

A new subfamily of operculate stylasterine (Coelenterata: Hydrozoa) from the Subantarctic

STEPHEN D. CAIRNS

Research Associate, Department of Invertebrate Zoology,
Smithsonian Institution, Washington, D.C. 20560

Introduction

In the course of a faunistic revision of the Stylasterina of the Antarctic and Subantarctic, a very unusual species was discovered from four seamounts in the Subantarctic South Pacific and southwest Atlantic. This species differs from all other Stylasterina in having hinged opercula, one of which covers each gastropore. The stylasterine genera *Crypthelia* and *Calyptopora* are superficially similar in having a fixed lid covering part of each gastropore; however, this Subantarctic species has hinged opercula, which freely articulate with the coenosteum by a nub-and-socket mechanism. This kind of operculum is unique in the order Stylasterina and the coelenterate phylum and is rare in the Animal Kingdom, the closest analogous structure being found in certain cheilostome Bryozoa.

The classification of the Stylasterina, consisting of one family, three subfamilies, and 19 genera, is highly artificial and in need of revision, especially at the higher taxonomic levels. However, despite taxonomic confusion within the order, it is felt that the presence of a hinged operculum warrants the creation of a new taxon, at least at the subfamilial level.

The holotype and most paratypes are deposited at the United States National Museum, Washington, D.C. Paratypes are also deposited at the British Museum (Natural History), London; Rijksmuseum van Natuurlijke Historie, Leiden; and the Royal Ontario Museum, Toronto.

ADELOPORINAE, subfam. nov.

Diagnosis

Gastropores and dactylopores not arranged in cyclo systems. Gastropores occur at branch tips and axils, each gastropore covered by a hinged operculum. Type-genus: *Adelopora*, gen. nov.

Discussion

Because of the random arrangement of dactylopores in *Adelopora*, it would appear to be most closely related to the subfamily Errininae. *Adelopora* shows individual similarities to various genera within the Errininae, as well as to the Stylasterinae, but does not closely resemble any particular genus. For instance, *Adelopora* is similar to several species of *Errina* (*Inferiolabiata*) in coenosteal texture and position of gastropores at axils, but differs considerably with regard to shape of dactylopores, absence of gastrostyles, and nature of ampullae. It has the coenosteal structure and absence of gastrostyles in common with *Conopora pauciseptata*, but differs in lacking cyclo systems and nematopores, and having differently shaped gastropores. It is similar to *Pliobothrus* in shape of dactylopores and in lacking

gastro- and dactylostyles, but differs in coenosteal texture, position of gastropores, and shape of ampullae. In short, *Adelopora* incorporates many typical stylasterine characters present in both subfamilies but does not closely resemble any one genus and is consistently different from all genera with regard to the presence of hinged opercula. In the order Hydroida, within which the Stylasterina are sometimes placed as a family, the presence of an unhinged, movable operculum is considered to be a family level character (Naumov 1960: 93). In my opinion, *Adelopora*, because of its hinged operculum, has the potential to effect an adaptive radiation paralleling the diversity achieved within either the Stylasterinae and/or the Errininae, and therefore I propose a new subfamily for this taxon.

Opercula occur in other members of the coelenterate phylum but the freely articulated, hinged operculum of *Adelopora* is unique. In the closely related order Hydroida, several thecate families, including the Sertulariidae and Campanulinidae, have one or more opercular flaps covering the hydrothecal apertures. The campanulinids usually have 5–14 flexible, triangular flaps, which fold together in a pyramidal cover over the hydrotheca. Often there is no boundary between the flap and the rest of the perisarc. This type of closure is analogous to the four-part infolding of some conularid (Cam.-Trias.) 'scyphozoans'. Four genera within the Sertulariidae have one-part, rounded opercula closing each hydrotheca; however, none has a hinged articulation. Their opercula are a direct continuation of the exoskeleton, separated only by a slight crease in the perisarc. Sertulariid opercula are discussed in detail by Nutting (1904: 19–25).

Another operculate coelenterate group is the rugosan family Goniophyllidae (Sil.-Dev.), which is partly characterized by having 1–4 heavy opercular plates covering each calice. *Calceola* and *Rhizophyllum* have single plates but their articulation is similar to that of some bivalves, composed of numerous parallel ridges and grooves, which guide the operculum into place. There are no muscle scars on the operculum, indicating that it might have been free of the corallum, perhaps attached to the side of the polyp (pers. comm., William Oliver).

The structure most similar to the hinged operculum occurs in the cheilostome bryozoans. Most cheilostome opercula articulate on two opposing condyles (cardelles) and do not appear to be interlocked with the zooecia. However, the opercula of *Lagarozoum* (see Harmer 1926, pl. 22, fig. 7) and particularly of *Microporella* (*Flustramorpha*) (see Shrock and Twenhofel 1953: fig. 7–34K) are very similar in shape to *Adelopora*, having a thickened outer edge, a straight, bar-shaped hinge edge, and extensions from the bar in the form of nubs to aid in articulation. The opercula of *Flustramorpha* and *Adelopora* are a remarkable example of convergent evolution in two distant phyla.

