Diagnosis.—Colonies flabellate or bushy; branches round in cross section, occasionally anastomosing, especially in flabellate colonies. Coenosteum linear-imbricate, composed of broad, flat platelets; no granules. Gastropores occur at branch tips, branching axils, and, in thicker branches, on lateral surfaces. Gastropore tube cigar shaped, with no style or tabulae; pore covered by a hinged operculum, which, when closed, is flush with the coenosteal surface. Dactylopores are randomly arranged, apically perforate mounds; no dactylostyles. Ampullae large and superficial, some with a lateral, tubular efferent canal.

Discussion.—The complete lack of coordination between the gastro- and dactylopores of Adelopora and its long dactylopore tubes clustered along branch axes, suggests an affinity with the more simple genera of the Errininae. It is most similar to Pliobothrus, both genera having apically perforate dactylopore spines, linear-imbricate coenosteal texture, and no gastrostyles. However, Adelopora differs significantly in having much better developed and organized coenosteal platelets, smaller coenosteal pores, better-formed gastropore tubes without tabulae, superficial ampullae with large efferent ducts, and gastropores located primarily at branch axils, each covered by a hinged operculum.

Occurrence.—Subantarctic seamounts from off South America and South Pacific. 298-915 m.

Type Species.—Adelopora pseudothryon Cairns, 1982, by original designation.

Adelopora pseudothryon Cairns, 1982

Diagnosis.—Colonies up to 3.8 cm tall; distal branches about 0.9 mm in diameter, basal branches up to 1 cm in diameter. Branching axils often U-shaped. Coenosteal strips 53–70 μm wide, composed of broad platelets extending the entire width of one or two strips; 75–90 leading platelet edges occur per mm. Gastropore tubes at least 1 mm deep and 0.3 mm in diameter, ending in a gently rounded cul-de-sac. Opercula 0.39–0.58 mm long and 0.35–0.64 mm wide with length to width ratios of 0.71–1.34, but averaging about 1.1. Opercula 70 μm thick at their edges but considerably thinner toward the center because of the concavity of their lower sides. Dactylopores 25–35 μm in diameter, occurring only on small diameter distal branches. Dactylopores elevated on mounds up to 0.15 mm tall and 0.15 mm broad at their bases; the pores extend down the center of the branch axis in fascicles for a considerable distance. Ampullae 1.06–1.22 mm in diameter, the efferent canal up to 0.5 mm long and 0.23 mm in distal diameter.

Gastrozooids large, bottle shaped, with a crown of 7–9 relatively long tentacles below a tapered hypostome. Dactylozooids simple and long. Rod-shaped nematocysts measuring 11.8–12.5 × 2.5–3.0 μm occur in the ectoderm, and oval nematocysts, 6.1–7.0 × 3.0–3.5 μm, occur on gastrozooid tentacles. Two short
opercular retractor muscles attach to narrow slits, one on each side of the operculum adjacent to the lower, outer edge (Fig. 28G).

Discussion.—A. pseudothyron has been more thoroughly described and illustrated by Cairns (1982a); however, three corrections are made here: (1) the larger coenosteal canals 50–90 μm in diameter described by Cairns (1982a: fig. 22) are actually dactylopore tubes, (2) the gastropore tube is not 1 mm in diameter, but 1 mm long and about 0.3 mm in diameter, and (3) slightly different nematocyst measurements are given in the diagnosis.

Adelopora is a monotypic genus.

Distribution.—Subantarctic seamounts from Scotia Ridge, Drake Passage, Chile Rise, and Eltanin Fracture Zone (South Pacific). 298–915 m.

Types.—Holotype and most paratypes deposited at the USNM. Single paratypes also at BM, ROM, and RMNH.

Subfamily Distichoporinae Stechow, 1921

Diagnosis.—Gastropores linearly arranged, usually on the lateral branch edges, flanked on either side by a row of dactylopores.

Distichopora Lamarck, 1816

Millepora: Pallas, 1766: 288 (part).
Madrepora: Nardo, 1844: 68 (part).

Diagnosis.—Colonies usually flabellate, sometimes slightly bushy; branches closely spaced but rarely anastomotic. Branches usually elliptical to rectangular in cross section, the greater branch axis in the plane of the colony; branch tips usually blunt. Coenosteal texture tuberculate to reticulate, always covered by low granules; low, longitudinal supporting ridges sometimes present. Color of coenosteum highly variable. Gastro- and dactylopores extend for a long distance down the center of the branch. Gastropores aligned or slightly staggered in pore rows, which run along the lateral branch edges, sometimes meandering over the branch faces. Gastropores usually flanked on both sides by a row of dactylopores; however, sometimes only one side has pores or one side has a greater frequency and/or height of dactylopores. Gastropores round to polygonal, sometimes sunken along a recessed sulcus or flush with the coenosteum. Dactylopores oval to elliptical, their greater axis perpendicular to the pore row; dactylopores may be elevated (in which case a short dactylotome is present), conical, or flush with the surface. No dactylostyles. Gastrostyles needle shaped (H:W often over 10) and very prominently ridged, the ridges bearing tall, pointed spines. A diffuse ring palisade is often present and tabulae sometimes stabilize the style. Female ampullae superficial and often ridged in a stellate or longitudinal fashion; male ampullae smaller. Ampullae are often clustered.

Discussion.—Distichopora is most similar to the genus Sporadopora. Both have very long gastro- and dactylopores, and sacs which completely enclose the gastrozooids, characters shared only by the simple Errininae. Furthermore, both have extremely long, ridged gastrostyles supported by tabulae (a character shared only by these two genera), reticulate coenosteum on the older branches, flush gastro- and dactylopores (some Distichopora), blunt branch tips, and no dactylostyles. Distichopora differs primarily in its linear coordination of gastro- and dactylo-
pores, elliptical dactylopores, and superficial ampullae. One species, *D. providentiae* (Hickson and England, 1909), seems to be transitional between the two genera. It has distichoporine-shaped dactylopores and partially buried ampullae, but the coordination of its dactylo- and gastropores is not as intimate as in the other *Distichopora*, and in some places it is almost random (Fig. 16H). Both Hickson and England (1909) and Boschma (1959) considered *D. providentiae* to represent an intermediate between the two genera, the former placing it in *Sporadopora*, the latter transferring it to *Distichopora*. I agree with Boschma, that *D. providentiae* is more similar to the other species of *Distichopora* and that it may resemble a transitional stage between *Sporadopora* and *Distichopora*.

**Occurrence.**—Eocene: Paris; Miocene: New Zealand; Pliocene: Japan; Recent: Indo-West Pacific, North Pacific, off Galapagos (undescribed species from Albatross station 2818: 0°29'S, 89°54'30"W, 717 m, USNM), western Atlantic. 1–717 m.

**Type Species.**—*Millepora violacea* Pallas, 1766, by monotypy.

*Distichopora* (*Distichopora*) *violacea* (Pallas, 1766)

Figures 15A–H, 26C, 27D

*Millepora violacea* Pallas, 1766: 258.


*Madrepora violacea*: Nardo, 1844: 68.


?*Distichopora rosea* Kent, 1871: 281.—Boschma, 1959: 139.

*Distichopora fisheri* Broch, 1942: 14–16, pl. 2, fig. 2, 30a.—Wells, 1954: 476, pl. 185, figs. 1–2.

Not *Distichopora violacea*: Broch, 1942: 9–14, pl. 1, figs. 1–2 (=*D. nitida* and *D. coccinea*).—Wells, 1954: 476, pl. 185, fig. 3 (=*D. nitida*).

