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OBSERVATIONS ON SPECIES OF THE FOSSIL GENUS AXOPORA (COELENTERATA: HYDROZOA) AND ITS EVOLUTIONARY SIGNIFICANCE TO THE STYLASTERIDAE

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Abstract. – Two species of Axopora are redescribed and the remaining valid species are diagnosed and discussed. Three species are illustrated by scanning electron photomicrographs. Special emphasis is given to the morphology of the gastrostyles, and their supposed homology to those of the stylasterids is discussed. A hypothetical evolutionary scheme is proposed suggesting the evolution of the axoporids from a hydractiniid ancestor by the acquisition of calcification and the transformation of its protective spines to gastrostyles. An ancestor to the axoporids is suggested to have evolved into the stylasterids also, the major changes being the encasement of its gonozooids and dactylozooids in specialized calcareous structures. The Axoporidae is considered to be a family of athecate hydroids with close affinities to the Hydractiniidae and Stylasteridae.

The Axoporidae is a small family of calcified hydrozoans (13–14 nominal species in 1–2 genera), known only from the Oligocene to Eocene of Europe and South West Africa. They were originally described as Scleractinia (*Pocillopora* of Defrance (1826), and *Holaraea* of Milne Edwards and Haime (1849)) and some were even classified as tabulate corals and sponges (*Alveolites* and *Geodia* of Michelin (1844)). Michelin (1844) also identified a species as a milleporid, and, until 1963, most axoporids were assigned to the order Milleporina. Boschma (1963b) removed the axoporids from the Milleporina and created a new order, the Axoporina, for them, which, according to him, had closer affinities to the Stylasteridae than to the Milleporina.

The classification and phylogenetic position of the axoporids are based strongly on the characteristics of their gastrostyles. Until 1963, all axoporid gastrostyles were considered to be longitudinally grooved, nonspinose, fasciculate structures. However, Boschma (1963b) revealed that they are deeply ridged spinose cylinders, not at all fasciculate. Scanning electron microscopy allows an even more detailed analysis of gastrostyle morphology and a detailed comparison to other stylasterid gastrostyles.

Following a redescription of two species of *Axopora* and diagnoses of the other valid species, the interrelationships of the axoporids, stylasterids, and athecate hydroids will be discussed.

Class Hydrozoa

Order Hydroida Family Axoporidae Boschma, 1951

Diagnosis. - Calcified hydrozoans with long spinose gastrostyles and with no skeletal evidence of dactylozooids (dactylopores) or gonophores (ampullae). Eocene

to Oligocene (?Miocene): Europe, South West Africa, (?New Zealand). One or two genera.

Genus Axopora Milne Edwards and Haime, 1850

Diagnosis.—Characteristics of the family. Type-species: *Geodia pyriformis* Michelin, 1844. Five to seven species.

Axopora solanderi (Defrance, 1826) Figs. 1–7

Pocillopora solanderi Defrance, 1826:48.

Palmipora solanderi. – Michelin 1844:166, pl. 45, fig. 9.

Lobopora solanderi. - Milne Edwards and Haime 1850:lix.

Axopora solanderi. – Milne Edwards and Haime 1851:151; 1857:243–244, pl. F3, fig. 2. – Boschma 1951:25, fig. 3; 1961:F94, fig. 78–1, 2; 1963a: 107, figs. 2a–

b, d; 1963b:122, 125, pl. 1, fig. 1, pl. 2, figs. 1-2, pls. 3-8.

Axopora michelini Duncan, 1866:50, pl. 7, figs. 11-15.-Boschma 1963b:124, 126.

Axopora fisheri Duncan, 1866:64, pl. 10, figs. 20–22. – Boschma 1963b:124–125, 126.

Millepora mamillosa d'Archiardi, 1867:11.

Axopora mamillosa.-Steinmann 1903:5.-Boschma 1963b:125-126.

Description.—Corallum composed of flattened lobes (typical form) (Figs. 1–2) or lumpy masses (*michelini* form), but never forming laminar encrustations. In both lumpy and lobate forms, gastrostyles originate on both sides of a midline (Fig. 3), a plane in center of lobe or lump, not differing in porosity from rest of corallum. Surface coenosteum usually smooth but may be ridged, especially at tips of lobate specimens. Coenosteal ridges subparallel and roughly perpendicular to lobe edge, up to 1 mm tall and 1.5 mm broad. Lower relief ridges sometimes cross between adjacent parallel ridges producing reticulate pattern (Fig. 1). Coenosteal texture appears to be reticulate-granular, but preservation of specimens examined did not allow a definitive categorization.

