

Type locality: Given by LINNAEUS (1767) as Mediterranean and Norwegian Sea. This should be restricted to Mediterranean. As pointed out by BOSCHMA (1953a, 1953b), the indication Norwegian Sea was due to a misunderstanding arising from a correspondence LINNAEUS had with GUNNERUS: referring to LINNAEUS, GUNNERUS (1768) added to his description of *Millepora norvegica* (as the name says, a species from Norway) that he considered this as being the same as LINNAEUS' *M. aspera*. In fact, these are distinct species (see account of *Stylaster norvegicus*).

Errina aspera mascarina: This subspecies is said to come from the Indian Ocean (Mauritius) and to differ from typical Mediterranean *E. aspera aspera*; it was described by BOSCHMA (1965a) from 2 slender colonies up to 37 mm high and 33 mm wide, one designated by him holotype, the other paratype, both at MNHN. Originally these colonies were attached to a telegraph cable (substrate not mentioned by BOSCHMA).

Type locality: Given by BOSCHMA (1965a) as Mauritius (Indian Ocean), from unrecorded depth. The origin, as indicated on the label found with the specimens (" *Spinipora*, île Maurice, 1883, échange VIMONT "), is certainly misleading. The 2 types look like slender Mediterranean material and closely resemble another slender colony of *E. aspera* at the MNHN that also had grown on a telegraph cable. The latter specimen (Fig. 9 B), found unidentified in the bryozoan collection, was labeled " Toulon — sur le cable transatl. ", meaning probably that it had been detached from a telegraph cable in the Mediterranean (or Straits of Gibraltar ?) and eventually landed at Toulon. Possibly the types of *E. aspera mascarina* and the " Toulon " specimen were collected together from the same cable.

MATERIAL STUDIED

Specimens of various sizes (colonies, branches, fragments) of *E. aspera* without exact collecting data are present in many museum collections (e.g. in coral collections, or together with *Pedicularia sicula* in mollusc collections): many colonies (MZUC). — 5 colonies already mentioned by BOSCHMA (1965a), Mediterranean or without indication (MNHN); types of *E. aspera mascarina* (MNHN); colony " Toulon — sur le cable transatl. " (MNHN); branch with *P. sicula*, Palermo (MNHN). — colony (MZUS). — Messina, H. FOL, colony (MHNG). — 2 colonies (NHMW 15714). — 2 branches with *P. sicula* (IRSNB IG 10591). — colony studied by BOSCHMA (1954) (ZMA Coel 7401). — branch with *P. sicula* (BMNH 1846.12.8.1) and several colonies, either Sicily or without locality (BMNH 1842.3.29.47/49, 1843.3.6.147/148/150). — 2 colonies (UZMC). — colony (ZMUO B 879). — photo (RMNH; by BOSCHMA) of colony in Manchester Museum mentioned by HICKSON (1912 a, as sent by J. MORGAN). — colony USNM 75602 (ex BMNH 1842.3.29.47). — Messina, branches with *P. sicula* (USNM 189433, 189435). — Sicily, branches with *P. sicula* (AMNH 14084, 14085). — fragment (YPM 5368).

Straits of Messina, more recently collected samples: G. FREDJ, 1964, colony (MNHN). — " Bannock " 1972, stn 23, off Punta Pezzo, 95 m, photo received from P. COLANTONI showing colony bearing *P. sicula*. — I. DI GERONIMO, 1986, several colonies from rocky bottom + many small colonies on fouled fishing line, ca. 100 m (MNHN; USNM 75603).

Straits of Gibraltar and approaches: Geological cruise, W.N. NESTEROFF (no details), small colony (MNHN). — " *Calypso* " 1958, stn SME-1282, several colonies + branches (most MNHN; USNM 59931). — " *Al Mounir* " stn B6-D6, B8-D2, dead colonies + branches (MNHN; USNM 48889). — " *Cryos* " 1984, cruise BALGIM stn DR-40, DR-49, DR-115, DR-116, dead branches + fragments (MNHN).

Atlantic coast of Morocco: " *Al Mounir* " stn B10-D3, several colonies + branches (most MNHN; USNM 48889; BMNH 1980.1.4.1).

Cape Verde Islands: " *Talisman* " drag. 114, 4 branches (MNHN) + fragment (BMNH 1950.1.11.94).

DESCRIPTION

Colonies primarily uniplanar but sometimes bushy (Fig. 9 A-B). Examined specimens up to 20 cm high and wide. Branches cylindrical, gradually tapering to pointed tips about 0.7 mm in diameter. Coenosteum white and porous. Coenosteal texture predominantly reticulate-