**Diagnosis.**—Colonies flabellate, rarely exceeding 8–9 cm in height. Branches compressed in plane of fan, blunt tipped, and closely spaced. Colony form variable: forma *violacea* s.s. broadly flabellate with thick terminal branches (2.5 × 3.0–5.0 mm in diameter); forma *fisheri* flabellate but vertical branch growth predominates, terminal branches as in *violacea* s.s.; forma *tenella* broadly flabellate but terminal branches slender (1.5 × 2.5 mm in diameter). Intergrades and other variations of colony form and branch thickness also occur. Base of colony usually forms a broad encrustation. Coenosteum at branch tips tuberculate, composed of discrete convex tubercles measuring 0.15–0.20 mm in diameter, each surrounded by 5–8 round coenosteal pores 35–39 μm in diameter; tubercles covered by rounded granules 8–10 μm in diameter. Towards the colony base the tubercles fuse, creating a reticulate texture. Coenosteum usually violet or red but may be vermilion, pink, orange, brown, yellow, or white. Pore rows generally restricted to lateral branch edges but occasionally meandering over anterior or posterior faces; short rows running perpendicular to the lateral rows are common at branch tips; isolated rows of 1–4 gastropores also occur on the branch faces near the base of the colony, often resembling cyclosystems. Pore rows 0.8–1.0 mm in width, sulcus depth varies from shallow to deep. Gastropores round to polygonal, 0.3–0.5 mm in
diameter, usually arranged unilinearly. Dactylopores about 0.19 mm long and 0.06-0.08 mm wide, the pores narrowing to a lesser width near the gastropore. Dactylopores only slightly raised; dactylotomes correspondingly short. Approximately 2.1-2.9 gastropores per mm and 4.0-4.5 dactylopores per mm, the dactylopores of equal frequency on either side of the pore row, thus 3-4 dactylopores per gastropore. Illustrated gastrostyle 0.55 mm tall, 0.064 mm wide (H:W = 8.5), bearing tall (up to 35 µm) sharp, upcurved, claw-like spines on its ridges. Diffuse ring palisade composed of clavate elements measuring up to 54 µm tall and 16-18 µm in diameter; no tabulae noted. Female ampullae 0.6-1.0 mm in diameter, usually bearing radiating ridges; male ampullae smaller and usually clustered into a large mass.

Gastrozooids with 4-6 tentacles; dactylozooids adnate. Ectodermal nematocysts oval, 6.5-8.0 × 3.2-4.0 µm; those of gastrozooid tentacles and dactylozooids rod shaped, 4.0 × 1.5-2.0 µm. Sexes usually separate but hermaphrodites do occur. Male ampullae may have 4-5 gonophores apiece.

Discussion.—The history of the synonymy of *D. violacea* and a comparison to other species is given by Boschma (1959); remarks on its gonophores are made by Hickson (1893) and England (1926); and a description of the histology of the polyps and coenosteum is given by Hickson (1892).

Fifteen Recent species are assigned to *Distichopora* (Table 1): nine in the Indo-West Pacific region, one in the North Pacific, and five in the western Atlantic. In addition, three fossil species are known from the Eocene of Paris, Miocene of New Zealand, and Pliocene of Japan. I have examined representatives of all but three (*D. livida, D. sepens, D. profunda*) of the Recent species.

Distribution.—From the western Indian Ocean to the central Pacific, but not Hawaii (see Boschma, 1959: 144). Shallow water to 122 m.

Types.—Deposition unknown.

Subgenus *Distichopora* (Haplomerismos) Cairns, 1978


*Diagnosis.*—Colonies small and flabellate, the flabellum sometimes slightly curved. After initial bifurcation of main stem no further branching occurs; instead, two vertically flattened lobes are produced which grow in opposite directions and parallel to the substrate. Coenosteum flat and granular (not reticulate), bearing low longitudinal ridges. Gastro- and dactylopores are both very long, extending for a great distance down the center of the lobes. Pore rows occur on lateral edges of lobes and main stem. Dactylopores occur in about equal number on both sides of pore rows. Gastrostyles have a very high H:W and are ridged, the ridges bearing tall, slender, often fused, spines; no ring palisade. Ampullae internal, opening to surface by irregularly shaped pores.

Discussion.—*Haplomerismos* differs from the nominate subgenus primarily in its unusual colony shape and its nonreticulate coenosteal texture. Other points of
difference include its gastrostyle spines, which are more slender and often fused, and its internal ampullae, both characters shared with the aberrant D. providentiae. The bilobate colonial form is unique among the Stylasterina. Several species of Distichopora, particularly D. borealis, have broad, flattened branch tips approximating a small lobe, but eventually bifurcation occurs producing an arborescent colony. Only one other species is known to have plate-like fronds: some specimens of Errinopora nanneca have large, vertical, solid labella. Stylanthea porphyra also has a broad, flat coenosteal surface, but it is an encrusting species.

Occurrence.—Known only from off Laysan, Hawaiian Islands. 658–736 m.

Type Species.—D. (Haplomerismos) anceps Cairns, 1978, by original designation.

Distichopora (Haplomerismos) anceps Cairns, 1978
Figures 16A–G, 24C, 25F, 28E

Distichopora (Haplomerismos) anceps Cairns, 1978: 84–86, pi. 1, figs. 1–6.

Diagnosis.—Colonies up to 26.4 mm tall and 49.2 mm broad; main stem 4–5 mm in diameter and about 12 mm tall. Lobes 2.5–3.5 mm thick and usually slightly asymmetrical, one being larger than the other. Coenosteal granules rounded to conical, 15–30 μm in diameter and equally tall; coenosteal pores irregular in outline, 20–30 μm in diameter. Both granules and pores randomly scattered over the coenosteum, the pores much less numerous. Coenosteum white. Pore row about 1 mm wide, containing a recessed sulcus about 0.6 mm deep. Gastrostyles elliptical to rectangular, up to 0.75 mm long and 0.36 mm wide, the greater axis aligned with the sulcus. Gastrostyles regularly and unilaterally arranged, separated by thin septa; up to 15 pores per cm. Dactylolopores elliptical in cross section, up to 0.35 mm long and 0.18 mm wide, oriented with their greater axes perpendicular to the pore row; no dactylotome; up to 30 pores per cm. Sometimes the dactylolopores on one side of the pore row are taller and fewer in number. Gastrostyles sometimes exceed 5.5 mm in length with an average diameter of 0.085 mm, producing H:W ratios in excess of 65. Styles bear elongate, slender spines up to 75 μm long and 6 μm in diameter, which project perpendicularly or slightly toward the tip of the style. Internal diameter of female ampullae 1.0–1.14 mm.

Gastrozooids short and squat in the contracted state, concentrated near the tip of the gastrostyle; gastrozooids orange in alcohol. Adnate dactylozooids long and slender, attached to an adhesive basal structure which is robust below the junction but long and ribbonlike above. Nematocysts of gastrozooid tentacles and dactylozooid tips small, measuring 5.0–6.0 × 2.3–2.5 μm; those of coenosteal canals only slightly larger: 7.3–8.0 × 2.7–3.0 μm. Gonophores not examined.

Discussion.—Haplomerismos is monotypic; the type-species has been more thoroughly described by Cairns (1978).

Distribution.—As for the genus.

Types.—The holotype and three paratypes are deposited at the USNM.

Figure 16. D. (Haplomerismos) anceps (A–G, paratypes from off Laysan): A, colony, ×1.4; B, E, pore row, ×15, ×34, respectively; C, midsection of a gastrostyle, ×270; D, cross section of an internal ampulla, ×40; F, coenosteal surface with ridge, ×30; G, coenosteal granules, ×500. Distichopora providentiae, H, syntype from Percy Sladen Trust Expd. station D-8: off Providence Island, 229 m, BM 1957.2.18.2, branch segment with irregular pore row, ×20.
Subfamily Stylasterinae Gray, 1847

Diagnosis.—Gastro- and dactylopores arranged in distinct cyclosystems.

Stylaster Gray, 1831
Group A ("Allopora")


Dendracis: Römer, 1863: 243 (part).
Cryptaxis Reuss, 1865: 620.

