are bilaterally symmetrical animals. The edwardsians, however, stop at the eight-mesentery stage and retain this type of symmetry throughout their lives. In the further developmental process the remaining anemones turn to radial (mainly hexamerous) symmetry by completing the lateral pairs and by developing paired mesenteries of the next cycles in the exocoels (Hertwig & Hertwig, 1879; Boveri, 1890). Boveri (1890) examined *Halcampia chrysanthelium* (Peach in Johnston, 1847) in detail. Although it forms twelve mesenteries as in hexactinians, they are unevenly developed: eight strong ones,

corresponding to *Edwardsia* mesenteries, and four weak ones forming pairs with four lateral mesenteries. Like Hertwig (1882), Boveri (1890) considered *Halcampia* Gosse, 1858 to be a transitional form between *Edwardsia* and hexactinians. Regressive development seemed unlikely to him.

McMurrich (1891), discussing issues of anemone phylogeny, also wrote that representatives of the order Actiniaria descended from ancestors close to modern *Edwardsia*. He believed that a form similar to but different from the scyphozoan larva should be placed at the root of the Anthozoa tree. From this ancestor, a transition occurred to a polyp with octomerous symmetry, which gave rise to *Edwardsia* and all Alcyonaria. Since the stage with eight mesenteries was described in the ontogeny of all non-skeletal coral polyps, including the ceriantharians and zoantharians, McMurrich (1891) thought that their origin was associated with an *Edwardsia*-like form. Considering the development of the first hexamerous cycle of mesenteries, he also described the stage in which four lateral mesenteries reach a pharynx and in which smaller mesenteries that form pairs with them do not reach it, i.e. remain imperfect. Although no adult sea anemone with this structure is known, this stage represents an important period in evolution. It gave rise to the genera *Scytophorus* Hertwig, 1882, *Gonactinia* Sars, 1851 and *Oractis* McMurrich, 1893, forming the group Protactiniae Carlgrén, 1891, whose representatives had an incomplete second cycle of mesenteries. Moreover, an important feature of Protactiniae was the preservation of bilateral symmetry. They gave rise to hexamerous anemones, in which, upon completion of development of the second mesenterial cycle, radial symmetry replaces the original bilateral symmetry. However, forms belonging to the genus *Halcampia* disturbed the strictness of the phylogenetic scheme. Some members of this genus had only six pairs of mesenteries and could be considered more primitive. Other *Halcampia* spp. and representatives of closely related genera also exhibited secondary imperfect mesenteries. This would make them more advanced. The first of these, according to McMurrich, could be close to *Scytophorus*, *Gonactinia* and *Oractis*, but this was unlikely because all species of the genus *Halcampia* were very similar to each other and differed sig-

nificantly from the three other genera. Therefore, *Halcampa* and closely related genera with secondary mesenteries most likely originate from hexactinians due to a stopped development that led to the reduction of the second cycle of mesenteries (McMurrich, 1891).

As noted above, Carlgren (1898, 1900) proposed dividing the sea anemones into Thenaria and Athenaria based on the presence of basilar muscles in the former and their absence in the latter. Carlgren (1905) considered this presence to be a more advanced trait that arose later in evolution, and was characteristic of “higher” anemones with a well-developed flat pedal disc (Figs 14, 15). The absence of basilar muscles, in contrast, is a primitive character of “lower” Actiniaria–Athenaria. Greater mobility and elongated body shape contributed considerably to the development of longitudinal muscles on the mesenteries in Athenaria (Fig. 16). These retractor muscles are homologous to those of other anemones. Carlgren believed that the parietal muscles, lying on one side of the mesentery, were the modified parieto-basilar muscles, and those on the other side were part of the longitudinal muscles of the mesentery. Importantly, the musculature of the Athenaria mesenteries did not have a homologue to the basilar muscles of higher anemones (Figs 14–16) (Carlgren, 1905, 1921).