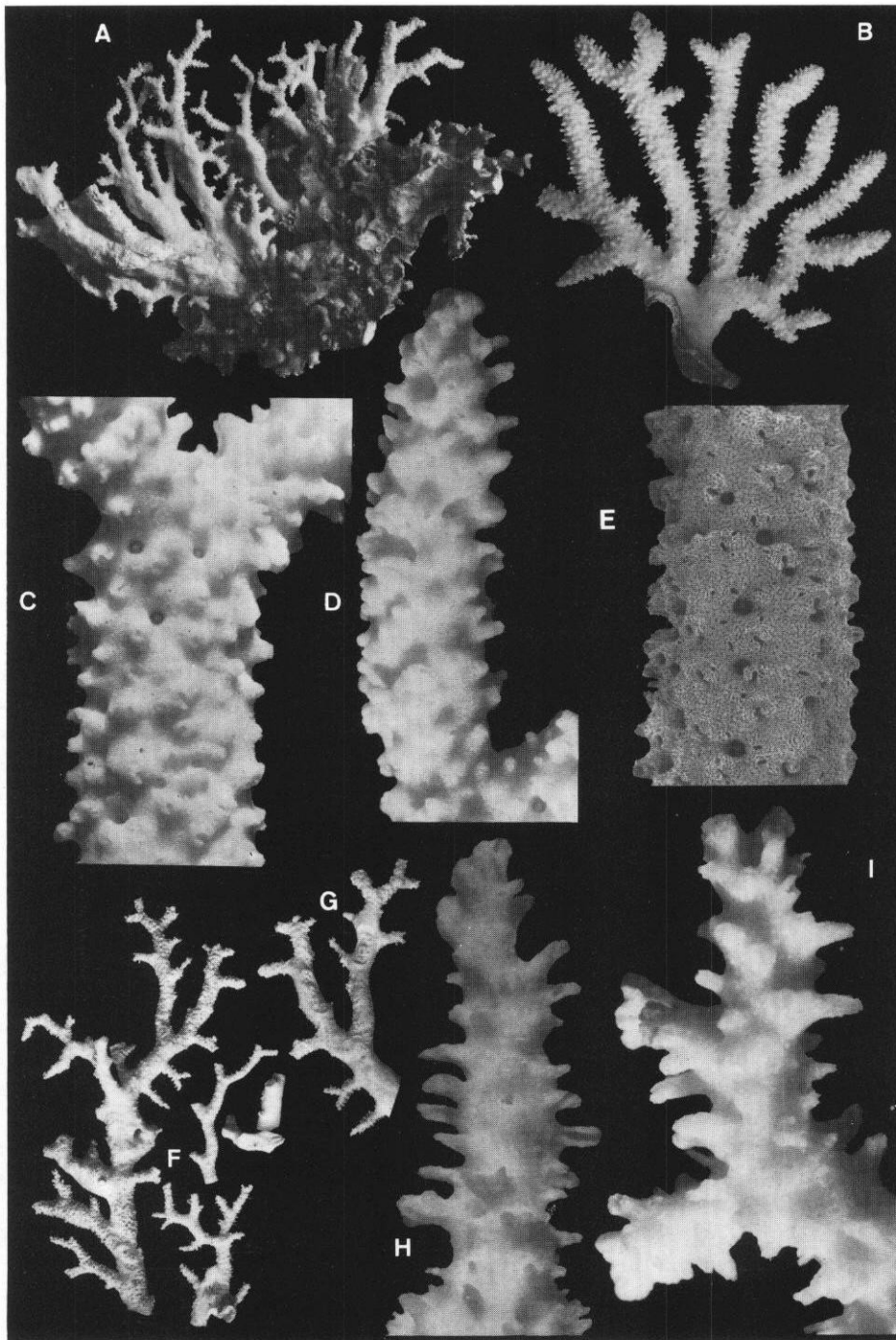


FIG. 9. — *Errina aspera* (A, from Messina, coll. H. FOL, MHNG; B, from unknown locality, "Toulon", MNHN; C-D, from "Calypso" 1958, SME-1282, MNHN; E, from "Al Mounir" B10-D3, USNM 48889; F-I, from "Talisman" drag. 114, F-H: MNHN, I: BMNH 1950.1.11.94); A, large colony ($\times 0.7$); B, small slender colony very similar to types of *E. aspera mascarina* ($\times 1.8$); C-E, details of branches showing dactylopore spines and gastropores with gastrostyles (all $\times 10$); F, four branches and fragments ($\times 1.1$); G, distal part, opposite face of larger branch under F showing two *Pedicularia* traces ($\times 1.1$); H, tip of slender branchlet from larger branch under F ($\times 12$); I, distal part of another branch ($\times 14$).

granular (Fig. 10 E), but sides of dactylopore spines and inner gastropore tube surface usually imbricate (Fig. 10 F, H), a rare combination of coenosteal textures in one species. Coenosteal strips 45-75 μm wide; granules irregular in shape.

Gastropores circular, 0.18-0.25 mm in diameter, without proximal lip. Gastropore tube cylindrical, lacking a ring palisade. Gastrostyle occupies lower half of gastropore tube. Gastrostyle lanceolate: up to 0.27 mm tall and 0.09 mm in diameter, H:W ratios ranging from 1.5-3.3. Gastrostyles bear short, vertical ridges, which are covered by large pointed spines up to 26 μm long. Individualized dactylopore spines project perpendicularly from branch surface, predominantly with groove directed proximally (Fig. 9 C-E); however, some dactylopore spines directed obliquely, particularly when 2 or 3 are clustered.

On distal branches dactylopore spines occur on all sides of branch but are rare on posterior face of larger basal branches. Dactylopore spines up to 0.65 mm tall; width, about 0.27 mm; width of dactylopore groove, 0.06-0.08 mm, or about one-quarter width of spine. Smaller slit-shaped dactylopores, unaccompanied by spines, are common, measuring 0.13-0.16 x 0.06 mm.

Female ampullae hemispherical, 0.5-0.7 mm in diameter, and often spinose as a result of short dactylopore spines. Female efferent pores about 0.11 mm in diameter, but were rarely observed. Male ampullae internal (Fig. 6 G), elliptical in shape, and about 0.4 mm in greater internal diameter. Each male ampulla communicates to surface by a narrow irregularly shaped efferent pore 30-40 μm in diameter (Fig. 10 E).

COMPARISONS

There are 17 valid Recent species of *Errina*, a genus known from the Atlantic, off South Africa, the Galápagos, and particularly from the New Zealand region, Subantarctic, and Antarctic (CAIRNS, 1983b, 1986a, 1986 b). The 5 Atlantic species are compared in Table 1. *E. aspera* is most similar to *E. atlantica* but can be distinguished by its taller dactylopore spines (which are imbricate in texture); the presence of numerous unspined dactylopores; and a tendency to be uniplanar in colony shape.

REMARKS

E. aspera is recognizable in the brief original description of *Millepora aspera* by LINNAEUS (1767), which certainly was based on material from the Mediterranean. LINNAEUS also referred to MARSILI (1725) and to GUALTERI (1742), believing that his species had already been figured by these authors. However, as pointed out by BOSCHMA (1953b), who analyzed and reproduced the pertinent passages and figures from all these older publications, MARSILI's and GUALTERI's illustrations are difficult to interpret, and bryozoans may be involved as well, at least in part.