Gastropores round, 0.15–0.35 mm in diameter, flush with coenosteal surface (Fig. 5). Gastropores randomly arranged, occurring at a density of 1.6–2.2 pores per mm². Very diffuse ring palisade occurs in upper part of gastropore tube, elements measuring about 25 μ m in diameter. Gastrostyles extend almost to coenosteal surface and occupy most of space within gastropores, unlike in the stylasterids, where there is always considerable space around the style.

Length of gastrostyles and number of tabulae per gastrostyle vary with width of lobe or lump in which they occur (Figs. 4, 7). In thick coralla, gastrostyles up to 3.8 mm long and have over 18 tabulae. Styles rarely exceed 0.21 mm in diameter; maximum H:W observed was 23.5. According to Boschma (1963b: 121), gastrostyles sharply ridged, with spines occurring on ridges; however, scanning electron microscopy reveals that base of styles definitely not ridged, but spinose. Above base of style, spines vertically aligned, sometimes 1–3 across, and separated from adjacent rows by shallow groove. Spines so long, and sometimes bifurcate, that it is difficult to distinguish actual ridges on style (Figs. 6, 7). Gastrostyle spines cylindrical, up to 0.13 mm long and about 30 μ m in diameter.



Figs. 1–6. Axopora solanderi from Valmondois (USNM 68437). 1–2, distal lobes, $\times 1.8$, $\times 1.3$, respectively; 3, Cross section of lobe showing midline and gastrostyles, $\times 6$; 4, A gastrostyle and tabulae from colony of Fig. 3, $\times 27$; 5, Coenosteum and gastropores, $\times 40$; 6, Detail of gastrostyle, $\times 250$.



Figs. 7–9. Gastrostyles. 7, Stereo view of gastrostyle and tabulae of *Axopora solanderi*, British Museum R 50812, \times 140; 8, Gastrostyle and tabulae of *Sporadopora dichotoma* from the Drake Passage (*Hero* 715–895), \times 100; 9, Gastrostyle tip of *Lepidopora granulosa* from Drake Passage (*Eltanin* sta 740), \times 190.

Tabulae invariably present, occurring at irregular intervals, averaging about every 0.25 mm. Tabulae about 6 μ m thick, completely sealing off lower gastropore tube from upper tube.

Discussion. — Axopora solanderi is distinguished from the other species in the genus by its nonencrusting growth form and massive corallum. Its gastrostyles are superficially similar to those of Sporadopora dichotoma, particularly with regard to the high H:W, similar tabulae, and apparent ridges (Fig. 8); however, the gastrostyles of S. dichotoma are distinctly ridged and bear much smaller and sharper spines. The characteristics of the tabulae are quite variable and not usually considered to be of generic or even specific value. Of all the stylasterines, Lepi-dopora granulosa (Fig. 9) has gastrostyles most similar to those of A. solanderi. Distribution.—Eocene to Oligocene: England, France, Italy.

Material examined.—Auvers-sur-Oise, Seine et Oise, France, 7 fragments (*michelini* form), USNM 80889 (Invertebrate Paleontology Series); Valmondois, France, 2 fragments (typical form), USNM 68437; Sands of Beauchamps, Auvers, France, 2 fragments (*michelini* form), USNM 68438; Parnes, Beavoir, France, 1 fragment (*michelini* form), USNM 80891 (Invertebrate Paleontology Series); Le Bois Gouet, Lutecien, France (typical form), USNM 68439; Paris Basin, France, 1 fragment (*michelini* form), British Museum R 50812.

Axopora parisiensis (Michelin, 1844) Figs. 10–15

Alveolites parisiensis Michelin, 1844:166, pl. 45, fig. 10. Holaraea parisiensis. – Milne Edwards and Haime 1849:259; 1850:1vi, 40, pl. 7, fig. 2.

Axopora parisiensis. – Milne Edwards and Haime 1851:151; 1857:244. – Boschma 1951:25; 1963a:107–109, fig. 1; 1963b:122–123, 126.