Other invertebrate groups, such as the Bivalvia, Hyolitha, Brachiopoda, and Rudistacea, have hinge mechanisms joining valves, but in no case is the hinge an interlocking nub-and-socket mechanism as in *Adelopora*. In most cases, when the animal dies, the valve or operculum disarticulates, whereas, in *Adelopora*, the operculum remains interlocked with the coenosteum.

Adelopora, gen. nov.

Diagnosis

Gastropores and dactylopores without styles. Dactylopores small perforated tubercles. Coenosteal texture composed of broad, imbricated platelets. Type-species: *Adelopora pseudothyron*, sp. nov.

Etymology

Adelopora is a combination of *adelos* (Greek: unseen) and *poros* (Greek: hole) referring to the unseen gastropores when the operculum is in the closed position. Gender: feminine.

Adelopora pseudothyron, sp. nov.

(Figs. 1–22)

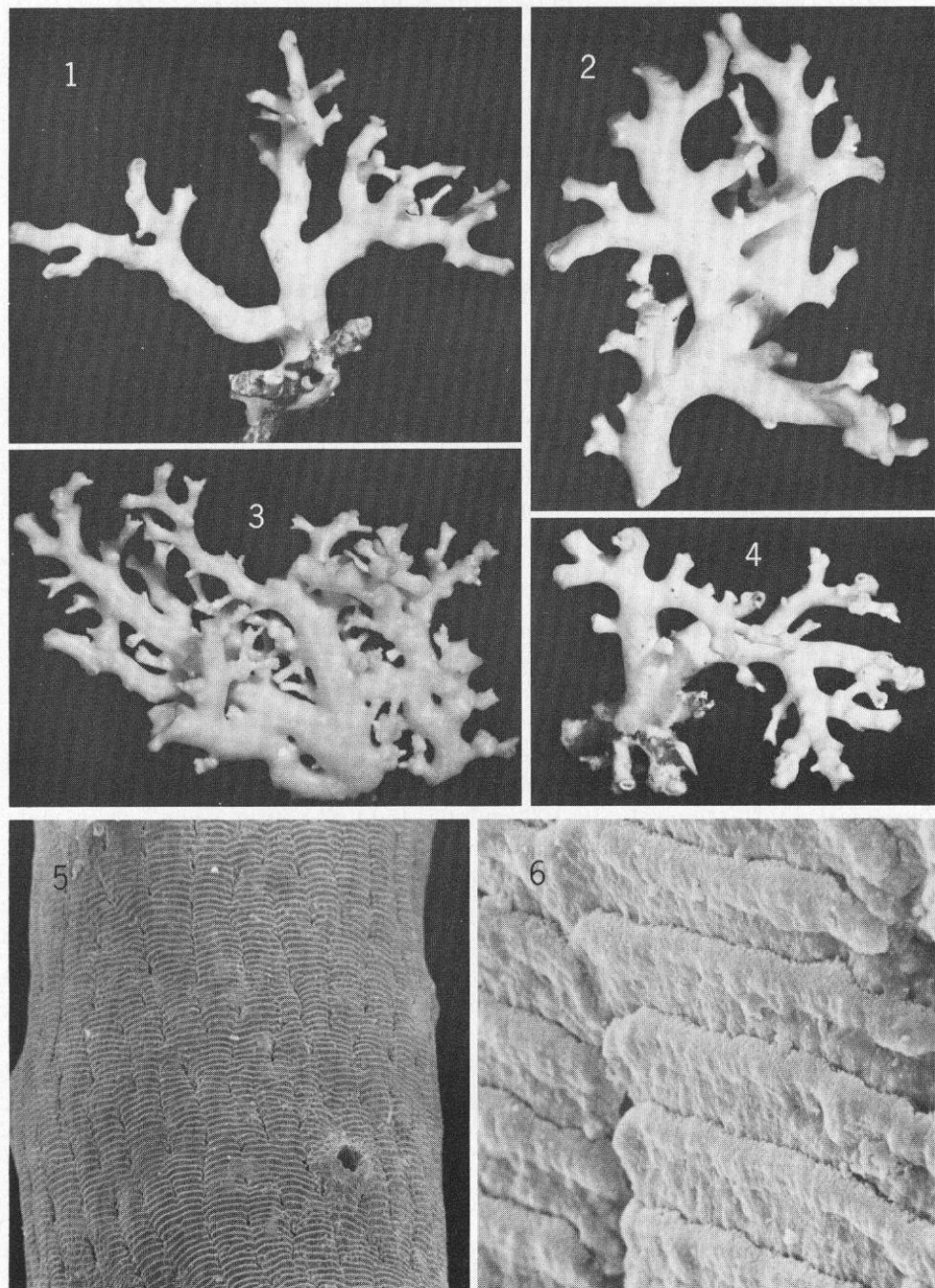
Description

Corallum usually uniplanar; however, some colonies maintain a loose, bushy branching (figs. 1–4). Largest colony 3.8 cm tall but other fragments with greater basal branch diameters indicate that larger colonies do exist. Branches tend to avoid coalescing; however, in densely branched colonies the branches sometimes anastomose, forming a reticulate fan (fig. 3). Branches round in cross section except toward the base of the colony, where the thick basal branches are slightly elliptical in cross section. Distal branches about 0.9 mm in diameter, largest