The oldest known stylasterid from European seas, *E. aspera* has been the subject of considerable confusion. Confusion with the morphologically very different *Stylaster norvegicus* is explained above (see Types).

E. dabneyi (Pourtalès, 1871), from the Azores, had first been mentioned as *E. aspera* by VERRILL (1864) and POURTALES (1867) before it was described as a distinct species.

BOSCHMA's (1965a) subspecies *masarina* is discussed above (see Types).

E. aspera sensu BOSCHMA & LOWE (1969) from Antarctica proved to be *E. gracilis* Marenzeller, 1903, as indicated by CAIRNS (1983a: 98, 100; 1983b: 459).

E. aspera sensu BROCH (1942), said to come from the West Indies, was also misidentified. The small branch of slightly pink colour (SMNH 45) does not belong to either the Mediterranean — eastern Atlantic *E. aspera*, or to any species known from the West Indies (see CAIRNS, 1986a), but represents some other species, possibly of Antarctic or Subantarctic origin.

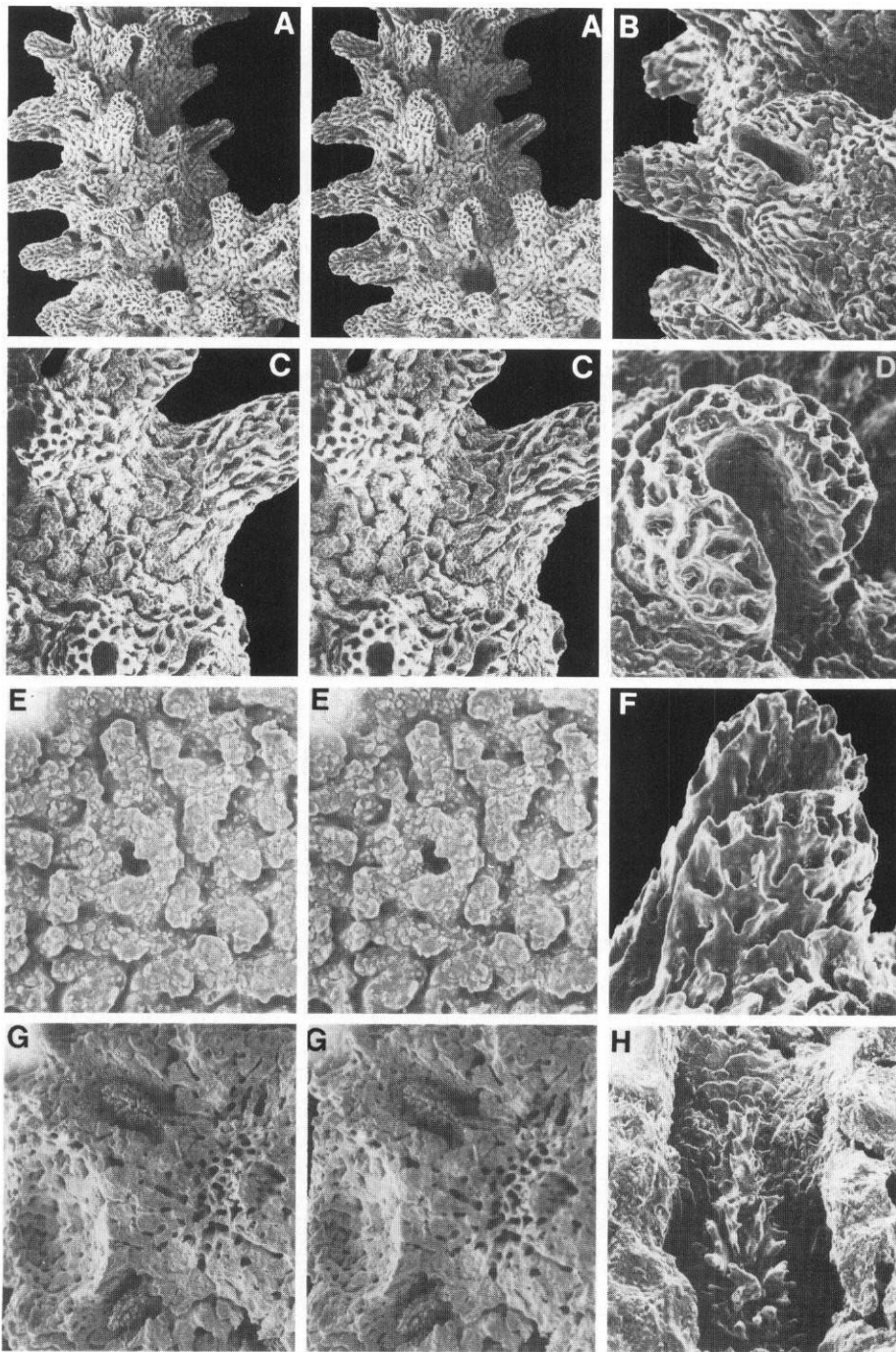


FIG. 10. — *Errina aspera* (A, C, H, from Straits of Messina, female, USNM 75603; B, D, F, from “*Calypso*” 1958, SME-1282, USNM 59931; E, G, from “*Al Mounir*” B10-D3, female, USNM 48889): A, branch segment illustrating a gastropore and numerous dactylopore spines ($\times 17$, stereo pair); B, C, D, F, aspects of dactylopore spines and coenosteal texture ($\times 45$, $\times 47$, $\times 120$, $\times 120$, respectively, C being a stereo pair); E, coenosteal texture ($\times 120$); G, transverse branch fracture revealing two gastrostyles and internal male ampullae ($\times 36$); H, gastrostyle ($\times 140$).

DISTRIBUTION AND ECOLOGY

As demonstrated above (see Types, Remarks), *E. aspera* has been reported by error from Norway, the Azores, the West Indies, Mauritius, and Antarctica.