Stephenson (1920, 1921, 1922) wrote that a potential ancestor for all Anthozoa was a small planktonic organism characterised by eight mesenteries and bilateral symmetry. Several forms could have derived from it and given rise to all the anthozoan groups. With regard to the anemones, Stephenson (1921) believed that Edwardsiaria were the first to separate from the common stem; they acquired a burrowing lifestyle and became worm-like. The main branch led to the appearance of a *Halcampa*-like organism, from which most anemones originated. According to Stephenson (1920, 1921), primitive forms were small and had few mesenteries, the macrocnemes, which performed all the functions and had mesenterial filaments, gonads and muscles¹. The evolution of anemones was marked by a tendency to increase the size of the individual and, accordingly, to develop a large

number of mesenteries that have undergone specialization. The first cycles consisted of sterile perfect mesenteries with weak muscles; imperfect fertile mesenteries formed subsequent cycles (Stephenson, 1920, 1921). Thus, Stephenson also separated *Edwardsia* from the other anemones and considered the halcampids to be more primitive forms that gave rise to all large hexamerous polyps. Nevertheless, he cautiously assumed that the edwardsians still belong to the Nynantheae (according to Carlgren’s (1898, 1900) suborder, including Athenaria and Thenaria), in which some mesenteries became rudimentary and form only bilateral couples. The histological structure of *Edwardsia* also shows similarities with Nynantheae (Stephenson, 1920, 1921, 1922).

2.2. The burrowing sea anemones originate from large hexamerous actinians

Faurot (1895) revealed that *Edwardsia* in fact had more than eight mesenteries. His work largely changed the notions about evolution within Actiniaria and sought to find common and distinctive features of “Actinines pivotantes” and “Hexactinies” using embryology and anatomy data. Although the author did not consider the relationship of different groups of anemones, he showed that all have a common organization plan, which changes from group to group. He suggested that *Edwardsia*, like *Halcampa* or *Peachia* Gosse, 1855, showed a stoppage in development, but more pronounced. In Faurot’s thinking, his discovery by of microcnemes in *Edwardsia* showed the inconsistency of isolating these anemones in a separate branch, and the groundlessness of their affinity to the ancestral form (Faurot, 1895).

Beneden (1897) agreed that the description of the micromesenteries by Faurot (1895) in *Edwardsia beautempsi* and *Edwardsianthus pudicus* (Klunzinger, 1877) negated the assumption about the primitiveness of *Edwardsia*. Van Beneden recognised the *Edwardsia* species as representatives of Hexactiniaria whose development stopped, that retained only the eight perfect mesenteries and became sexually mature. Since these

¹I reserve the right to use the terms “gonads” and “organs” following their traditional application in the literature on sea anemones (e.g. Sanamyan et al., 2018).

species have a total twelve primary mesenteries, as do hexactinians, and in addition an incomplete second cycle of mesenteries, van Beneden considered it impossible to separate the edwardsians from all other anemones and to regard them as an ancestral form. The presence of even rudimentary mesenteries did not allow *Edwardsia* to be considered as a transitional form from an ancestor to hexactinians because, according to van Beneden, these mesenteries could hardly be preserved until the present. Consequently, the edwardsians originated from the hexamerous anemones with a large number of mesenteries and tentacles, as evidenced by the presence in the genus of species with many tentacles and by their hexamerous arrangement. They are hexactinians with underdeveloped mesenteries of the fifth and sixth bilateral pairs of the first cycle and rudimentary mesenteries of the second cycle (Beneden, 1897).

Subsequently, Carlgren & Stephenson (1928) emphasised that the consideration of the genus *Edwardsia* by most zoologists as an example of a primitive eight-ray form, from which all sea anemones originated, is in fact incorrect. On the one hand, *Edwardsia* has more than eight mesenteries (Faurot, 1895), and there are no anemones that have only eight mesenteries in the adult state. On the other hand, *Gonactinia* can be identified as a more primitive form, with an organization closer to the primitive state than *Edwardsia*. Unlike *Gonactinia*, *Edwardsia* is in many ways a more specialised and advanced form. Its few mesenteries indicate, rather, a reduction or cessation of development associated with a worm-like body shape. Moreover, Stephenson rejected Bourne's (1916) assumptions and concluded, based on his own observations, that *Edwardsia*'s microcnemes adjacent to four lateral macrocnemes correspond to the fifth and sixth couples of other anemones, and that the rest of the microcnemes arise as ordinary pairs, but not couples (Carlgren & Stephenson, 1928).