Description.—Corallum always encrusts an elongate cylindrical object, such as a gorgonian stem, which, when the stem is lost, produces a cylindrical corallum with a hollow center (Figs. 10–11). Largest specimen examined 14 mm long and 6.5 mm in diameter, with hollow center 2.5×2.0 mm in diameter. Coenosteal encrustation always thin, with no side branches or lobes. Coenosteum papillose (Fig. 13), producing spongy coenosteal texture.

Gastropores round, 0.45–0.55 mm in diameter, surrounded by round to polygonal, infundibuliform calices (Fig. 12). Otherwise constant-diameter cylindrical gastropore becoming flared near coenosteal surface. Calices closely packed in honeycomb arrangement, each calice measuring about 1.2 mm in diameter. The density of gastropores therefore less than one pore per mm². Diffuse ring palisade present, similar to that of *A. solanderi*. Tips of gastrostyles extending only to base of funnel-shaped section of gastropore and thus each occupying only about onehalf of gastropore (Figs. 14–15).

Because the corallum is never thick, gastrostyles are relatively short and rarely have tabulae. A large gastrostyle is 0.9 mm long and 0.18 mm in diameter (H:W = 5); however, H:W ratios usually lower than 5. Spination of gastrostyle is similar to that of *A. solanderi*, with cylindrical spines up to 1.25 mm long and 19–26 μ m in diameter arranged in poorly defined vertical rows. The "ridges" of these styles are virtually nonextant.

Discussion.—*Axopora parisiensis* is easily distinguished by its large infundibuliform calices and its cylindrical encrusting growth form.

Distribution.-Eocene: France and England.

Material examined.—Vandane, France, 3 fragments, USNM 68440; Parnes, France, 2 fragments, USNM 68441; Campbon, France, 15 fragments, USNM 68442; Cuise, France, 2 fragments, USNM 68443; St. Lucien de la Haye, France, 1 fragment, USNM 68444; Grignon, Seine-et-Oise, France, 35 fragments, USNM 68445.

Axopora kolosvaryi (Boschma, 1954) Figs. 16–17

Axopora ramea. - Kolosváry 1949:189, pl. 20, fig. 2.

Axoporella kolosváryi Boschma, 1954:101–103, figs. 2a–c; 1956:F-94, fig. 78-3a–c; 1963a:114–115.

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Figs. 10–15. Axopora parisiensis from Parnes (USNM 68441). 10, encrusting piece of colony, $\times 9$; 11, Cross section of encrustation, $\times 13$; 12, Infundibuliform calice, $\times 50$; 13, Papillose coenosteal texture within a calice, $\times 385$; 14–15, Gastrostyle, $\times 230$, $\times 60$, respectively.

Axopora kolosváryi. – Boschma 1963b:127.

Diagnosis.—Corallum encrusting (Boschma 1963b:127). Gastropores round, about 0.35 mm in diameter, flush with surface. Gastrostyle $80-90 \mu m$ in diameter, extending almost to surface of coenosteum. Style covered with short clawlike spines, curved both upwards and downwards on style (Fig. 16). Spines only about 35 μm long, tapering to point from broad base up to 20 μm in diameter (Fig. 17). Spines not aligned in rows; gastrostyles not ridged. Tabulae present.

Discussion. — Axopora kolosvaryi is distinguished from the other species of Axopora by its very short clawlike gastrostyle spines, which are not arranged in rows. Only one tiny specimen was available for examination, inadequate for a redescription of the species.

Distribution.-Lower Eocene: Hungary.

Material examined.—One fragment from Gánt, Hungary (topotypic), USNM 68447.

Axopora pyriformis (Michelin, 1844)

Geodia pyriformis Michelin, 1844:178, pl. 46, fig. 2.

? Millepora parasitica Catullo, 1856:79, pl. 18, fig. 4.

Axopora pyriformis. – Milne Edwards and Haime 1850:1ix; 1857:244. – Boschma 1951:25; 1956:F94; 1963a:123, 126, pl. 1, figs. 2–5, pl. 2, figs. 3–4.

Diagnosis.—Corallum always encrusting, usually on gastropod shells. Gastropores 0.25-0.40 mm in diameter, occurring with a density of 1.4-1.5 per mm². Otherwise similar to *A. solanderi*.