The occurrence of typical *E. aspera* is confirmed only for the Straits of Messina, the Straits of Gibraltar with its Atlantic approaches, and a locality further south on the Atlantic coast of Morocco (33°43.5'N). A few branches from the Cape Verde Islands differ slightly from the typical Mediterranean form (see below).

In the Mediterranean the occurrence of *E. aspera* is sufficiently confirmed only for the Straits of Messina. ARADAS & BENOIT (1876) reported the associated gastropod *Pedicularia sicula* (on *Millepora aspera*) as frequently obtained there by the red coral fishermen. Abundant material of *Errina*, probably that examined by those authors, is present in the collection of the MZUC. FOL (1885), who observed the red coral fisheries aboard a boat from Messina, collected *Errina* and *Pedicularia* (MHNG). Thanks to the red coral fisheries once prosperous in and near the Straits of Messina, the fortuitously caught *E. aspera* and *Pedicularia sicula* are represented in many museum collections, generally with poor (if any) indications on the origin, such as Mediterranean, Sicily, or, at best, Messina.

Referring to observations from submersible dives, FREDJ & GIERMANN (1982) reported *E. aspera* to be very abundant on rocky bottom exposed to strong currents at depths of about 110-130 m in the straits between Ganzirri (Sicily) and Punta Pezzo (Calabria). In this part of the straits (off Punta Pezzo, 95 m) the hydrocoral with its gastropod symbiont has also been dredged by the "Bannock" in 1972 (photo communicated by P. COLANTONI; ARNAUD & ZIBROWIUS, 1979; SELLI *et al.*, 1980), and more recently by I. DI GERONIMO (material studied). The depth range of the species was extended by DI NATALE & MANGANO (1985) on the basis of sampling down to 181 m, and of a video-record from a submersible dive down to 236 m off Capo Annunciata, south of Messina (Sicily). The characteristic *E. aspera* hard bottom of the straits was again mentioned by GIACOBBE & LEONARDI (1985).

On the basis of dredgings and the previously mentioned submersible observations, DI GERONIMO & FREDJ (1988) summarized the depth distribution of *E. aspera* as being roughly 80-90 m to 200 m. They further pointed out that the stylasterid occurs together with the large barnacle *Pachylasma giganteum* (Philippi, 1836), which also abounds and coexists with *E. aspera* in the Straits of Gibraltar on deep hard bottoms. Previously DARWIN (1854) had mentioned and illustrated the co-occurrence of both species ("Sicily, deep water").

E. aspera has been recorded as a Plio-Pleistocene fossil from several localities in Sicily and Calabria (see Records of fossil stylasterids from Europe).

From various old collections and mainly old malacological literature (presence in the Mediterranean of *Pedicularia* implies that of its host *E. aspera*) the following list of hypothetical *Errina* localities has been compiled: coast of North Africa, Alger, Maltese Islands, Palermo, Lipari or Eolian Islands, Capri, Nice area, Hyères, Toulon (the latter 3 localities on the coast of France). These indications do not prove the extended range of *E. aspera*; specimens may have been obtained there by naturalists from red coral fishermen or dealers, or the origin may be confused for other reasons. It is particularly unlikely that the stylasterid (included by RISSO, 1826, in the fauna of the Nice area) occurs in the northern Mediterranean. It is more likely to be found along the coast of North Africa since it also occurs in the Straits of Gibraltar.

Like the Straits of Messina, the Straits of Gibraltar is known for its hard bottom exposed to strong currents. Although few samples of *Errina* have yet been collected in the straits and its approaches (see Material studied) — the irregular and steep bottom is difficult to dredge — we can conclude that the stylasterid must be rather common there. In fact, shells of *Pedicularia* have been found abundantly (together with rare fragments of *Errina*) in coarse sediments under the Mediterranean outflow slightly west of the sill ("Cryos" 1984, cruise BALGIM). Apparently, the coral branches, when dead and detached, remain close to where they lived, whereas the lighter shells are sorted by the current and transported further away.

In the nearby Atlantic, *E. aspera* has been obtained from Spartel Bank, in the western approaches of the Straits of Gibraltar (first mentioned by PÉRÈS, 1964, as "Hydrocoralliaire"), and from farther south on the coast of Morocco (33°43.5'N). *Pedicularia sicula* from that station had been reported independently by BELLON-HUMBERT & GOFAS (1977), who did not mention that it was an obligate symbiont of the stylasterid.

The occurrence of *E. aspera* in the Cape Verde Islands requires further confirmation. The few branches obtained there by the "Talisman" at the unusual depth of 600 m differ from typical Mediterranean *E. aspera* by their more spinous aspect, which we have interpreted as intraspecific variation (Fig. 9 F-I).

SYMBIONTS

Throughout its geographical range *E. aspera* is found with traces of *Pedicularia*. The symbiotic *P. sicula* has been obtained, either on live branches or as dead shells, from the sediment in the Straits of Messina, the Straits of Gibraltar and its western approaches (Spartel Bank), and further south on the Atlantic coast of Morocco (33°43.5'N). Only the traces of the symbiont are known from the Cape Verde Island material (Fig. 9 G).

In the Straits of Messina *P. sicula* is a common symbiont. Dead shells swept away by the currents have been obtained from the sediments at greater depths and at greater distances north and south of the sill (SELLI *et al.*, 1980): towards the Tyrrhenian Sea at 329 m off Scilla, and at 220 m towards the Ionian Sea off Villa San Giovanni.

Pedicularia is known as a fossil from the Lower Pleistocene of Sicily and Calabria (see Records of fossil stylasterids from Europe).

Errina dabneyi (Pourtalès, 1871)

Fig. 11 A-I, 12 A-F, 13 A-B

Synonymy:

- Lepidopora dabneyi* Pourtalès, 1871: 41, pl. 7, fig. 10-11.
Hornera verrucosa Calvet, 1903: 161-162, pl. 18, fig. 6a-c.
Errina amoena Boschma, 1956a: 281, text-fig. 1-3, pl. 1-2, pl. 3, fig. 1-4.