Diagnosis.—Colonies flabellate to bushy, often massive. Branches cylindrical to slightly compressed and blunt; branch anastomosis occurs in some species. Coenososteum reticulate, covered by rounded or irregularly shaped granules; coenososteum white, orange, red, pink, purple, yellow, or blue. Coenostomal papillae (small mounds) and short, flattened coenostomal outgrowths present in some species. Cyclosystems uniformly spaced on all sides of branches. Gastrostyles quite variable in shape, ranging from almost hemispherical (H:W = 1), to bullet shaped (H:W = 2–5), to lanceolate (H:W up to 10). Gastrostyles longitudinal ridged and usually highly spinose; ring palisade often present; tabulae rarely present. Three to seventeen dactylopores per cyclosystem; however, 7–9 are the most common numbers; diastemas rare. Additional isolated dactylopores often present, sometimes in great numbers. Dactylostyles well developed, composed of long cylindrical elements, but not present in isolated dactylopoires. Ampullae low superficial bulges, sometimes ridged.

Group B (Annectant group)


Diagnosis.—Like Group C, but in addition to the regularly sympodially arranged cyclosystems at the branch tips there are additional cyclosystems on the anterior and posterior branch faces, especially on the larger diameter branches. Colonies usually slightly more robust, sometimes bushy.

Group C ("Stylaster")


Cyclopora Verrill, 1866: 38.
Decentopora Hall, 1893: 117.

Diagnosis.—Colonies flabellate and delicate. Branches usually slender, terminating in a characteristic zigzag, sympodial shape. Branches elliptical in cross section and sometimes anastomose, even approaching the fenestrate growth form of Erinopsis. Coenososteum variable in texture, including reticulate-granular, linear-imbricate, and very irregular reticulate-imbricate. Papillae (nematopores ?) and
short ridges are sometimes present on the coenosteum. Coenosteum orange, beige, purple, or white. Cyclosystems occur in a regularly sympodial pattern resulting in two rows, one on each lateral branch edge. These rows may be displaced to the anterolateral edges of large diameter branches but cyclosystems do not occur on the anterior or posterior branch faces. Cyclosystems usually slightly raised above the coenosteum, especially the abcauline side, which gives them an anteriorly projecting aspect. Gastrostyles lanceolate and ridged, with a medium to high H:W ratio, and invariably with a well-developed ring palisade. Usually 10–15 dactylopores per cyclosystem; adcauline diastemas not uncommon; dactylostyles rudimentary. Ampullae large and superficial, sometimes ridged.

Discussion.—The problem of distinguishing Stylaster from Allopora has been discussed by many authors and has undoubtedly been the cause of great frustration. Typical representatives of the two genera are clearly quite different but species with intermediate characters are common. Milne Edwards and Haime (1857: 131) were the first to suggest dividing Stylaster into three groups: the first corresponding to my Group C, their second to my annectant Group B, and their third to my Group A. They also maintained the genus Allopora, distinguishing it by a more irregular branching and a smoother coenosteum. Studer (1878) accepted this scheme as did Hickson and England (1905: 6–7), who introduced a fourth group (D), which we now know as Stenohelia. Moseley (1881: 90–91, 97) acknowledged the problem but maintained two separate genera: Stylaster (my Groups B and C) and Allopora (my Group A). He differentiated them on the regularity of arrangement of cyclosystems and number of tentacles per gastrozooid. Broch (1914: 7; 1936: 8–11) admitted that there was no definite hiatus between Allopora and Stylaster but nonetheless established subgenera to name his groups: S. (Eustylaster), my Groups C and B; S. (Allopora), my Group A; and S. (Stenohelia), Stenohelia. Fisher (1938: 498–499) pointed out that establishing subgenera does not solve the inherent problem of where to place an annectant species. His faunistic account employed only Stylaster (my Group C) and Allopora (my Groups A and B). Boschma (1956: F99–100) presented the two genera as distinct with no further explanation, and in 1965c he discussed the problem and gave a short history of the debate. All recent papers have used Allopora and Stylaster as distinct genera.

I have examined representatives of about two-thirds of the valid taxa that I have listed for this species complex and, like those before me, can find no discontinuity between the two genera. Intermediates exist which have cyclosystem arrangements typical of both genera on the same colony. I have therefore synonymized Allopora with Stylaster but, because this produces a large genus containing about one-third of the stylasterine species, I have divided the genus into three groups, a variation of the solution of Milne Edwards and Haime (1857). The groups have no taxonomic standing and are created for convenience only.

To reiterate, my Group A (“Allopora” of others) is characterized by having bushy to flabellate, robust colonies; thick cylindrical branches; reticulate-granular coenosteum; low or flush cyclosystems on all sides of the branches; well-developed dactylostyles; and low, superficial ampullae. Group C (“Stylaster” of others) is characterized by having delicate flabellate colonies; thin, flattened branches; variable coenosteal texture (including imbricate); raised cyclosystems arranged in two rows on the lateral branch edges; rudimentary dactylostyles; and large, superficial ampullae. The annectant Group B has characters intermediate between the two. The most significant character separating Groups A and C is the arrangement of the cyclosystems. No other character consistently distinguished the two; however, if more species are examined histologically and by scanning electron microscopy, a more valid division may be proposed in the future.
Stylaster (Group A) is very similar to Errinopora, as previously stated. Both Group A and certain species of Errinopora (i.e., E. pourtalesii, E. stylifera) have similar colony and branch shapes, coenosteal texture (including papillae), gastro- and dactylostyles, isolated dactylopores flush with the coenosteum, and superficial ampullae. The main difference between the two is the greater coordination of gastro- and dactylopores as distinct cyclosystems in Group A; however, as previously noted, isolated gastropores on basal branches of Errinopora are sometimes surrounded by dactylopores, resulting in rudimentary cyclosystems (pseudocyclosystems). Although cyclosystems are characteristic of all Stylaster and rudimentary ones are found in some Errinopora, it is not difficult to hypothesize that the ancestor of Group A evolved from an Errinopora-type stock by a selection for the pseudocyclosystem arrangement of pores and a consistent lateral fusion of dactylopore spines, as has occurred in E. cestoporina and Gyropora, resulting in true, highly coordinated cyclosystems.

**Occurrence.** — Group A is known from the Oligocene of Germany and Washington; the Atlantic, Pacific, and Antarctic Oceans; and off South Africa (not Indian Ocean). Group B is known from the Miocene of Czechoslovakia and from the Atlantic, Pacific, and Antarctic Oceans (not Indian Ocean). Group C is known from the ?Oligocene of Italy, Eocene of Madagascar and Tonga, Miocene of Australia and Japan, and from all ocean basins. (Undescribed species in the USNM collections are from Hawaii and the Galapagos.) 1-1,400 m.

**Type Species.** — Madrepora rosea Pallas, 1766, by subsequent designation (Milne Edwards and Haime, 1850); a member of Group B.