basal branch up to 1 cm in greater diameter. Small diameter branches result from gradual tapering of larger branches or grow directly from the sides of larger diameter branches. A cross section of a distal branch reveals three to four large coenosteal canals of 50–90 μm diameter and numerous smaller canals of 15–20 μm diameter (fig. 22). Axils of branching usually U-shaped. Colonies firmly attached by a thin, encrusting base to objects such as medium pebble-sized rocks, the scleractinian coral *Solenosmilia variabilis*, and the stylasterine *Errina* sp.

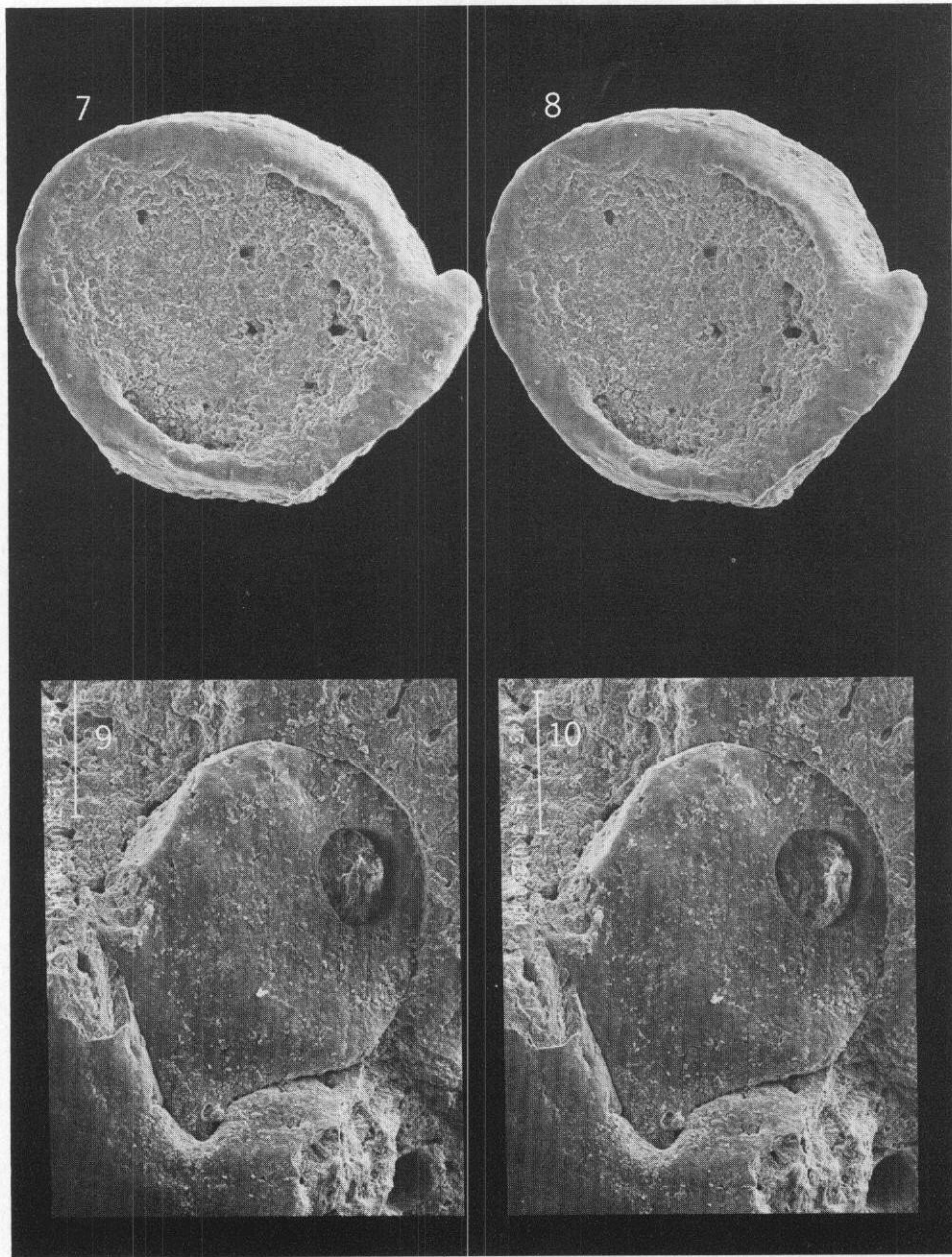
Coenosteum smooth, dense, and porcelaneous; always white. Discontinuous rows of coenosteal slits define longitudinal, parallel strips of coenosteum, often bifurcating and rejoining adjacent strips in their progression toward the branch tip (fig. 5). Coenosteal slits 3–4 μm wide, 10–100 μm long, and up to 50 μm deep. Larger, more continuous slits in thicker, older branches. The slits define strips of coenosteum between 53–70 μm wide. Texture of coenosteum composed of imbricated platelets, the free edges of which are directed distally (fig. 6). Width of each platelet is width of coenosteal strip; approximately 75–90 leading edges occur per mm. There are no coenosteal granules. On older branches of greater diameter, the imbricated platelets are often worn down, the platelets appearing as transverse rugae without the overlapping effect.