Chresonymy:

- Errina aspera* — VERRILL, 1864: 46. — POURTALÈS, 1867: 116.
Errina dabneyi — MOSELEY, 1879: 479; 1881: 84. — HICKSON, 1912a: 893; 1912b: 463-464, pl. 8, lower fig. — BOSCHMA, 1953b: 313, 314; 1954: 148; 1956a: 286-288; 1957a: 53; 1963a: 337; 1963c: 398, text-fig. 1-4, pl. 1, fig. 1-8; 1964f: 284-285; 1965a: 2; 1967: 331; 1968b: 113. — CAIRNS, 1983b: 428.
Errina dabneyae — BOSCHMA, 1953b: 313.
Errina (Errina) dabneyi — ZIBROWIUS, 1982: 981-982.
Hornera verrucosa — CALVET, 1931: 45. — BORG, 1944: 203. — BELLOC, 1960: 12.
Errina amoena — BOSCHMA, 1957a: 50; 1963a: 335.
Errina (Errina) amoena — VERVOORT & ZIBROWIUS, 1981: 26.
Errina spec. 2 — BOSCHMA, 1967: 330-331.

TYPES

Lepidopora dabneyi: In the original description, POURTALÈS (1871) mentioned several large colonies sent to the MCZ by Miss DABNEY (of the family of the American consul at Faial) that were obviously collected by local Azorean fishermen. No precise type status was given to the specimens by POURTALÈS. The type lot (here considered as syntypes) preserved at the MCZ comprises 3 large fan-shaped colonies 20-30 cm high and wide, and various smaller branches and minor fragments, at least in part broken off the larger colonies. Two fan-shaped branches from the type lot (the larger 58 mm high, 27 mm wide) were transferred to the BMNH (1891.2.4.29). Some branches and fragments from the type lot are also at RMNH (Coel 13907) (Fig. 11 A) and USNM (75608).

Type locality: Faial, Azores. Upper bathyal depths (no depth indication in POURTALÈS, 1871; but remarks on *Caryophyllia cyathus* as epifauna permit this bathymetric extrapolation).

Hornera verrucosa: CALVET (1903) mentioned 4 colonies, all from one station, and figured one (29 mm high, 22 mm wide). No precise type status was given to these specimens, here considered as syntypes. Only part of the material mentioned was found at the MOM: 8 small fragments (possibly from a single branch or colony, but apparently not from the figured one), the largest about 20 mm high (Fig. 11 E).

Type locality: Prince of Monaco stn 247, 30.8.1888, 38°24'N, 28°01'25"W, 318 m. Azores.

Errina amoena: BOSCHMA's (1956a) original description was based on a single, large, fan-shaped colony (29.5 cm high, 31.5 cm wide) of which larger parts and smaller sectors have been figured. Being the only specimen mentioned, it must be considered as the holotype, which is preserved at MNHN, together with some detached branches. Some smaller branches from the holotype at RMNH (Coel 15855) (Fig. 11 B) and USNM (75605).

Type locality: Given by BOSCHMA (1956a) as "China Sea, depth not recorded" based on old label found with type colony ("*Stylaster flabelliformis*, Mer de Chine, Mr. MONTIGNY"). In view of the otherwise confirmed distribution (*E. amoena* being a synonym of *E. dabneyi*), it is most likely that the indicated origin was wrong, as was the identification on the old label (*S. flabelliformis* being a large fan-shaped, morphologically convergent, species from the Mascarene Islands; see BOSCHMA, 1957b), and that the holotype of *E. amoena* came from the Atlantic.

MATERIAL STUDIED

Azores: Types of *Lepidopora dabneyi*, *Hornera verrucosa*, and *Errina amoena*. — Azores, SAVIGNY, 1843, 4 pieces of large fan-shaped colonies (ZMB 1066). — Origin not given but undoubtedly from local Azorean fisheries, large fan-shaped colony on piece of volcanic rock (MCM 63). — "Talisman" drag. 123, ca. 15 colonies, branches, fragments (MNHN); branch (figured by HICKSON, 1912b: pl. 8, lower fig.) + small branch (BMNH 1950.1.11.93; 1964.9.17.10). — "Jean Charcot" 1971, cruise BIAÇORES stn 49, 13 small branches + fragments (most MNHN; USNM 75606).

Mid-Atlantic Ridge: "Bartlett" 1975, stn 14, 4 branches (ZMUK).

DESCRIPTION

Colonies uniplanar, up to 30 cm high and wide; branches cylindrical and occasionally anastomose. Small diameter branches project perpendicularly from the larger diameter main branches. Distal branch tips about 0.60 mm in diameter. Coenosteum white and reticulate-granular in texture. Strips 55-100 μ m wide, covered by rounded granules about 8 μ m in diameter. Coenosteal papillae 63-100 μ m in diameter and up to 0.15 mm tall sometimes occur on and adjacent to male ampullae (Fig. 11 G, 12 E). Papillae are assumed to contain additional nematocysts or a different type of nematocyst and therefore to serve a defensive function.

Gastropores circular, 0.15-0.20 mm in diameter, and bordered by a broad proximal lip. Gastropore tube cylindrical, lacking a ring palisade; gastrostyle occupies lower half of chamber. Gastrostyle lanceolate: illustrated style (Fig. 13 B) 0.31 mm high

and 0.091 mm wide (H:W = 3.4). Gastrostyle strongly ridged, the ridges bearing pointed spines up to 27 μ m long. Dactylopore spines individualized, almost exclusively with groove directed proximally, and occurring uniformly on all sides of distal branches but infrequently on larger diameter branches. Dactylopore spines also very common on undersides of gastropore lips (Fig. 12 C). Dactylopore spines short, projecting perpendicularly from branch surface up to 0.13-0.15 mm. Width of spine about 0.15 mm; width of groove 44-50 μ m, or about one-third spine width. There are no unspined dactylopores.