**Stylaster roseus** (Pallas, 1766)

**Figures 17A-I, 25A, 26D, 28F, H**

**Madrepora rosea** Pallas, 1766: 312.

**Oculina rosea:** Lamarck, 1816: 287.


**Millepora rosacea:** Nardo, 1845: 637.

**Allopora rosea:** Dana, 1848: 694.


**Not Stylaster (Eu-Stylaster) roseus:** Broch, 1936: 15 (= S. erubescens).

**Stylaster (Eustylaster) duchassaingi:** Laborel, 1971: 224, pl. 8, fig. 4.

**Diagnosis.** — Colonies flabellate to bushy, up to 7 cm tall and 11 cm broad. Branches slightly elliptical in cross section and nonanastomotic; distal branches not much larger in diameter than diameter of a cyclosystem (about 1 mm). Coenosteum linear-imbricate with a tendency toward reticulate structure near ampullae and cyclosystems. Strips usually 65–80 μm wide, covered by a very irregular arrangement of platelets measuring 5–34 μm in width. Slits separating strips narrow and
deep, bearing elongate granules. Coenosteum rose, red, light purple, or yellowish. Cyclosystems variable in their arrangements. Usually on distal branches they are arranged in a regularly sympodial manner which may continue throughout the colony or be augmented by additional cyclosystems on the anterior and posterior sides. Some colonies have entirely regularly sympodially arranged cyclosystems; on others they are mostly randomly arranged; and yet others have both arrangements on different branches of the same colony. It appears that bushy colonies have a greater tendency for the irregular arrangement. Cyclosystems round to slightly elliptical, 0.75-1.0 mm in diameter. Gastrostyles lanceolate and highly ridged, measuring 0.32-0.50 mm tall and 0.11-0.20 mm in diameter (H:W = 2.1-3.6). Gastrostyle spines fused along ridges; they are slender and pointed, up to 32 \( \mu \)m long. A distinct ring palisade is present, encircling the upper third of the style, composed of vertical ridges up to 52 \( \mu \)m long and 15 \( \mu \)m wide. Based on 1,003 cyclosystems, Boschma (1965c) found the range of dactylopores per cyclosystem to be 5-15, average = 9.7, and mode = 10. Both dactylotomes and pseudosepta are about 60-70 \( \mu \)m wide; however, a small adcauline diastema is sometimes present, measuring 3-4 times the width of a pseudoseptum. Dactylostyles rudimentary, composed of widely spaced, linearly arranged, cylindrical to clavate elements 25-27 \( \mu \)m tall and 11 \( \mu \)m in greatest diameter. Ampullae very prominent, 0.5-0.7 mm in diameter, with a thin, porous surface which may be smooth or warty. Sometimes there is a small porous indentation about 0.17 mm in diameter near the base of the ampulla: the future efferent duct. Ampullae are often clustered on both the anterior and posterior sides.

Gastrozooids are short, blunt cylinders, each with several tentacles. Dactylozooid tentacles within cyclosystems are usually adnate (Goedbloed, 1962a); however, some are simple and greatly elongated (hair dactylozooids of Kruijf, 1977). Isolated simple dactylozooids also occur with varying frequency. Nematocysts of gastrozooid tentacles and dactylozooids about 6 \( \times \)2 \( \mu \)m; slightly larger swollen nematocysts measuring 7 \( \times \)4 \( \mu \)m occur on the pseudosepta. Colonies may be hermaphroditic, but individual ampullae are exclusively male or female (Goedbloed, 1962b).

Discussion.—As I have divided the genus *Stylaster* (Table 1), Group A contains 24 species, 1 subspecies, and 1 forma; Group B has 16 species and 4 subspecies; Group C has 26 species, 5 formae, and 2 unnamed species; two more species are nomina nuda. *Stylaster* s.l. thus contains 68 species (plus 2 nomina nuda), 5 subspecies, and 6 formae, or a total of 79 taxa. *S. roseus* belongs in the annectant Group B, “a rather unfortunate choice” of the type-species, according to Boschma (165c: 232), because of its intermediate position between *Stylaster* and *Allopora*.

Boschma (1955; 1965c) discussed the synonymy and morphology of *S. roseus* in great detail. Goedbloed (1962a; b) examined its dactylozooids and gonophores, and Kruijf (1977) reported on its polyp behavior and sweeping tentacles. Other important works dealing with the soft anatomy or natural history of other species of *Stylaster* s.l. include: Moseley (1881: 57-65), Hickson (1890), Broch (1914: 8–19; 1942: 73–77), England (1926), and Ostarello (1973; 1976).

Distribution.—Caribbean and off Brazil to Pernambuco (not Gulf of Mexico or Florida Keys). Most common between 0.5-4 m.

Types.—Pallas’s types have not been traced.

*Stylantheca* Fisher, 1931


**Diagnosis.**—Colonies encrusting, forming thin laminae on rocks and shells. Coenosteum reticulate-granular, purple to light pink, and bears numerous small, apically perforate papillae. Cyclosystems round to elliptical, each bearing 1–12 gastrozooids and gastrostyles. Gastrostyles globose to conical, squat (H:W usually less than 2), and vertically ridged; the ridges bearing long, slender spines. A prominent ring palisade originates from the common spongy horizontal gastropore floor, below which the gastrostyles are housed in individual gastrostyle chambers. Three to sixteen dactylopores per cyclosystem; isolated dactylopores uncommon. Inner edge of dactylotome deep, revealing a well-developed dactylostyle. Ampullae internal, often massed together or encircling a cyclosystem, alternating with the dactylopores.

**Discussion.**—Stylantheca is very similar to Stylaster (Group A); several authors have synonymized the two or treated Stylantheca as a subgenus. It differs from Stylaster (Group A) primarily in its encrusting habit and its tendency to have more than one gastrozooid per cyclosystem, both of which are characters unique in the Stylasterina. For these reasons Stylantheca is kept as a separate genus. Stylaster verrillii (Dall, 1884) also forms lumpy encrustations but also develops into upright lobes and normal arborescent colonies (Fisher, 1938: 521). In the case of S. verrillii the encrusting colonies are probably just a stage in the development of larger branched colonies. Two other characters that unite the species of Stylantheca, and serve to differentiate them from most Stylaster, are their well-developed coenosteal papillae and their very deep dactylotome slits.

**Occurrence.**—Recent: Northeast Pacific from California to Alaska. 0–18 m.

**Type Species.**—Stylantheca porphyra Fisher, 1931, by monotypy.

Stylantheca porphyra Fisher, 1931
Figures 18A–I, 24H, 27G, J

Stylantheca porphyra Fisher, 1931: 395–397, pl. 15, fig. 1, pl. 16, fig. 5, pl. 17, fig. 6.—Boschma, 1956: F100, text-fig. 81, 1; 1957: 33; 1960: 426–427, text-fig. 1e–f; 1961: 221.
Allopora porphyra: Fisher, 1938: 528–530, pl. 59, figs. 1–2, pl. 60, pl. 61, fig. 1, pl. 70, fig. 2.
Stylaster (Stylantheca) porphyra: Boschma, 1951: 39, text fig. 5b.

**Diagnosis.**—Encrustations up to 30 × 25 cm, about 2.5 mm thick. Coenosteal strips flat, 25–55 μm wide, separated by deep slits about 7.5 μm wide; granules 3–7 μm in diameter, pointed. Coenosteal papillae uniformly spaced about 1 diameter from each other, fused into parallel rows, or absent altogether from portions of the colony. Papillae 0.07–0.19 mm in diameter and up to 0.24 mm tall, having an irregularly shaped apical pore measuring about 17 μm in diameter. Cyclosystems round to elongate; the most elongate appear to be multiple cyclosystems fused together. Round cyclosystems 1.0–1.1 mm in diameter, elongate ones up to 2.7 × 1.0 mm in size. Cyclosystems usually only slightly raised above coenosteum, more rarely elevated up to 2 mm with short coenosteal costae radiating from the dactylotome edges. One to 12 gastrostyles per cyclosystem (Fisher, 1938): in a sample of 31 cyclosystems examined from the type-specimens, a range of 1–8 was found, average = 3.3 (σ = 1.59), mode = 3. Gastrostyles globose and very irregular, 0.40–0.43 mm high, 0.26–0.33 mm broad, with H:W ranging from 1.2–1.6. Gastrostyle spines up to 80 μm long and 7 μm in diameter, pointed, and usually fused to adjacent spines near the underlying ridge. In a sample of 34 cyclosystems, the range of dactylopores per cyclosystem was 6–16, average 9.11
(σ = 2.08), mode = 10. Dactylostyles up to 0.35 mm long and 0.09 mm wide, composed of long, blunt, cylindrical elements up to 50 μm long and 10 μm in diameter. Elements of ring palisade similar but shorter. Male ampullae about 0.3 mm in internal diameter, female 0.4 × 0.6–0.8 mm in internal diameter.

Gastrozooids squat and clavate, with 5–8 short tentacles attached about midway down the polyp. Dactylozooids adnate with only a tiny free part. Nematocysts of gastrozooid tentacles and dactylozooids measure about 6 × 2 μm; there are larger nematocysts (9 × 2.5 μm) in the epidermis, but unfortunately a surface papilla was not sectioned.