Gastropores occur only on branch tips (figs. 11–12) and at branching axils. The presence of a gastropore on a branch tip seems to cause the branch to bifurcate, which establishes it at this axil. Gastropore tubes cigar-shaped: straight, cylindrical, about 1 mm in diameter, and abruptly truncated in a gently rounded cul-de-sac (fig. 18). There is no gastrostyle. Small diameter coenosteal canals penetrate the wall and base of the gastropore.

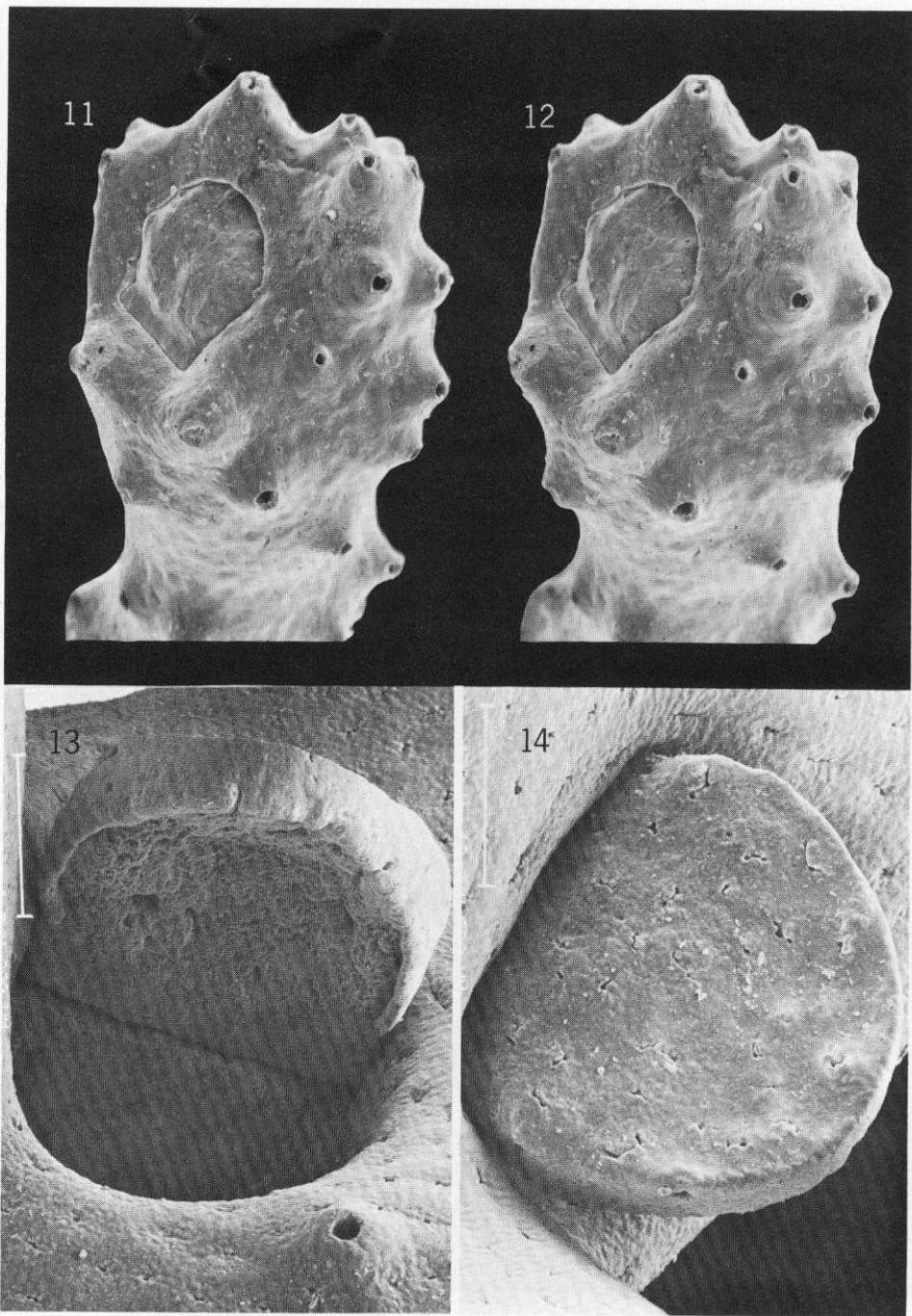
Each gastropore is covered by a freely hinged operculum (figs. 7–14). Opercula are variable in shape but generally are round to elliptical, with one edge of the ellipse modified into a straight articular edge. The length of an operculum (measured from the hinge to the free end) varies from 0.39–0.58 mm, the width from 0.35–0.64 mm. Usually the length is greater than the width of any given operculum (*i.e.*, length: width ratio about 1.1); however, this ratio varies from 1.34–0.71, with both extremes occurring on the same branch. Opercula are approximately 70 μm thick at their edges but considerably thinner toward the centre because of the great