Female ampullae (Fig. 12 F) hemispherical, 0.6-0.7 mm in diameter, with an efferent pore diameter of about 0.17 mm. Male ampullae (Fig. 12 E) smaller, slightly irregular protuberances, 0.4-0.5 mm in diameter, each with 1-3 small apical efferent pores.

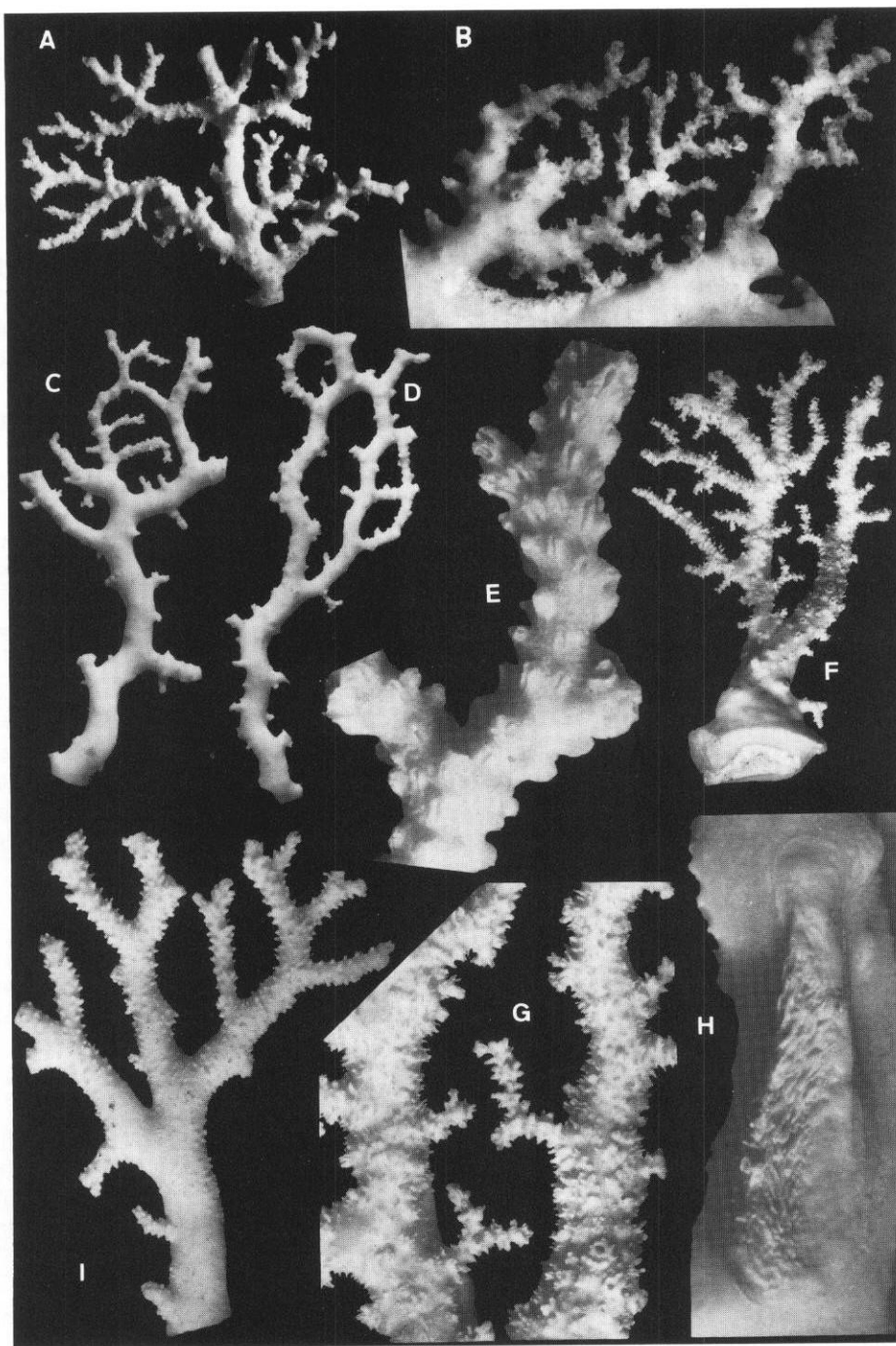


FIG. 11. — *Errina dabneyi* (A, syntype of *Lepidopora dabneyi*, RMNH Coel 13907; B, holotype of *Errina amoena*, RMNH Coel 15855; C-D, from "Jean Charcot" 1971, stn 49, MNHN; E, syntype of *Hornera verrucosa*, MOM; F-G, from "Talisman" drag. 123, MNHN; H, from "Talisman" drag. 123, BMNH 1950.1.11.93; I, from "Bartlett" 1975, stn 14, ZMUK): A, colony fragment ($\times 2.0$); B, colony fragment ($\times 3.0$); C-D, branches with anastomoses (both $\times 1.9$); E, distal part of slender branchlet ($\times 15$); F, colony having overgrown colony of *Pliobothrus* ($\times 1.5$); G, detail of F showing abundance of coenosteal papillae ($\times 4.0$); H, *Pedicularia* trace ($\times 13$); I, branch with abundant coenosteal papillae ($\times 3.0$).

COMPARISONS

Among the Atlantic *Errina*, *E. dabneyi* is clearly most similar to the western Atlantic *E. cochleata* Pourtalès, 1867 (Table 1) but can be distinguished by its ridged gastrostyles, reticulate-granular coenosteal texture, and occurrence of numerous dactylopore spines on the underside of each gastropore lip.

REMARKS

Previous to its description as a distinct species, the type series of *E. dabneyi* had been referred to *E. aspera* (Linnaeus, 1767) by VERRILL (1864) and POURTALÈS (1867).