In the second half of the 20th century, with accumulation of new data on anemone diversity, interest in the study of the athenarian polyps was revived. An original view of its origin was expressed by Hand (1966). He believed that Athenaria, long considered as primitive anemones, should be considered as secondarily simplified forms. In his opinion, all the sea anemones originated from the

scleractinians (Scleractinia = Madreporaria). Accordingly, the first sea anemones (which lost their ability to form a skeleton) could, in the late stages of ontogenesis, develop a pedal disc with muscles. These muscles enabled them to attach to a solid substrate, a characteristic of higher anemones. Thus, in Hand's interpretation, it is more correct to consider Thenaria, whose members have numerous mesenteries, to be closer to the ancestor than Athenaria. Hand also concluded that Haeckel's (1966) interpretation of evolution, from simple to complex (from a few to many mesenteries), is incorrect in the case of sea anemones. Hand was the first to draw attention to the similarity of burrowing sea anemones and the polyps of the subtribe Acontiarina (now the superfamily Metridioidea), which goes beyond the presence of acontia in polyps of both groups. Among Acontiarina, representatives of the genera *Flosmaris* Stephenson, 1920 and *Mimetricidium* Hand, 1961, resemble the athenarian polyps in body shape and burrowing lifestyle. Hand therefore concluded that the burrowing lifestyle and the correlated elongation of the body (characteristics of Athenaria) first arose in the acontiarian anemones. In the course of evolution, the latter could lose a muscular base and develop physa. Therefore, the athenarians derived from members of Acontiarina. The athenarians without acontia, such as *Edwardsia* and *Halcampoides*, lost these organs and at the same time, began to mature at earlier ontogenetic stages, therefore reducing the number of mesenteries (Hand, 1966).

Schmidt (1972) also suggested that *Edwardsia* cannot be considered primitive because it has only eight perfect mesenteries. On the contrary, it belongs to the phylogenetically "later", higher anemones. Schmidt (1974) then argued that the presence of basilar muscles is neither an advanced nor a primitive feature: these muscles develop in anemones that settle on a solid substrate and are reduced in the burrowing forms. Thus, the athenarian anemones may have arisen independently in several families due to reduction of the basilar muscles during a transition to soft sediments. Having studied the distribution of nematocysts and certain anatomical traits, Schmidt (1974) divided the athenarians into two actiniarian superfamilies: Endomyaria (now the superfamily Actinioidea), equipped with an endodermal mar-

ginal sphincter muscle, and Mesomyaria (now the superfamily Actinostoloidea), whose mesogloal marginal sphincter muscle consists of muscular fibers embedded in a thick layer of mesogloea.

Based on the strongly differing structure of the edwardsians and the endomyarians, an affinity of these sea anemones as proposed by Schmidt (1972, 1974) seems unlikely. Nonetheless, the description of a new genus *Segonzactis* Riemann-Zürneck, 1979 (Condylanthidae) became a serious argument for conjunction of *Edwardsia*-like anemones with Endomyaria (Riemann-Zürneck, 1979). This genus differs significantly in morpho-anatomical features from the remaining condylantids. It has no basilar muscles, and its eight macrocnemes are located as in *Edwardsia* (Riemann-Zürneck, 1979; Dimitris & Chariton, 2002). Riemann-Zürneck concluded that members of the family Condylanthidae were transitional forms between the endomyarians and the edwardsians. This view was based on the similarity between *Segonzactis* and *Edwardsia* as well as the fact that the family presents a combination of features and their variation between genera (namely dimorphism of mesenteries and their number, the distinctness of body division, and the presence of basilar muscles and a marginal sphincter). Speculating on a direction of the evolution of the group and on the ancestral form, Riemann-Zürneck concluded that the ancestor was probably very close to a typical *Actinia*-like endomyarian sea anemone. One branch of descendants is today represented by the sea anemones (Athenaria), which reduced the size and number of mesenteries and specialised in becoming flexible and contractile animals. They ultimately succeeded in conquering a new habitat, loose sediment. Examples of possible stages of this evolutionary trend are evident in Condylanthidae (Riemann-Zürneck, 1979).

The growing number of works based on molecular markers increasingly support the polyphyly of Carlgren's Athenaria (e.g. Daly et al., 2002, 2008, 2010; Rodríguez et al., 2012, 2014).