Discussion.—Three species are assigned to Stylantheca, all endemic to shallow water in the northeastern Pacific. S. porphyra is most similar to S. petrograpta (Fisher, 1938), the latter differentiated only by its lower number of gastrozooids per cyclosystem (range 1–3, average 1.35 for the type-specimens), fewer dactylozooids per cyclosystem (range 4–9, average 5.8), and smaller cyclosystems (0.73–0.77 mm in diameter). The fewer gastrozooids and dactylopores per cyclosystem can probably be attributed to the smaller size of the cyclosystem, which, in turn, may be environmentally controlled. Therefore, it is possible that S. petrograpta may be synonymized or reduced to a subspecies or forma of S. porphyra. Fritchman (1974) has studied the planula and early settlement of S. petrograpta. The third species, S. papillosa (Dall, 1884), is known only from the tiny type-specimen which contains only 28 complete cyclosystems. Each cyclosystem has but one gastrostyle; dactylopores per cyclosystem range from 3–5 (average = 4.0); and the asymmetrical cyclosystems measure 0.82–0.85 mm in diameter. Because of its encrusting mode and only one gastrostyle per cyclosystem, it lies intermediate between typical Styliaster (Group A) and Stylantheca, but based on its coenosteal texture, gastrostyle, and general aspect, S. papillosa is tentatively assigned to Stylantheca. Obviously more specimens are needed to correctly resolve its position.

Distribution.—Known only from the Monterey Bay area, California, 0–1+ m.

Types.—The holotype and 13 paratype colonies are deposited at the USNM (43018, 43019, 43276, 43277). Presumably another paratype is at the BM. The types of all three species have been examined by the author.

Calyptopora Boschma, 1968

Stylaster: Pourtalès, 1867: 115.
Stenohelia: Kent, 1870: 123 (part: S. complanata).

Diagnosis.—Colonies flabellate. Branches round to elliptical in cross section, sometimes posteriorly carinate; branch anastomosis may occur. Coenosteum reticulate-granular and white, bearing numerous small papillae (nematopores), especially on larger diameter branches. Cyclosystems unilinearly or sometimes slightly

Figure 18. Stylantheca porphyra (A–I, syntypes from Carmel Bay, California): A, colony, ×1.1; B, coenosteal surface with cyclosystems and papillae, ×15; C, cyclosystem, ×36; D, longitudinal fracture of a cyclosystem revealing two gastrostyles and several dactylostyles, ×36; E, coenosteum bearing papillae, ×67; F, reticulate coenosteal texture, ×270; G, gastrostyle, ×93; H–I, dactylostyle and dactylostyle elements, ×144, ×1,190, respectively.
sympodially arranged, but in both cases the cyclosystems are all on the anterior side. Cyclosystems usually have one or more diastemas and one or more fixed lids of variable size. The lids are broad, tongue-shaped projections or simply the overdevelopment of several adjacent pseudosepta which overhang the gastropore. Lids are predominantly abcauline. Gastropores broad and deep with a small gastrostyle chamber containing a lanceolate, ridged gastrostyle of small-medium H:W. A ring palisade is present. Dactylostyles well developed. Ampullae superficial, sometimes with an efferent duct.

Discussion. — *Calyptopora* is very similar to *Stylaster* (Group C), differing primarily in its exclusively anterior facing and usually unilaterally arranged cyclosystems, and its cyclosystem lids. These character states are approached by various species of *Stylaster* e.g., some species of *Stylaster* have two rows of anterolaterally arranged cyclosystems indicating a distinct anterior side, and the pseudosepta of *S. alaskensis* are sometimes strongly exsert, approximating a lip. Nonetheless, the three species now placed in *Calyptopora* are considered as a distinct genus.

Occurrence. — Recent: New Zealand region and northern Caribbean. 183–2,010 m.

Type Species. — *C. reticulata* Boschma, 1968, by original designation.

*Calyptopora reticulata* Boschma, 1968

Figure 19A–I


Diagnosis. — Colonies large, up to 17 cm tall and 20 cm broad; basal branches up to 2.3 × 1.9 cm in diameter. Distal branches often have a continuous ridge along their posterior sides; larger diameter branches round to slightly elliptical in cross section and frequently anastomotic, producing a well reinforced flabellum. A commensal polychaete, *Malmgreniella dicirra* Hartman (identified by M. H. Petthibone), induces flattened calcareous tubes to be formed on both the anterior and posterior colony faces. Coenosteal strips 50–90 μm broad, covered by irregularly shaped, angular granules. Nematopore mounds 0.14–0.20 mm in diameter and about 0.05 mm tall, each apically perforated with irregular slits. Cyclosystems 0.9–1.6 mm in diameter; one or two short diastemas often present on the abcauline perimeter of the cyclosystem, usually adjacent to an ascending branch. Pseudosepta often highly exsert, those on abcauline side often fused into a broad lid which overhangs the cyclosystem. Expression of lid quite variable, ranging from slightly overdeveloped pseudosepta to two broad lids (one ab- and one adcauline), which fuse over the cyclosystem, forming a canopy. Three to 17 dactylopoeres per cyclosystem; of 16 cyclosystems examined from the penultimate position on distal branches, the average was 11.3 (σ = 2.27), mode = 9.5. Gastrostyles up to 0.33 mm tall and 0.14 mm in diameter (H:W = 1.3–2.9). Dactylostyles consist of two to three adjacent rows of closely spaced pillars, measuring about 24 μm tall by

Figure 19. *Calyptopora reticulata* (A–E, Eltanin-1851: 49°40’S, 178°53’E, 476–540 m, 3 Jan. 1967; B, F–I, Eltanin-1991: 54°30’S, 170°22’E, 1,860–1,940 m, 2 Jan. 1968; C–D, G, Eltanin-2143: 49°51’S, 178°55’E, 2,010–2,100 m, 26 Feb. 1968): A, colony, ×0.43; B–C, distal branch showing cyclosystem lids, ×14; D, cyclosystem with lid, ×28; E, cyclosystem with lids completely fused over gastropore, ×38; F, coenosteal papillae, ×73; G, dactylostyle, ×390; H–I, cross section of gastrostyle chamber containing a gastrostyle, ×43, ×133, respectively.
16 μm in diameter. Female ampullae 0.65–1.06 mm in diameter, sometimes with a short, tubular, lateral efferent duct. Male ampullae 0.49–0.61 mm in diameter, often clustered on the outside of the worm tube.

The soft parts were poorly preserved in the specimen sectioned; however, the tiny gastrozooids have several tentacles and the dactylozooids are adnate. Nematocysts measuring \(7 \times 2.5\) μm are common in gastrozooid tentacles and dactylozooids.

**Discussion.**—Two other species are placed in *Calyptopora*. *C. complanata* was previously assigned to *Stenohelia*, but with the establishment of *Calyptopora* for the unifacial stylasterines with gastrostyles and fixed lids (Boschma, 1968a), and the added fact that *Calyptopora* does have dactylostyles (Cairns, in press), it becomes clear that *C. complanata* belongs in this genus. Examination of the types of both *C. complanata* and *C. virginis* show them to be synonymous, as Broch (1936) suspected. *C. pachypoma* (Hickson and England, 1905) is quite different from the other two species in coenosteal texture, gastropore shape, and lack of dactylostyles and should probably form the basis of a new genus.

**Distribution.**—Macquarie Ridge; New Zealand Plateau; off Antipodes, Bounty, and Chatham Islands. 349–2,010 m.

**Types.**—The holotype and some paratypes are deposited at the New Zealand Oceanographic Institute; other paratypes are at the RMNH (Vervoort and Zibrowius, 1981: 30). Types not examined by the author.

*Stenohelia* Kent, 1870

*Allopora*: Johnson, 1862: 196 (part).


*Stylaster (Stenohelia)*: Hickson and England, 1905: 8, 15.—Broch, 1936: 10 (part: not *S. (S.) complanatus*).