POURTALÈS' (1871) original description of *E. dabneyi* (as *Lepidopora*) is very brief. A more detailed description, based on the types, was given by BOSCHMA (1963c), who also mentioned this species in several other papers.

E. amoena Boschma, 1956, based on an old museum specimen said to come from the China Sea, proved to be identical with *E. dabneyi* (BOSCHMA, 1963c, 1964f, 1968b). As for the unlikely disjunct distribution, we presume that the type of *E. amoena* was in fact of Atlantic origin and had been mislabeled.

Yet another synonym of *E. dabneyi* is *Hornera verrucosa* Calvet, 1903, described as a bryozoan from the Azores. Only much later CALVET (1931: 45-46) became aware that his *H. verrucosa* was a stylasterid hydrocoral. This rectification has been reiterated in the bryozoan literature by BORG (1944: 203) and COOK (1968: 238). The "transphylectic" synonymy of CALVET's (1903) bryozoan with POURTALÈS' (1871) stylasterid was noted by ZIBROWIUS (1982).

HICKSON (1912b) tentatively referred specimens from the Azores ("Talisman") to *E. dabneyi*, a species which at that time had not yet been illustrated, and of which he had not seen the types. Having seen these, BOSCHMA (1963c, 1967) concluded that HICKSON's identification of the "Talisman" material was incorrect, and that the form in question (*Errina* sp. 2 in BOSCHMA, 1967) was more similar to *E. aspera* (Linnaeus, 1767). We have reexamined the 2 branches seen by BOSCHMA, as well as additional material from the same station; we cannot follow his interpretation and refer the whole lot to *E. dabneyi*.

DISTRIBUTION AND ECOLOGY

E. dabneyi is known from the Azores (recorded depths of 3 stations ranging from 215-225 m to 500 m) and from the Mid-Atlantic Ridge southwest of the Azores (recorded depths of one station 140-2200 m).

For other samples the depth had not been recorded. According to POURTALÈS (1871), *Caryophyllia cyathus* (Ellis & Solander, 1786) was growing on the thicker branches (type lot of *Lepidopora dabneyi*) received from Faial. In the Azores this scleractinian is common in depths of a few hundred meters (ZIBROWIUS, 1980). JOURDAN (1895: 10) also mentioned a specimen of *C. cyathus*, and DAUTZENBERG (1889: 39) specimens of *Pedicularia* taken from the same coral substrate (unidentified "polypier") from off Faial, 400-500 m), and offered to the Prince of Monaco by W.S. DABNEY in 1887. The coral substrate in question (no longer preserved either with *C. cyathus* or *Pedicularia* at the MOM) might well have been another colony of *E. dabneyi*.

To summarize, in the Azores *E. dabneyi* appears to be a species mainly of upper bathyal depths.

SYMBIONTS

The characteristic traces of *Pedicularia* (Fig. 11 H) have been found on branches of most lots of *E. dabneyi* from the Azores (or presumably from the archipelago), including the types of *Lepidopora dabneyi*, *Hornera verrucosa*, and *Errina amoena*, and branches from "Talisman" drag. 123 and "Jean Charcot" 1971, cruise BIAÇORES stn 49. When examined in 1979, a large colony at the MCM (no. 63) still had several small *Pedicularia* attached.