2.3. Hypotheses on the origin of the burrowing sea anemones

My review shows two main hypotheses on the origin of the burrowing sea anemones. In the framework of the first hypothesis, the burrowing

forms are considered as primitive, the closest to the ancestor. A number of researchers (see Hertwig & Hertwig, 1879; Hertwig, 1882; Boveri, 1890; Carlgren, 1905), however, have explained their primitiveness in terms of various anatomical features. For example, Hertwig (1882), based on the discovery of only eight mesenteries in *Edwardsia*, considered the edwardsians as being the closest to the ancestor. He defined the remaining burrowing forms (having at least one complete hexamerous cycle of mesenteries) as transitional between *Edwardsia* and attached hexamerous polyps. However, the presence of more than eight mesenteries in the edwardsians contradicts their relationship to Octocorallia, which are generally considered the closest to ancestors of all Anthozoa.

Carlgren (1905) also believed that burrowing sea anemones are a primitive group. Nevertheless, in contrast to Hertwig (1882), he relied on the presence or absence of the basilar muscles. Accordingly, Carlgren (1905) divided the sea anemones into "higher" Thenaria with basilar muscles and a well-developed pedal disc and "lower" Athenaria without such muscles and with a rounded aboral end. Subsequent researchers questioned Carlgren's (1905) assumption about the primitiveness and monophyly of the athenarians. This revived the views of Faurot (1895) and Beneden (1897) and established a new hypothesis suggesting that the burrowing sea anemones are advanced forms (see Carlgren & Stephenson, 1928; Hand, 1966; Schmidt, 1972, 1974).

The first to suspect that burrowing sea anemones could have come from large hexamerous polyps (based on stopped individual development) were Faurot (1895) and Beneden (1897). This view was extended by Hand (1966), who suggested that they originate from Acontiaria. As a result of the transition to life on soft substrates, they lost the basilar muscles, reduced the number of mesenteries and became mature in the earlier ontogenetic stage. Schmidt (1972, 1974) held a similar opinion, the only difference being that the athenarians arose independently from different families of the thenarian sea anemones, and not only from Acontiaria. Other authors (e.g. Daly, 2002; Rodríguez et al., 2012, 2014) disagree that this group originated from anemones with basilar muscles in the course of adaptation to a burrowing lifestyle.

Based on molecular markers, the researchers (Daly et al., 2008; Rodríguez et al., 2012, 2014) showed the polyphyly of athenarian sea anemones. Accordingly, an elongated body, a rounded aboral end and the absence of basilar muscles arose (or were lost) multiple times within Nynanthaeae (Rodríguez et al., 2014). The discovery of sea anemones that both have basilar muscles and a burrowing lifestyle (*vs* those lacking such muscles and not burrowing) led to the opinion that Carlgren's (1898, 1900, 1905) division into higher Thenaria and lower Athenaria is incorrect (Daly et al., 2002; Rodríguez et al., 2014). To confirm polyphyly and that incorrectness, the researchers (e.g. Daly, 2002) usually concentrated on the presence or absence of the basilar muscles in different groups of sea anemones. Nevertheless, the remaining morpho-anatomical features and the burrowing behaviour itself are, as a rule, not taken into account, which makes it possible to combine the athenarian and thenarian sea anemones.

Burrowing behaviour is poorly studied and described only for certain representatives of the four athenarian families (Haloclavidae, Halcampoididae, Halcampidae, Edwardsiidae) and only for two representatives of the thenarian polyps: *Oulactis concinnata* (Drayton in Dana, 1846), Actiniidae Rafinesque, 1815, and *Iosactis vagabunda* Riemann-Zürneck, 1997, Iosactinidae Riemann-Zürneck, 1997 (see Williams, 2003; Durden et al., 2015). Even based on such insufficient data, I consider that the burrowing behaviour of the athenarians and thenarians undoubtedly arose independently. This is supported by a significantly different morphology and anatomy of the two groups and by the related differences in their burrowing methods (see Ansell & Trueman, 1968; Magnum, 1970; Pickens, 1988; Ansell & Peck, 2000; Williams, 2003).