**Diagnosis.**—Colonies flabellate and delicate; distal branches round in cross section and usually very thin, sometimes half the diameter of a cyclosystem in thickness. Sometimes polychaete commensals induce perforated tubes to be produced, which usually leads to a more robust and slightly bushy corallum. Coenosteum white and usually longitudinally ridged, especially on distal branches; larger diameter branches are either ridged or reticulate in texture. Usually the coenosteum is covered by irregularly shaped granules but in one case (*S. robusta*) a linear-imbricate texture is present. Nematopores often occur on the outside of worm tubes but are otherwise rare; coenosteal spines sometimes present. All cyclosystems originate on the anterior side and project perpendicular to the branch. Cyclosystems are usually unilinearly arranged on a branch and measure 0.8–2.0 mm in diameter. Gastropores very long and invariably curved 90° along the branch axis, sometimes extending all the way to the wall of the more proximal cyclosystem. In the latter case, the gastropore is not visible from the outside; however, usually the gastropore is shorter and the tip of the style can be glimpsed projecting through a well-developed ring palisade. Gastrostyle of medium to high H:W, irregularly ridged, and bears fused spines. Seven to 20 dactylopores per cyclosystem; no diastemas or lids. Dactylostyles rudimentary. Ampullae superficial hemispheres, usually clustered around a cyclosystem, but may also be scattered irregularly over the anterior and posterior surfaces.

**Discussion.**—*Stenohelia* is most similar to *Stylaster* (Group C), differing from it by having: (1) all cyclosystems on the anterior side, (2) a curved gastropore, (3)
slightly concave upper edges of the pseudosepta, and (4) ampullae clustered around the base of the cyclosystems.

Occurrence.—Western Pacific, Antipodes, Galapagos, Madeira, Cape Verde Islands, Lesser Antilles. 91–1,901 m.

Type Species.—*Allopora maderensis* Johnson, 1862, by subsequent designation (Broch, 1936: 8).

**Stenohelia maderensis** (Johnson, 1862)

*Figure 20A–B, D–G*


*Allopora madeirensis* Studer, 1878: 633.


*Stylaster tilius* Hickson, 1912b: 461–462.

Not *Stenohelia maderensis* Boschma, 1964b: 64–69, pl. 1, figs. 13–14 (=*S. profunda*); 1964c: 80–84, pl. 2 (=*S. profunda*).

**Diagnosis.**—Colonies up to 9 cm tall and 5.7 cm broad, supported by a basal branch up to 5 mm in diameter. Branches anastomose infrequently and there is no polychaete commensal. Coenosteal strips 75–85 μm wide and usually slightly convex to ridged; sometimes ridged strips alternate with flatter ones. Coenosteal slits deep, about 10 μm wide. Strips covered by slender, rudimentary, imbricated scales. Cyclosystems elliptical in cross section, about 1.0 mm in greater diameter and 0.8 mm in lesser, the greater diameter transverse to the branch. Gastrostyles lanceolate, about 0.4 mm tall and 0.16 mm in diameter (H:W = 2.5), the tip easily visible from the outside. Ring palisade well developed. Of 100 cyclosystems examined, Boschma (1967) found a range of 9–19 dactylopores per cyclosystem, average = 13.5, and mode = 14. Dactylostyles composed of a unilinear row of slightly clavate elements about 42 μm tall and 12 μm in diameter. Ampullae quite prominent, expressed as globose hemispheres 0.75–0.85 mm in diameter surrounding the cyclosystems, and also sometimes found on the posterior side of the branch opposite a cyclosystem. Ampullae warty and often ridged. Female efferent ducts are indicated by a shallow circular depression about 0.17 mm in diameter on the sides of each ampulla.

Alcohol-preserved specimens of *S. maderensis* were not available for study, but examination of the soft parts of the closely related *S. profunda* from ALBATROSS-2753 (Figs. 20C, H–I, 24D, 26E, 27E–F) revealed a robust, cylindrical gastrozooid about 0.5 mm tall with a whorl of seven tentacles below an extended hypostome. Dactylozooids adnate. Nematocysts measuring 5.0–5.5 × 2.0–2.5 μm common in gastrozooid tentacles and dactylozooids.

**Discussion.**—Ten species are assigned to *Stenohelia* (Table 1), only two of which occur in the Atlantic. *S. maderensis* is distinguished from the western Atlantic *S. profunda* Moseley, 1879, by its smaller, more regularly shaped cyclosystems; less dactylopores per cyclosystem; larger, more conspicuous ampullae; coarser coenosteal ridges; and shorter gasteropore, which allows the gastrostyle tip to be seen from the outside. Boschma's (1964b: c; 1967) records of *S. maderensis* from the West Indies are *S. profunda*.

*Stenohelia boschmai* Wells, 1977 (Eocene, Tonga), is removed from *Stenohelia* and placed incertae sedis. Wells (1977) did not observe gastrostyles in his specimens and examination of his material suggests that gastrostyles were never pres-
ent. *S. boschmai* has the appearance of a *Cryptothelia* without lids. No currently defined genus is appropriate to receive *S. boschmai*.

**Distribution.**—Known only from Madeira and Cape Verde Islands. 91–275 m.

**Types.**—The holotype was originally deposited at the BM but can no longer be found there; it is presumed to be lost.

**Conopora** Moseley, 1879

*Sylaster*: Studer, 1878: 635 (part).


**Group A**

**Diagnosis.**—Colonies flabellate unless modified by a commensal polychaete, which induces a somewhat bushy and more robust growth form. Distal branches delicate and slightly compressed in the plane of the colony, supporting sympodially arranged cyclosystems in alternating positions on the lateral branch edges; larger branches sometimes anastomose. Coenosteum irregularly linear-imbricate, covered by broad, flat platelets. Raised nematopores often present, sometimes in great density, especially on larger branches, the exterior of worm tubes, and the tops of pseudo-septa. Coenosteum white. Distal cyclosystems slightly exsert and oriented toward the branch tip, as in *Stylaster* (Group C). Gastropore consists of two chambers, the upper, larger chamber separated from the lower, thinner one by a constricted aperture analogous (?) homologous) to the ring palisade. Adecauline diastemas common in some species. Dactylotomes extend deeply into upper gastropore chamber. No gastro- or dactylostyles. Female ampullae usually superficial; male ampullae usually internal, communicating with the upper gastropore chamber via an efferent duct.

**Group B**

**Diagnosis.**—Colonies robust; branches large and round in cross section, supporting randomly arranged cyclosystems on all branch surfaces, as in *Stylaster* (Group A). Coenosteum reticulate-granular; nematopores common. No polychaete commensalism observed. Otherwise, similar to Group A.

**Discussion.**—*Conopora* is remarkably similar to *Stylaster*, differing primarily by its absence of gastro- and dactylostyles. Both genera even have a broad range of colony shapes and cyclosystem arrangement, which created the need for similar groups within the genera: *Stylaster* (Group A) and *Conopora* (Group B) are equivalent and *Stylaster* (Group C) and *Conopora* (Group A) are equivalent. *Stylaster* (Group B), the annectant group, has no counterpart in *Conopora*; however, it is interesting to note that two of the several hundred colonies of *C. verrucosa* examined had cyclosystems scattered irregularly on all sides of several distal branches.

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Figure 20. *Stenohelia maderensis* (A–B, D–G, specimens from Santiago de la Praya, Cape Verde Islands, BM 1950.1.11.81): A, part of colony, X3.8; B, F, branch fragment with ampullae, X20, X40, respectively; D–E, coenosteal texture, X83, X270, respectively; G, dactylostyle, X400. *Stenohelia profunda* (C, H–I, Albatross-2753: 13°34'N, 61°03'W, 514 m, 4 Dec. 1887): C, gastrostyle and ring palisade, X100; H, cyclosystem and ampullae around base of cyclosystem, X13; I, pseudo-septa of a cyclosystem, X100.
es, possibly indicating a similar transition within Conopora. In Stylaster, the groups were historically given separate generic names, but not in Conopora, an inconsistency noted by Boschma (1968a: 101). However, the inconsistency is circumvented by considering Stylaster as a genus with three groups and Conopora as a genus with two groups.

**Occurrence.**—Group A: Recent: Indo-West Pacific, Antarctic and Subantarctic, New Zealand. 110-2,355 m.—Group B: ?Paleocene: Denmark; Recent: Providence, Indian Ocean. 228 m.

**Type Species.**—C. tenuis Moseley, 1879 (=Conopora laevis (Studer, 1878)), by monotypy.

*Conopora laevis* (Studer, 1878)

Figure 21A–D

*Stylaster laevis* Studer, 1878: 635, pl. 2, fig. 5a–b.—Not Moseley, 1881: 81 (=C. verrucosa).—Boschma, 1957: 12.