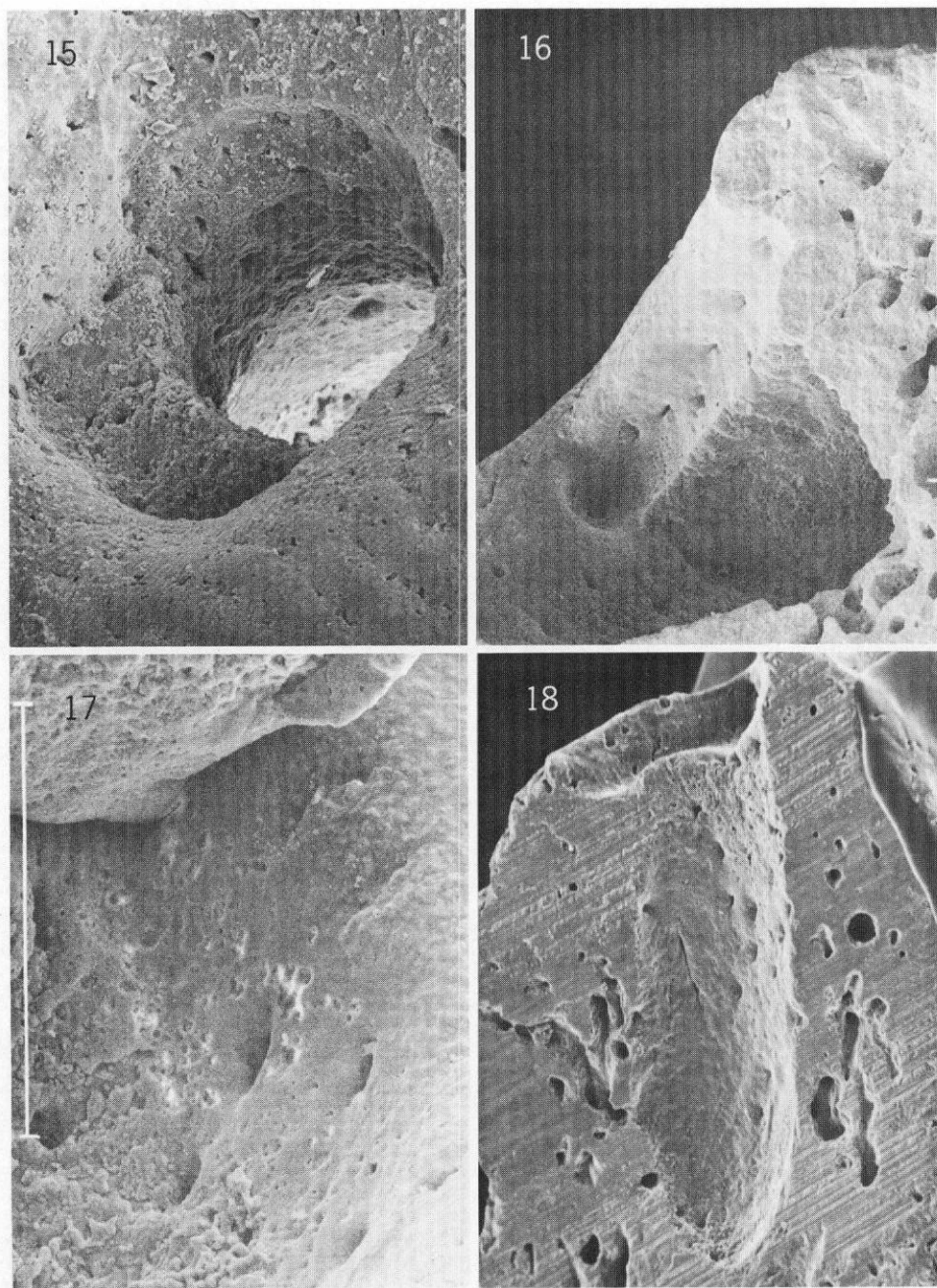
FIGS. 1-6. *Adelopora pseudothyron*: (1) Holotype, *Eltanin* sta. 254, USNM 60198, $\times 1.6$. (2) Paratype, *Eltanin* sta. 254, BMNH 1981.8.1.1, $\times 2.0$. (3) Paratype, *Eltanin* sta. 25-326, USNM 60133, $\times 2.0$. (4) Paratype, *Eltanin* sta. 254, ROMCN-B 102, $\times 1.6$. (5) Close-up of branch showing coenosteal strips, *Eltanin* sta. 254, USNM 60128, $\times 90$. (6) Coenosteal texture showing imbricated platelets, same specimen as before, $\times 1125$.