Discussion. – Boschma (1963b:126) noted that the only difference between A. pyriformis and A. solanderi was in growth form, which may in itself be a variable character. This allows for the possibility that A. pyriformis is a junior synonym of A. solanderi. Unfortunately, no specimens of A. pyriformis were available for study.

Distribution. - Eocene: France.

Axopora arborea Keferstein, 1859

Axopora arborea Keferstein, 1859:381, pl. 15, fig. 9.—Boschma 1951:26; 1963b: 124, 126.

? Axopora paucipora Keferstein, 1859:382, pl. 15, fig. 10.-Boschma 1963b:124, 126.

Axopora ramea d'Archiardi, 1867:11.—Not Kolosváry 1949:189 (=A. kolosvaryi).—Boschma 1963b:125, 126.

Diagnosis.—Corallum delicately branched; branches 3–6 mm in diameter. Details of gastrostyles unknown.

Discussion. – The poorly known A. arborea is distinguished from other species by its delicately branching growth form. No specimens were available for study. Distribution. – Oligocene: Germany.

Axopora cleithridium (Squires, 1958), new combination

Sporadopora cleithridium Squires, 1958:25–27, pl. 1, figs. 8–12. Axoporella cleithridium.—Squires, 1962:136–137.



Figs. 16–17. Axopora kolosvaryi from Gánt, Hungary (USNM 68447), details of gastrostyle spination, ×310, ×925, respectively.

Diagnosis.—Corallum with thick branches, up to 14 mm in diameter. Gastropores irregular in shape, 0.1–0.2 mm in diameter. Gastrostyles up to 5 mm long; tabulae present.

Discussion.—This is the only known *Axopora* with thick branches. Squires (1958) originally described it as a stylasterine, *Sporadopora*, and even described its dactylopores. When he (Squires 1962) later transferred it to *Axoporella* he did not mention the lack of dactylopores. Those referred to in 1958 were probably the superficial expression of coenosteal canals.

Only one specimen was available for study, a paratype from NZGS 5170. It does not appear to have dactylopores nor does it have any gastrostyles or tabulae. Perhaps the lack of styles and tabulae in this particular specimen is a result of poor preservation, but it does cast doubt on the placement of this species in the Axoporidae. Its occurrence in the Kapitean (Upper Miocene) of New Zealand would make it by far the youngest member of the family.

Apparently Boschma (1963b) overlooked this species in his revision of Axopora. Distribution. – Upper Miocene: New Zealand.

Material examined.—Whata, Rowallon, S. D., Southland, New Zealand, NZGS 5170, USNM 68446 (Paratype).

Other Species

Axopora microspora and A. alpina, both originally described by d'Orbigny (1850) in the genus Holaraea, were considered as species dubiae by Boschma (1963b) because of insufficient data. Both species are known from Faudon, France.

Diamantopora lotzi Weissermel, 1913, is the only species in its genus, and Diamantopora is the only other genus in the Axoporidae. It was distinguished from Axopora by its nongrooved gastrostyles (Boschma 1956); however, this characteristic was subsequently shown to be variable within Axopora. Diamantopora lotzi may therefore represent a seventh valid species of Axopora, but until specimens can be examined in detail, its position will remain in doubt. It is known only from the Eocene of South West Africa.

Discussion

Although traditionally allied with the milleporids (from 1844 to 1963) several authors had noted the similarities of axoporids and stylasterids, particularly with regard to their gastrostyles. Römer (1863) was perhaps the first to point this out when he observed the similarity of the gastrostyle of the fossil stylasterine Dendracis multipora (subsequently synonymized with Allopora compressa) with those of Axopora arborea. Reuss (1865) made a similar observation based on the same species. Steinmann (1903) was the foremost advocate of this point of view when he remarked that Axopora was undoubtedly the ancestor of the three Recent stylasterid genera Sporadopora, Errina (now Errina, Lepidopora, Lepidotheca, and Inferiolabiata) and Spinopora (now Stellapora). Boschma (1954) mentioned the resemblance of the gastrostyles of A. kolosvaryi with those of other stylasterids and finally he (Boschma 1963b) removed the axoporids from the Milleporina, creating a separate order for them, the Axoporina. He stated that the axoporids were more closely related to the stylasterids than to the milleporids because of their similar gastrostyles, and noted that the gastrostyles of Distichopora were most similar to those of Axopora.