*Stylaster obliquus* Studer, 1878: 633–636, pl. 2, fig. 7a–d.


*Conopora pauciseptata* Broch, 1951 is considered synonymous with C. laevis by Broch (1956: 486; 1957: 39; 1966: 115–116)

*Conopora verrucosa* Studer, 1878: 635–636, pi. 2, fig. 1a–b.

*Conopora bicarinata* Moseley, 1879; 1881: 82, pi. 12, figs. 5a–b, 6.—?Hickson and England, 1905: 25; 1909: 351.—?Brock, 1936: 88–91, pl. 13, fig. 37.—Boschma, 1956: F100, fig. 82, 2a; 1957: 39; 1966: 115–116.

*Stenohelia obliqua* Boschma, 1957: 32.

*Conopora laevis* Zibrowius, 1981: 274–277, pl. 3, figs. 8–11, pl. 4, figs. 1–5.

**Diagnosis.**—Colonies up to 6.5 cm tall with a basal branch diameter up to 5.5 mm. Coenosteal strips 62–115 μm wide, covered by equally broad, imbricated platelets with a frequency of 55–60 leading edges per mm. The free edges of the platelets are usually directed toward the branch tip, but occasionally a series is directed proximally, and at some point on the coenosteal strip the series meet with little disruption. No nematopores. Cyclosystems round to elliptical, 1.02–1.22 mm in greater diameter; no diastemas. Based on 19 cyclosystems from the holotype of *C. laevis*, the range of dactylopores per cyclosystem is 8–12, average = 10.0 (σ = 1.52). Dactylotomes are about 0.1 mm wide; pseudosepta are wedge shaped and sometimes concave. Male ampullae internal; female ampullae superficial, up to 0.6 mm in diameter. Soft parts unknown.

**Discussion.**—Only five species are assigned to Conopora (Table 1). I have examined the types of all but one of the nominal species (*C. major*) and herein synonymize *C. pauciseptata* Broch, 1951 with *C. verrucosa* (Studer, 1878) and strongly doubt the placement of *C. arborescens* Nielsen, 1919, in this genus. The poor preservation of a syntype and topotypic specimen of *C. arborescens* does not allow a decision on whether or not the cyclosystems have gastrostyles; in this case, Stylaster (Group A) cannot be ruled out.

*C. laevis* is most similar to *C. verrucosa*, but can be distinguished by its complete lack of nematopores, lack of cyclosystem diastemas and thus having slightly more...
dactylopores per cyclosystem, more exert cyclosystems, and more widely separated cyclosystems. The nematopores of *C. verrucosa* are sometimes very dense (separated from one another by only 1–3 diameters), tall (up to 0.15 mm), and distributed over the entire colony. The type of *C. verrucosa* is a specimen such as this. However, the nematopores may also be much less common (occurring only on the pseudosepta and worm tube), and flush with the coenosteum. The type of *C. pauciseptata* and most of the specimens reported by Cairns (in press) as *C. pauciseptata* are intermediate between these extremes. *C. verrucosa* is also characterized by adcauline diastemas, not on distal cyclosystems but on those cyclosystems of larger diameter branches. The diastema reduces the average number of dactylopores per cyclosystem to about 7.1 (Boschma, 1966). Finally, the cyclosystems on basal branches of *C. verrucosa* are flush or almost sunken into the coenosteum and the cyclosystems on distal branches are more crowded.

Soft tissue of *C. laevis* was not available for study, but tissue of *C. verrucosa* from Edisto TD 2-14 (Figs. 21E–H, 26A, H) revealed a compressed hemispherical gastrozooid occupying the lower gastropore chamber which led via a narrow neck to a mound-like hypostome. Instead of tentacles, the hypostome contains large inflated cells. Dactylozooids adnate. Nematocysts of nematophores about 29 X 4 μm; smaller nematocysts measuring about 8 X 1.2 μm are less common in the tissue.

**Distribution.**—Off New Zealand, Chatham Island, Kermadec Islands, ?Indonesia, ?Chagos Archipelago, ?western Indian Ocean, ?Japan. 110–951 m. (The distributional records of Hickson and England (1905, 1909) and Broch (1936) have not been verified.)

**Types.**—The types of *S. laevis* and *S. obliquus* are deposited at the Zoologisches Museum, Berlin (1776, 1778, respectively). The syntypes of *C. tenuis* are deposited at the BM (1880.11.25.184). All of these types were examined by the author.

**Cryptothelia Milne Edwards and Haine, 1849**


**Diagnosis.**—Colonies flabellate and usually small and delicate. About one-quarter of the species are associated with a commensal polychaete, which induces a more robust colony. Branches round in cross section and very thin; distal branches thinner in diameter than the cyclosystems they support. Coenosteum linear-imbricate on distal branches, although this pattern is sometimes obscured on basal branches; coenosteum white. Nematopores common on coenosteum, particularly on the lid and pseudosepta. All cyclosystems originate on the anterior side of the colony except in *C. trophostega*, which is bifacial; cyclosystems project at right angles to the branch. Cyclosystems round to elliptical in cross section, ranging from 0.7–5.0 mm in diameter. Gastropore composed of two chambers, the lower one very reduced. Every cyclosystem bears a fixed lid, usually attached at the abcauline position, which overhangs the gastropore to a variable degree. In the most extreme cases, the lid fuses to the coenosteum on the adcauline side, almost completely covering the cyclosystem and allowing the polyp to feed through only two lateral slits. Multiple lids are sometimes present. Seven to 25 dactylopores per cyclosystem; tops of pseudosepta often concave. No gastro- or dactylostyles.
Ampullae superficial and large, usually associated with the lid or encircling the cyclosystem. Efferent ducts from both male and female ampullae open into the cyclosystem.

**Discussion.**—Among the three genera of Stylasterinae that do not have gastrostyles, *Crypthelia* is easily distinguished by its prominent lids, which cover all or part of the cyclosystem. It is most similar to *Astya*, which has an homologous structure much lower in the gastropore chamber.

**Occurrence.**—Eocene: Tonga; Recent: Atlantic, Indo-West Pacific, North Pacific, Galapagos, off Panama (Pacific), Subantarctic. 183–2,789 m.

**Type Species.**—*Crypthelia pudica* Milne Edwards and Haime, 1849, by monotypy.

**Crypthelia pudica** Milne Edwards and Haime, 1849

Figure 22A–H

*Crypthelia pudica* Milne Edwards and Haime, 1849: 69; 1850: 93, pl. 3, fig. 1.—Broch, 1936: 95–99, pl. 13, fig. 39, text-fig. 31.—Boschma, 1956: F100; 1957: 36–38 (synonymy).—?Eguchi, 1965: 219, text-figs. 1–3.


**Diagnosis.**—Colonies very delicate, up to 7 cm tall; basal branches up to 2.2 mm in diameter. Coenosteal strips about 70 μm wide; platelets equally broad, about 75 per mm. Nematopores, about 40–45 μm in diameter, are restricted to the lids and pseudosepta. Cyclosystems round to slightly elliptical in cross section, 1.2–1.5 mm in diameter; 15–19 dactylopores per cyclosystem. Thin, lower chamber of gastropore spiny, separated from upper chamber by a ring palisade instead of a solid, annular constriction. Lid large, covering the entire cyclosystem; lid raised high above the gastropore as a horizontal canopy; top of lid slightly concave. Female ampullae large, superficial hemispheres up to 1.3 mm in diameter and 1.1 mm tall, occurring on the top of each lid, usually one per lid. Male ampullae much smaller hemispheres, about 0.55 mm in diameter, occurring in clusters of 3–5 on the tops of lids. Immature cyclosystems have no ampullae and their lids are very thin, as illustrated by Milne Edwards and Haime (1850). Both male and female ampullae have efferent ducts (pores) visible on the lower side of the lid, one pore corresponding to each ampulla.