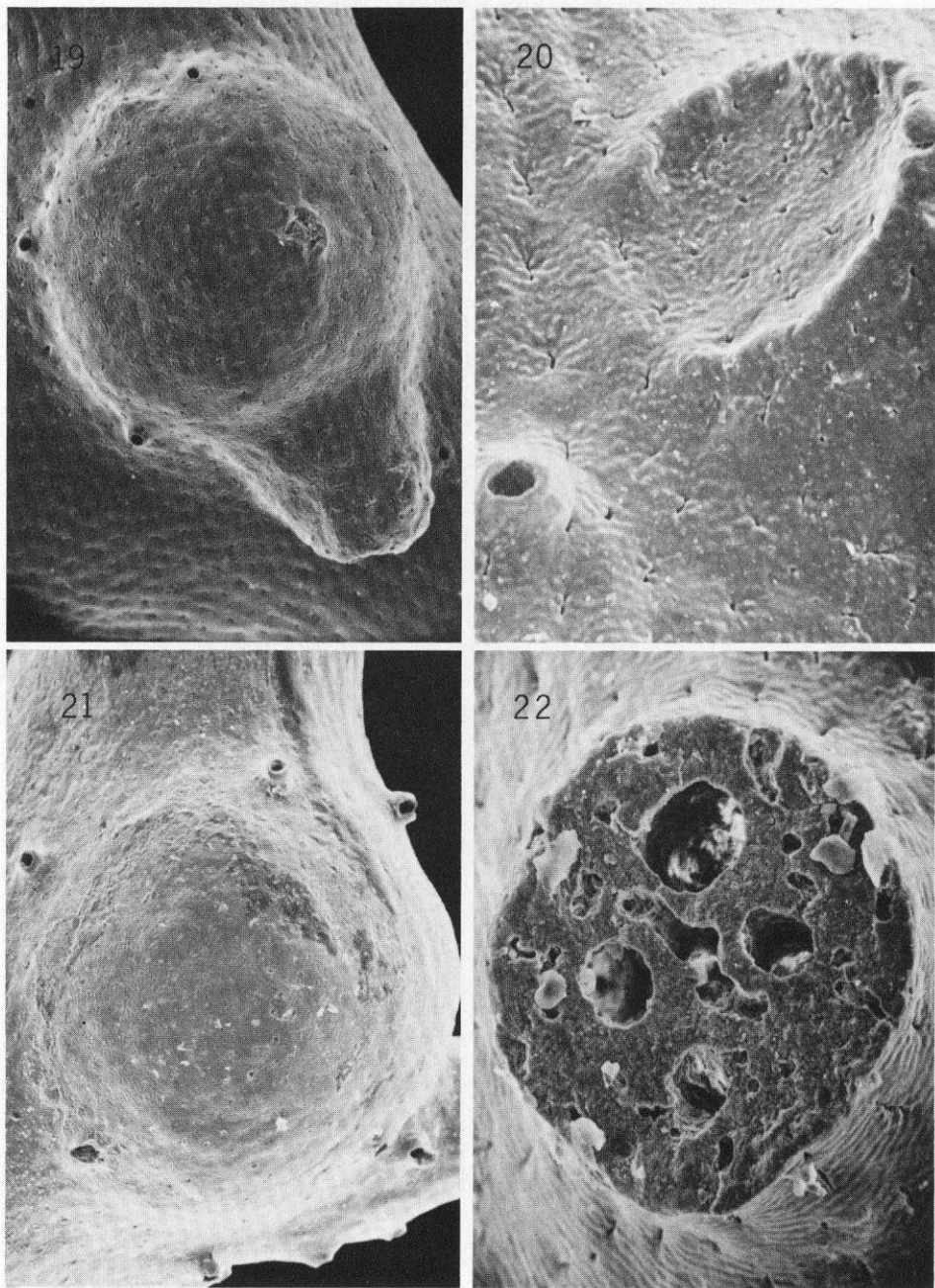
FIGS. 7-10. *Adelopora pseudothyron*, *Eltanin* sta. 254, USNM 60128: (7-8) Stereo pair of disarticulated operculum viewed from beneath (lower nub broken off), $\times 130$. (9-10). Stereo pair of operculum bored by unknown predator, $\times 110$, Scale bar = $200\mu\text{m}$.