In the literature, the term "burrowing" applies to both thenarian and athenarian polyps. Nevertheless, it has been proposed to call some thenarian species the "burying" sea anemones to emphasize their difference from the athenarian "burrowing" forms (Williams, 2003). Carlgren's Thenaria include many sea anemones that live on soft sediments, for example *Stichodactyla haddoni* (Saville-Kent, 1893) (Stichodactylidae Andres, 1883), *Actinostephanus haeckeli* Kwietniewski,

1897 (Actinodendronidae Haddon, 1898), *Oulactis concinnata* (Actiniidae). Nonetheless, the behaviour of many thenarians living in sand is generally the same as that of settled thenarians: they are also attached with their pedal disc to a solid substrate (stones, rock, shell fragments, etc.), the only difference being that they are hidden in the sediment. A burrowing behaviour may well not always be necessary for them: at least *Oulactis orientalis* was rather often found attached to a stone, not submerged into sand (Grebelny, pers. comm.; author's unpublished data). Thenarian sea anemones do burrow, as shown by *O. concinnata* (Magnum, 1970; Pickens, 1988), by contracting parieto-basilar muscles and peristaltic contractions. First, the parieto-basilar muscles contract and the pedal disc is swollen. Then, the column lengthens due to relaxation of parieto-basilar muscles and the passage of a peristaltic wave (the result of contraction of a circular muscles of body wall) and the pedal disc compresses. This is followed by a gradual relaxation of the disc and new contraction of parieto-basilar muscles. When the column initially plunges into the sediment, the retractor muscles sharply contract. As a result, the polyp decreases in size and settles in a larger hole. When a solid object is reached, the burrowing stops (Magnum, 1970; Pickens, 1988).

In contrast to the thenarians, the burrowing athenarians not only submerge into the sediment but also move inside it, as noted for the edwardsiids (see Manuel, 1975; Williams, 2003). Although its behaviour has not been described, *Limnactinia*, judging from the absence of tentacles in this genus, has probably become completely infaunal and no longer appears on the surface of the substrate. Furthermore, the burrowing behaviour of Athenaria differs significantly from that observed in Thenaria, reflecting their distinct anatomy. As shown for *Peachia hastata* Gosse, 1855 (Haloclavidae) (Ansell & Trueman, 1968), *Halcampoides* sp., (Halcampoididae) (Ansell & Peck, 2000) and *Nematostella vectensis* Stephenson, 1935 (Edwardsiidae) (Williams, 2003), burrowing involves peristaltic contractions of the column wall which lead to eversion of physa. With sufficient immersion in the sediment, when the physa can serve as an anchor, the column is straightened by contraction of the retractor mus-

cles in *P. hastata* (Ansell & Trueman, 1968) and *Halcampoides* sp. (Ansell & Peck, 2000) or of the parietal muscles in *N. vectensis* (Williams, 2003). In addition, the edwardsiids *Scolanthus callimorphus* Gosse, 1853, *Edwardsia ivelli* Manuel, 1975, and *E. clapedii* (Panceri, 1869) burrow head-first into mud, i.e. they burrow by alternately extending and introverting the distal end of the column, with the tentacles retracted, using a dilated scapus wall as a “penetration anchor” (Manuel, 1981; Williams, 2003). The only exception among the non-athenarians is the abyssal burrowing *Iosactis* Riemann-Zürneck, 1997 (Iosactiidae Riemann-Zürneck, 1997), which moves below the surface (see Durden et al., 2015). It can “jump out” of its hole by contracting the endodermal circular muscles and move along the substrate surface (Riemann-Zürneck, 1997). The athenarian sea anemones have no such ability. Moreover, *Iosactis* may have independently acquired burrowing behaviour based on the presence of peculiar anatomical features (sphincter muscles in the proximal part of tentacles, strong endodermal circular muscles of the column, altering character, shape and size of the longitudinal mesenterial musculature along the longitudinal extension (Riemann-Zürneck, 1997)) and habitation at great depths.

Hence, based on a few examples, it can be assumed that burrowing behaviour is not associated with the presence or absence of basilar muscles, but rely on the use of retractor muscles and the parieto-basilar or parietal muscles. The basilar muscles are involved in attachment/detachment and creeping, together with endodermal circular muscles of the pedal disc, lower parts of the retractor muscles and the parieto-basilar muscles, as was shown in *Metridium senile* (Linnaeus, 1761) (see Batham & Pantin, 1951).

Accordingly, burrowing in athenarian sea anemones should be associated mainly with the parietal and retractor muscles, with a rounded aboral end, and with an elongated body form. These features, in turn, are correlated with fewer tentacles and mesenteries, the latter divided into macro- and microcnemes.