I agree that the axoporids are closely related to the stylasterids, but most closely to the genus Lepidopora. Points of similarity and presumed homology between Lepidopora and Axopora include: 1) a structurally similar gastrostyle; including size, H:W, and spination, 2) a diffuse ring palisade, 3) a calcium carbonate skeleton with anastomosing coenosteal canals, and 4) a random (nonlinear) arrangement of gastropores on the corallum. Points of difference are that Axopora: 1) lacks dactylopores, 2) lacks ampullae, 3) has a less spacious gastropore, 4) has tabulae, 5) has a different coenosteal texture, and 6) has both an encrusting and branching growth form. The major differences are the first two: that Axopora lacks dactylopores and ampullae; however, this does not necessarily mean that Axopora lacked dactylozooids or gonozooids, only that it lacked skeletal evidence of these features. For instance, the Recent calcified hydroid Janaria has both dactylozooids and gonozooids but has no skeletal evidence of these structures because they are composed of tissue that projects above the coenosteum, as in Hydractinia and most other athecate hydroids. Thus, Axopora may well have had dactylozooids and gonozooids but they were not housed in specialized calcareous structures. Most assuredly Axopora did have gonozooids, which were probably superficial structures as in Hvdractinia.

In a phylogenetic analysis of the stylasterine genera (Cairns, in press), I chose the athecate hydroid *Hydractinia* as the out-group, or sister taxon, to the stylasterine corals. The most plesiomorphic (primitive) genus of stylasterine resulting from this analysis was *Lepidopora*, particularly *L. granulosa*. *Axopora*, because of its lack of skeletal evidence of dactylozooids and gonozooids and its encrusting growth form for some species, shows similarities to *Hydractinia*. On the other hand, of all the stylasterines, *Axopora* is most similar to *Lepidopora*, the most primitive stylasterine genus. I therefore propose that *Axopora* evolved from a hydractiniid ancestor in the early Tertiary (?Oligocene) and that a common ancestor gave rise to the stylasterines through *Lepidopora*. Furthermore, I consider the axoporids to be a family of athecate hydroids closely related to the Stylasteridae and Hydractiniidae.

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Fig. 18. Suggested evolution of the axoporids and stylasterids indicating significant character state changes. A and B are hypothetical ancestors.

As a hypothetical scenario I suggest the following (Fig. 18). In the Paleocene or Late Cretaceous a hydractiniid ancestor (A), which was encrusting and already had the gastrostyle homolog in the form of a chitinous spine, evolved the ability to calcify its skeleton and to protect its gastrozooids by enclosing them in rudimentary tubes: the gastropores. The chitinous spine transformed into the calcareous gastrostyle. The resultant hypothetical ancestor (B), with little further modification became the stem that resulted in Axopora. This evolutionary line developed a distinctive coenosteal texture, tabulae to stabilize its long gastrostyles, and, for some species, the ability to take advantage of the branching mode. Axopora became extinct in the Eocene (? Miocene), perhaps because it did not develop the further safeguards characteristic of the stylasterines: a protected gonozooid (ampullae) and a protected dactylozooid (dactylopores). (Stylasterines eventually evolved quite elaborate structures to protect their zooids, including fixed and hinged gastropore lids and dactylopore spines). In addition to the dactylopores and ampullae, the line leading to the stylasterines also evolved distinctive coenosteal textures (imbricate platelets and reticulate-granular coenosteum, among others), a more capacious gastropore tube, and an exclusively branching form. The characteristic of gastropore tabulae was probably independently acquired by several genera, such as Sporadopora, Distichopora, and Errina, and is therefore considered a convergent character.

The fossil record produces an apparent contradiction to the proposed scenario in that the earliest known stylasterids occur before the earliest known axoporids: the Paleocene (Danian of Denmark) and Eocene, respectively. As a test of my hypothesis, but not necessarily a confirmation, I predict the eventual discovery of *Axopora* from the Paleocene. An alternative explanation would be that the

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axoporids evolved through an intermediate Paleocene ancestor, which did not evolve *Axopora* until the Eocene and for which there is no known fossil record.

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