FIGS. 11–14. *Adelopora pseudothyron*: (11–12) Stereo pair of intact, closed operculum on branch tip surrounded by prominent dactylopore tubercles, *Eltanin* sta. 25–326, USNM 60133, $\times 53$. (13) Intact operculum in open position, dactylopore in foreground, *Eltanin* sta. 254, USNM 60128, $\times 144$, Scale bar = $200\ \mu\text{m}$. (14) The same operculum viewed from the back, $\times 162$, Scale bar = $200\ \mu\text{m}$.



FIGS. 15–18. *Adelopora pseudothyron*, *Eltanin* sta. 254, USNM 60128: (15) Gastropore cavity with operculum removed, $\times 130$. (16) Opercular hinge line in gastropore missing operculum, $\times 145$. (17) Underside of operculum (upper left) showing how one nub fits into coenosteum, $\times 347$, Scale bar = $200\ \mu\text{m}$. (18) Longitudinal section of gastropore tube, $\times 72$.



FIGS. 19-22. *Adelopora pseudothyron*, *Eltanin* sta. 254, USNM 60128: (19) Ampulla with lateral extension, $\times 53$. (20) Concave, truncated end of lateral extension, dactylpore tubercle in lower left, $\times 163$. (21) Hemispherical ampulla, $\times 56$. (22) Cross section of branch showing several coenosteal canals, $\times 170$.

concavity on the lower side. The straight, articular edge of the operculum is modified into a rod, which projects beyond the ellipse as a short nub on either side (figs. 7–8). The rod fits into a coenosteal groove (fig. 16) and the nubs are freely retained within coenosteal cavities (fig. 17), allowing an articulation of the hinged operculum. When closed, the top of the operculum is flush with the branch surface and the free edge rests on a small ledge encircling the upper gastropore tube. Opercula can swing open approximately 90° before being checked by the coenosteum behind the hinge. A linear depression along the surface of the articular edge of the operculum allows a later checking contact and therefore a slightly greater opening of the operculum. A slit, occupying the middle third of the lower side of the operculum, runs parallel and adjacent to each edge (figs. 7–8). These slits are presumed to be the scars of opercular retractor muscles.

Dactylopores, shaped as perforated tubercles, occur primarily on distal branches. The pores measure between 23–35 μm in diameter, whereas the tubercles may be up to 0.1 mm wide and 0.15 mm tall, the tallest dactylo pore tubercles occurring on branch tips (figs. 11–12). Tubercles away from the branch tip are usually only 0.02–0.03 mm tall.

Ampullae of two different shapes occur on most colonies. One form is hemispherical and quite prominent, 1.06–1.22 mm in diameter (fig. 21). These often occur in clusters. The other kind is similar in size and shape but augmented by a small lateral extension, which is abruptly truncated (fig. 19). The truncated face, about 0.23 mm in diameter, is concave (fig. 20) but was never observed to be ruptured or to have any pores. The orientation of the extension is random.

The tissue was studied by gross dissection and histological sections of decalcified branches, and by thin sections and acetate peels of epoxy-embedded whole branches. The complex, anastomotic coenosteal canal network remained intact in the decalcified branches, and even the opercular shape is maintained by its canal system; however, the preservation was not adequate to examine the polyp in any detail. All that was visible in the gastropore was a thin band of tissue (opercular retractor muscle?) extending from the base of the pore, continuing along the side of the pore away from the hinge, and joining with the free edge of the operculum.

At least two types of nematocysts are present. Near the coenosteal surface are elongate but slightly oval nematocysts measuring 17.2–21.9 μm \times 4.1–5.3 μm . Deeper in the branch (within a gastrozoid), a smaller rod-shaped form predominates, measuring 11.2–14.1 μm \times 2.9–4.2 μm .

Remarks

Two of the stations at which *A. pseudothyron* was collected (*Eltanin*-1343, 1345) were made on a seamount in the Subantarctic South Pacific, which supports a flourishing deep-water coral bank (Cairns, in press). The framework scleractinian coral, *Solenosmilia variabilis*, supports a wide diversity and great concentration of animal life, including 32 groups of benthic invertebrates representing 13 phyla. Ordinarily, deep-water corals are found in low density and in areas of low faunistic diversity. The enormous diversity and abundance of life on a deep-water bank probably exerts a much higher predation pressure on the coral and it is hypothesized that the evolution of a tightly fitted, defensive operculum is an adaptation to this predation pressure. It is ironic, therefore, that the operculum of *Adelopora*, perhaps the best defended stylasterine known, is sometimes penetrated by circular bore holes (figs. 9–10). These holes were originally thought to be produced by gastropod radulae

but the small diameter of the pores (0.12 mm) argues against a molluscan predator (pers. comm., E. Yochelson and J. Rosewater).