Soft tissue of *C. pudica* was not available for study; however, examination of tissue from an undescribed species from the Galapagos (Figs. 26F, 28B) revealed a crescent-shaped gastrozoid without tentacles, adnate dactylozooids with a long free part, and nematocysts measuring 20 × 2.5 μm in the nematophores and 7 × 2.0–2.5 μm in the dactylozooids. Moseley (1881) and Broch (1947) also reported gastrozooids without tentacles for other species of *Crypthelia*, and the former described the soft parts of *C. affinis* in great detail.

**Discussion.**—The 15 species of *Crypthelia* (Table 1) are differentiated primarily on the basis of cyclosystem diameter, size and shape of the lid, and size and position of the ampullae. *C. pudica* is characterized by relatively small cyclosystems with large lids and very conspicuous ampullae restricted to the top of the lid.

The type-specimen of *C. pudica* could not be obtained from the MNHN and is presumed to be lost. My diagnosis and most figures for this species are based
on topotypic (sensu lato) specimens from ALBATROSS-5423 (9°38'N, 121°11'E, 929 m), described and figured by Fisher (1938). They differ from the figured type in having conspicuous ampullae in their lids; however, it is suggested that the figures of Milne Edwards and Haime (1850) are those of immature cyclosystems before ampullae had formed.

Several of the synonymy entries are prefaced with a question mark because I
have not examined them; their distributional records are therefore also queried. Studer's (1878) specimen, however, was examined and found not to be *C. pudica* but an undescribed species similar to *C. fragilis*. Marenzeller's (1904) specimens (USNM 21285) also appear to be an undescribed species.

**Distribution.**—Indian Ocean (368 m), Kermadec Island (1,097 m), Philippine Islands (549–1,633 m), ?Japan, ?Sea of Okhotsk (1,240 m).

**Types.**—Muséum National d'Histoire Naturelle, Paris (presumed lost). The types of 10 of the 15 species have been examined by the author.

*Astya* Stechow, 1921


*Astya* Stechow, 1921: 233 (nom. nov.).—Boschma, 1956: F100.

**Diagnosis.**—Colonies small, delicate, and flabellate. Branches round in cross section and very thin; distal branches usually thinner in diameter than the cyclosystems they support. Coenosteum linear-imbricate, white. All cyclosystems originate on the anterior side of the colony and project at right angles to the branch. Cyclosystems slightly exert, round to elliptical in cross section, up to 1.9 mm in greater diameter. Gastropore composed of two chambers, as in *Conopora* and *Crypthelia*; however, in *Astya* a short, blunt pillar projects into the constricted aperture that separates the chambers. Seventeen to 19 dactylopores per cyclosystem. The upper, outer edge of each pseudoseptum bears a nematopore. No gastro- or dactylostyles. Ampullae restricted to a ring encircling the base of each cyclosystem, causing the cyclosystems to appear globose.

The gastrozooid fills the crescent-shaped lower chamber and also projects upward as a cylindrical tube. Mouth cruciform, no tentacles. Dactylozooids are adnate with long free tentacles. Nematocysts of nematophores about $23 \times 6$ μm. Tissue bluish green.

**Discussion.**—Three genera (*Astya, Crypthelia, and Conopora*) are characterized by having a double-chambered gastropore, prominent nematophores, and lacking gastro- and dactylostyles. *Astya* is most similar to *Crypthelia* in that they are both unifacial, have superficial ampullae clustered around the cyclosystems, and have a protective lid or small pillar covering the gastrozooid. They differ in that *Astya* has a small pillar overhanging only the gastrozooid, whereas *Crypthelia* has a lid...
overhanging the cyclosystem. Moseley (1881) suggested that they were homologous structures but did not predict the polarity of the character states.

**Occurrence.**—Eocene: Tonga; Recent: off Meangis Islands, Philippines. 914 m.

**Type Species.**—*A. subviridis* Moseley, 1879, by monotypy.

*Astya subviridis* (Moseley, 1879)

Figures 23C, 28A

*Astya subviridis* Moseley, 1879: 457-462, pl. 34, fig. 4, pl. 35, figs. 8, 15, pl. 41, fig. 1, pl. 43, figs. 10-11, pl. 44, fig. 2; 1881: 65-71, pl. 1, fig. 4, pl. 2, figs. 8, 15, pl. 8, fig. 1, pl. 10, figs. 10-11, pl. 11, fig. 2.

*Astya subviridis*: Stechow, 1921: 253.—Boschma, 1956: F100, fig. 82, 3; 1957: 40.

**Diagnosis.**—See that of genus.

**Discussion.**—There are two species in the genus *Astya*. Even though the preservation of the Eocene-aged *A. nielseni* Wells, 1977 (Fig. 23A–B), is not good enough to see the characteristic tongue-like projection between gastropore chambers, there is little doubt that it belongs to *Astya*. On the other hand, the placement of *Astya crassa* (Nielsen, 1919) is quite uncertain. It has sympodially arranged cyclosystems and randomly placed ampullae; the preservation is not good enough to judge presence or absence of gastrostyles. It may be either a *Stylaster* (Group C) or a *Conopora*, but probably not *Astya*; it is therefore placed incertae sedis.

*A. subviridis* is apparently known from only one specimen, the figured type, deposited at the BM (1880.11.25.185), which, unfortunately, has almost completely disintegrated. Moseley’s (1879) excellent description of both hard and soft parts forms the basis of our knowledge of this species. The only character I can add to Moseley’s description is the imbricate nature of the coenosleum, barely visible on one fragment.

**Distribution.**—Off Meangis Islands, Philippines. 914 m.

**Types.**—Holotype at the BM (see Discussion). The types of all three nominal species have been examined by the author.

*Incertae Sedis*

**Congregopora** Nielsen, 1919


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Diagnosis.—Colonies flabellate, up to 6 cm tall and 8 cm broad. Branches round in cross section and blunt; basal branches up to 5 mm in diameter. Coenosteum covered by shallow pits that are equally spaced about 0.21 mm apart, perhaps the preservation of coenosteal pores of a reticulate texture. Cyclosystems triangular or elongate, the greater axis of the latter parallel to the branch. Elongate cyclosystems about 0.7 mm long and 0.3 mm wide. One of the syntypes has cyclosystems arranged in three longitudinal rows. Dactylopores difficult to detect in the cyclosystems, but according to Nielsen (1919) they are few in number and irregularly scattered around the gastropore. No gastro- or dactylostyles. Craters of ruptured ampullae up to 1.34 mm in diameter.

Discussion.—Boschma (1968a: 100) defined Congregopora as “an Allopora without gastrostyles,” and another time (Boschma, 1951) implied that its closest affinity was to Conopora, differing from this genus primarily by its lesser number of dactylopores per cyclosystem. This is a good guess, but the preservation of the very few Paleocene specimens is not adequate to intelligently discuss its phylogeny, or even to adequately define the genus.

Occurrence.—Paleocene: Denmark (Danian of Fakse).

Type Species.—C. nasiformis Nielsen, 1919, by monotypy.

*Congregopora nasiformis* Nielsen, 1919

Figure 23D–F

*Congregopora nasiformis* Nielsen, 1919: 21–22, pl. 2, figs. 24–27, text-figs. 3.10.—Boschma, 1951: 40–42, text-fig. 6a–b; 1956: F100, text-figs. 82, 4a–c; 1957: 40.

Diagnosis.—See that of genus.

Discussion.—*Congregopora* is a monotypic genus; its single species has been reported only once.

Distribution.—Known only from the Paleocene of Denmark.
Types.—Deposited at the Geologisk Museum, Copenhagen. Examined by the author.

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LITERATURE CITED


Naumov, D. V. 1960. Hydroids and hydromedusae of the USSR. Keys to the fauna of the USSR published by the Academy of Sciences of the USSR, No. 70: 660 pp., 30 pls., 463 figs. (Translated from Russian to English by Israel Program for Scientific Translations, 1969.)


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NOTE: The paper referred to as Cairns, In press, on Antarctic Stylasterina should be published before this paper, as intended; however, because it was only in galley stage when this paper was written, complete citations are not given here.