The presence of the above-mentioned similar features in the athenarians potentially confirms their common origin. The presence of several characters that define, rather, individual families or genera than the infraorder as a whole can

probably be considered as an evidence for a further independent evolution of various athenarian families. Moreover, Athenaria should not be considered primitive because the appearance of this group is probably associated with the expansion of the ecological niche of the order Actiniaria.

Nevertheless, the athenarian sea anemones share many characters with Thenaria, potentially indicating the origin of the athenarians from several groups of the thenarians.

Almost all athenarians (except *Halcampoides*, which has only six pairs of mesenteries, and *Andresia* Stephenson, 1921, which has three mesenteric cycles) have a division of mesenteries into macrocnemes and microcnemes. Macrocnemes are strong, perfect mesenteries that bear retractors, filaments and gonads; microcnemes usually lack these organs, but can have parietal muscles. Among the thenarians, differentiated mesenteries are found in five families: Condylanthidae (Endomyaria), Isanthidae (Mesomyaria), Acontiphoridae, Bathypheiliidae, and Isophelliidae (Acontiarina). In both groups, microcnemes can appear both in the distal and proximal parts. Only *Andresia* lacks a differentiation into macro- and microcnemes, making this unusual polyp resemble most thenarians.

Interestingly, Athenaria and Thenaria are not always characterised by hexamerously arranged mesenteries. Decamerous and octomerous arrangements are also common in both groups. Some thenarians (e.g. *Zaolutus actius* Hand, 1955) are characterised by a weak development of the fifth and sixth couples of mesenteries (Hand, 1955), so that a bilateral arrangement of mesenteries further enhances their similarity with *Edwardsia* and certain other athenarians.

Another feature that binds the two groups is a marginal sphincter muscle, which constricts the distal part of the column. Within each infraorder, the sphincter may be endodermal, mesogloal or completely absent. Moreover, some representatives develop a double mesogloal sphincter (e.g. Halcampidae and Isanthidae) (see Carlgren, 1949; Hand, 1955).

One more overlapping feature is the presence of specialised stinging organs, the acontia. Among Athenaria, acontia develop in representatives of three families (Haliactinidae, Octineonidae, Andvakiidae). Among Thenaria, they occur in 14

families, which are combined into the superfamily Metridioidea.

Even though small size and a worm-like body are typical for Athenaria, that group does contain forms that are very similar to the thenarians. *Octineon* (Octineonidae) is the most remarkable example of this likeness: it has a wide, sticky, flat pedal disc with which it attaches to a solid substrate (Sanamyan et al., 2018). Vice versa, the thenarian anemones of various families can also be buried in the sediment and be elongated, in some cases forming a rounded aboral end. As a rule, however, they still need to attach the base to a hard object. In Athenaria, the development of a clearly defined attachment disc is probably an exception. Nonetheless, it cannot be denied that the athenarians can attach their aboral end to solid objects (see Williams, 2003).

Considering the totality of characters, the athenarians are most similar to representatives of the families Condylanthidae (Endomyaria), Isanthidae (Mesomyaria), Acontiophoridae, Bathypheiliidae, and Isophelliidae (Acontiaria). The athenarian sea anemones potentially come from a common ancestor with polyps of these five families.

Conclusions

An analysis of the systems of athenarian sea anemones proposed by various authors reveals that each classification scheme was based on only one feature, i.e. on the external organization, the arrangement of the mesenteries, the presence of the basilar muscles, or on a comparison of a few molecular markers. Clearly, focusing on only one specific feature yields heterogeneous groups: in every case it separates similar and joins unrelated forms. A detailed analysis of the recently proposed classification (Rodríguez et al. 2014), which many authors consider to be a replacement for the traditional system, confirms this conclusion. I consider that an integrated approach is currently needed to develop a natural classification that would include both morpho-anatomical features and molecular markers, supported by data on behaviour, embryology, etc. Solving the problem of the origin of Athenaria calls for taking into account not only their elongated shape and rounded body end, the absence of the basilar muscles, but also

the mesentery muscles, the separation of mesenteries into micro- and macrocnemes, peculiarities of behaviour, in particular how they burrow, and other characters. Considering a larger set of features allowed me to conclude that the burrowing sea anemones are characterised by a common origin and further divergence into the families within the infraorder Athenaria. In this interpretation, the similarities with certain representatives of Thenaria can be explained by convergence.

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