Etymology

The specific name *pseudothyron* (Greek: secret door), refers to the gastropore opercula, which, when closed, are usually quite inconspicuous.

Types

HOLOTYPE: *Eltanin* sta. 254, 59°49'S, 68°52'W (seamount in Drake Passage), 512–622 m, 10 Oct. 1962, USNM 60198.

PARATYPES: *Eltanin* sta. 254, USNM 60128, BMNH 1981.8.1.1, ROMCN-B 102, RMNH Coel. 14114; *Eltanin* sta. 1343, 54°50'S, 129°50'W, 567–824 m, 7 Nov. 1964, USNM 60131; *Eltanin* sta. 1345, 54°50'S, 129°48'W, 915–1153 m, 7 Nov. 1964, USNM 60132; *Eltanin* sta. 1521, 54°09'S, 52°08'W, 419–483 m, 30 Jan. 1966, USNM 60130; *Eltanin* sta. 25–325, 46°00'S, 83°59'W, 742 m, 9 Oct. 1966, USNM 60129; *Eltanin* sta. 25–326, 46°04'S, 83°55'W, 298 m, 9 Oct. 1966, USNM 60133.

Distribution

Known only from four Subantarctic seamounts from the Scotia Ridge, Drake Passage, off Chile (Chile Rise), and South Pacific (Heezen Fracture of Eltanin Fracture Zone). Bathymetric Range: 298–915 m.

Summary

A new species of Stylasterina is described, representing a new genus and new subfamily. The distinguishing feature of the taxon is the presence of freely hinged opercula, one covering each gastropore, which is unique in the Stylasterina. Other coelenterates have opercula but none are freely hinged and interlocked as in *Adelopora*. Some cheilostome bryozoans have a similar, obviously highly convergent, structure; however, even among the bryozoans the hinging mechanism is probably not interlocked. The operculate stylasterine is only known from four seamounts in the Subantarctic South Pacific and southwest Atlantic, one of which supports a deep-water coral bank. It is hypothesized that the selection pressure of high predation density favoured the development of a tightly fitted hinged operculum for defence of gastrozooids.

Acknowledgments

I would like to thank Drs. Frederick M. Bayer and Alan H. Cheetham (United States National Museum), and Helmut Zibrowius (Station Marine d'Endoume) for their assistance and encouragement throughout the project. Because the stylasterine nature of the specimens was not clear initially, I would also like to thank the following people who hypothesized about the identity of the animal and/or the nature of the hinged operculum: Drs. Gordon L. Hendler, Joseph Rosewater, Richard S. Boardman, Meredith L. Jones, Ms. Maureen E. Downey (all USNM), Ms. Renata Carson (Royal Ontario Museum), Drs. John W. Wells (Cornell University), William A. Oliver, and Ellis L. Yochelson (both United States Geological Survey). I am also grateful to Mr. George Robertson for his persistent encouragement and enthusiasm. Finally, I would like to thank Mrs. Susann Braden, Mr. Walter R. Brown, and Ms. Mary Jacque Mann for the scanning electron microscopy; Ms. Linda

J. Cullen for preparing the histological sections; Mr. Donald Dean for assistance in preparing the epoxy embedded specimen; and my wife, Peggy, for editing and typing the manuscript.

This work was supported by the Smithsonian Oceanographic Sorting Center's Cooperative Systematics and Analyses of Polar Biological Materials Program (National Science Foundation grant DPP 76-23979).

References

- CAIRNS, S. D., in press, Antarctic and Subantarctic Scleractinia, *Antarctic Research Series*, **34**, (1).
- HARMER, S. F., 1926, The Polyzoa of the Siboga Expedition. Part II. Cheilostomata Anasca, *Siboga-Expeditie*, 28 b, 182-501, pls. 13-34.
- NAUMOV, D. V., 1960, *Hydroids and Hydromedusae of the U.S.S.R.* (English translation, 1969), Keys to the fauna of the U.S.S.R. published by the Zoological Institute of the Academy of Sciences of the U.S.S.R., number 70, 1-660.
- NUTTING, C. C., 1904, American Hydroids. Part II. The Sertularidae, *Smithsonian Institution Special Bulletin*, 1-325.
- SHROCK, R. R., and W. H. TWENHOFEL, 1953, *Principles of Invertebrate Paleontology*, 2nd ed., New York: McGraw-Hill Book Company, 816 pp.