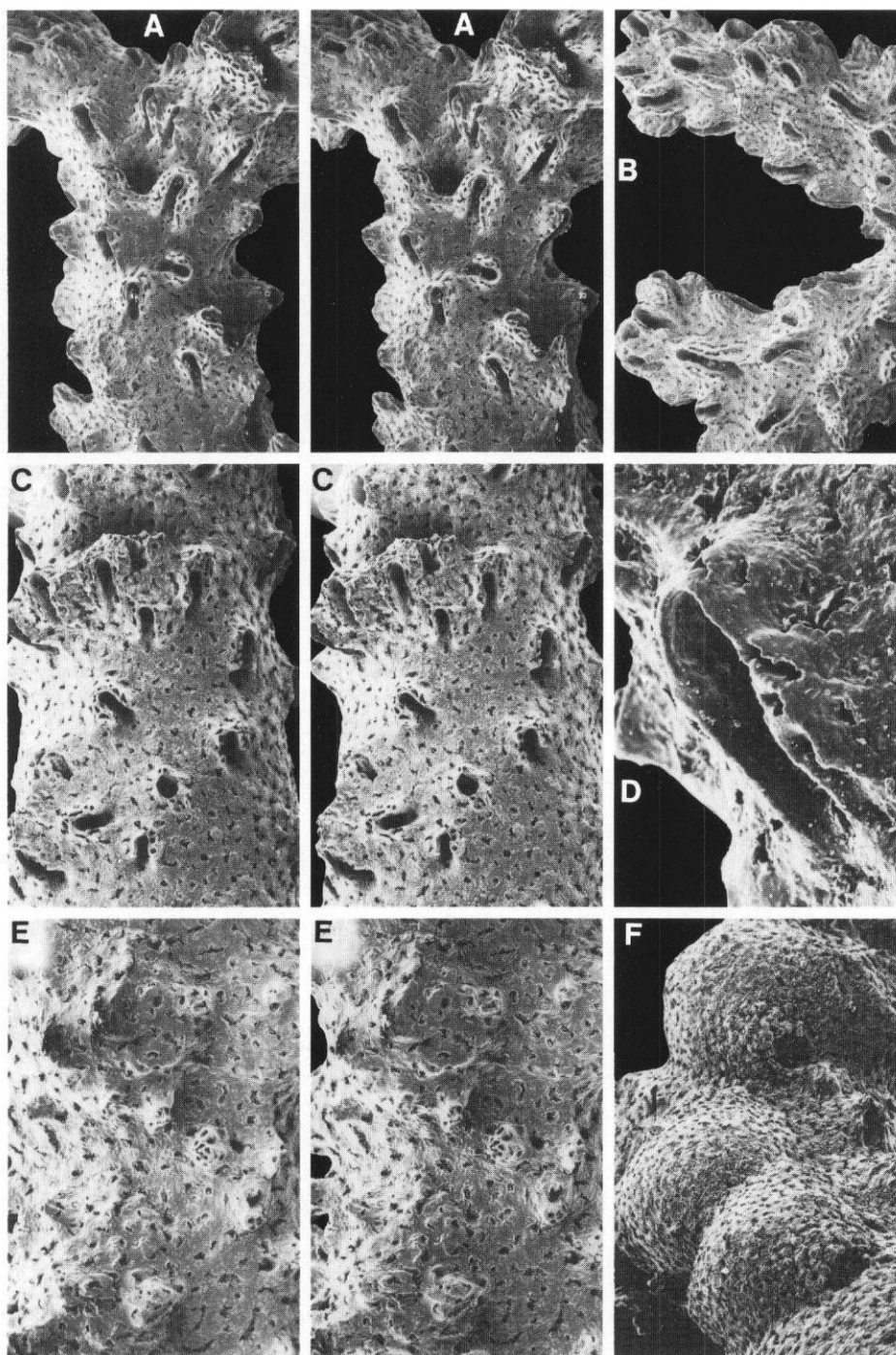


FIG. 12. — *Errina dabneyi* (A-B, holotype fragment of *Errina amoena*, USNM 75605; C, from "Jean Charcot" 1971, stn 49, female, USNM 75606; D, F, syntype of *Lepidopora dabneyi*, female, USNM 75608; E, from "Talisman" drag. 123, male): A, branch face illustrating gastro- and dactylopores ($\times 27$, stereo pair); B, branch tips ($\times 26$); C, branch face showing dactylopore spines and underside of proximal gastropore lip ($\times 38$, stereo pair); D, dactylopore spines ($\times 158$); E, male ampulla ($\times 38$, stereo pair); F, female ampullae ($\times 32$).

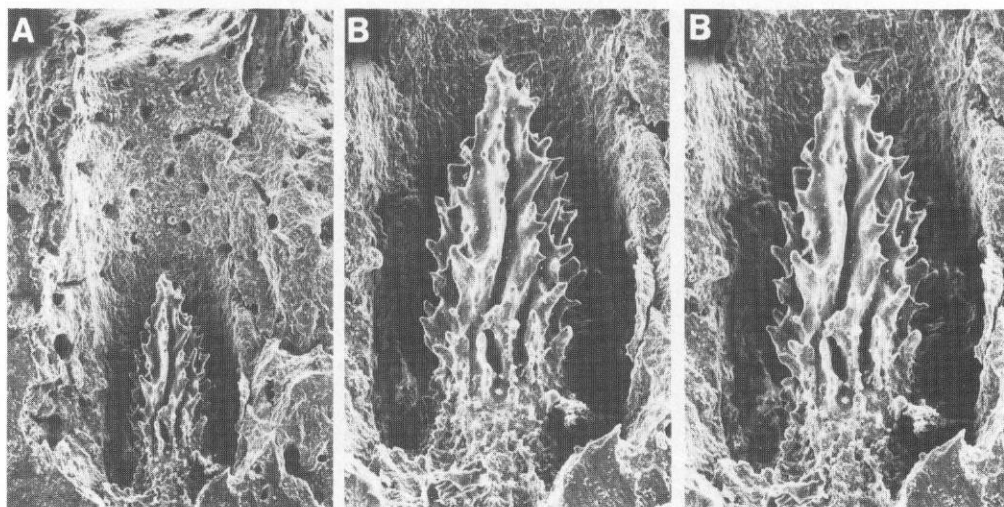


FIG. 13. — *Errina dabneyi* (A-B, from “*Jean Charcot*” 1971, stn 49, female, USNM 75606): A, gastrostyle and gastropore tube ($\times 91$); B, gastrostyle ($\times 175$, stereo pair).

Errina atlantica Hickson, 1912

Fig. 14 A-F, G-I ?, 15 A-G

Synonymy:

Errina atlantica Hickson, 1912b: 464-465.

Chresonymy:

Errina atlantica — BOSCHMA, 1957a: 52; 1967: 331-333, text-fig. 3a-b, pl. 1, fig. 7-10; 1968c: 206. — CAIRNS, 1983b: 428.

Errina (Lepidopora) atlantica — BOSCHMA, 1963a: 338-339; 1963b: 395; 1964a: 60-61.

TYPES

Errina atlantica: In the original description (HICKSON, 1912b), which was based on several branches from the Azores (“*Talisman*”), no specimens had been figured or otherwise individually characterised by size, or given a precise type status. Material identified by HICKSON as *E. atlantica* is present at the MNHN (various branches and fragments, including those figured by BOSCHMA, 1967: pl. 1, fig. 7-8), at the BMNH (1950.1.11.87, 1950.1.11.99, small branch and tiny fragment), and at the USNM (75609, fragment from BMNH 1950.1.11.87). When rediscovered in 1977, the largest pieces at the MNHN were branches 90 mm and 60 mm high, but have subsequently been accidentally broken into smaller pieces. The various old labels with these samples indicating dredge number, date, depth, and locality, are confusing and at variance with the official station list of the expedition. The greater part of the material certainly comes from “*Talisman*” drag. 128 (syntypes; Fig. 14 E), the remaining part possibly from drag. 127.

Type locality: Herewith designated as “*Talisman*” drag. 128, 16.8.1883, 38°07'N, 27°11'45"W, 983 m. Azores.

MATERIAL STUDIED

Azores: Origin not given but undoubtedly from the local Azorean fisheries, large colony (MCM 62). — “*Talisman*” drag. 127 (?), branch originally 90 mm high, now broken (MNHN); drag. 128, syntypes of *Errina atlantica* (see above). — “*Jean Charcot*” 1971, cruise BIAÇORES stn 197, several

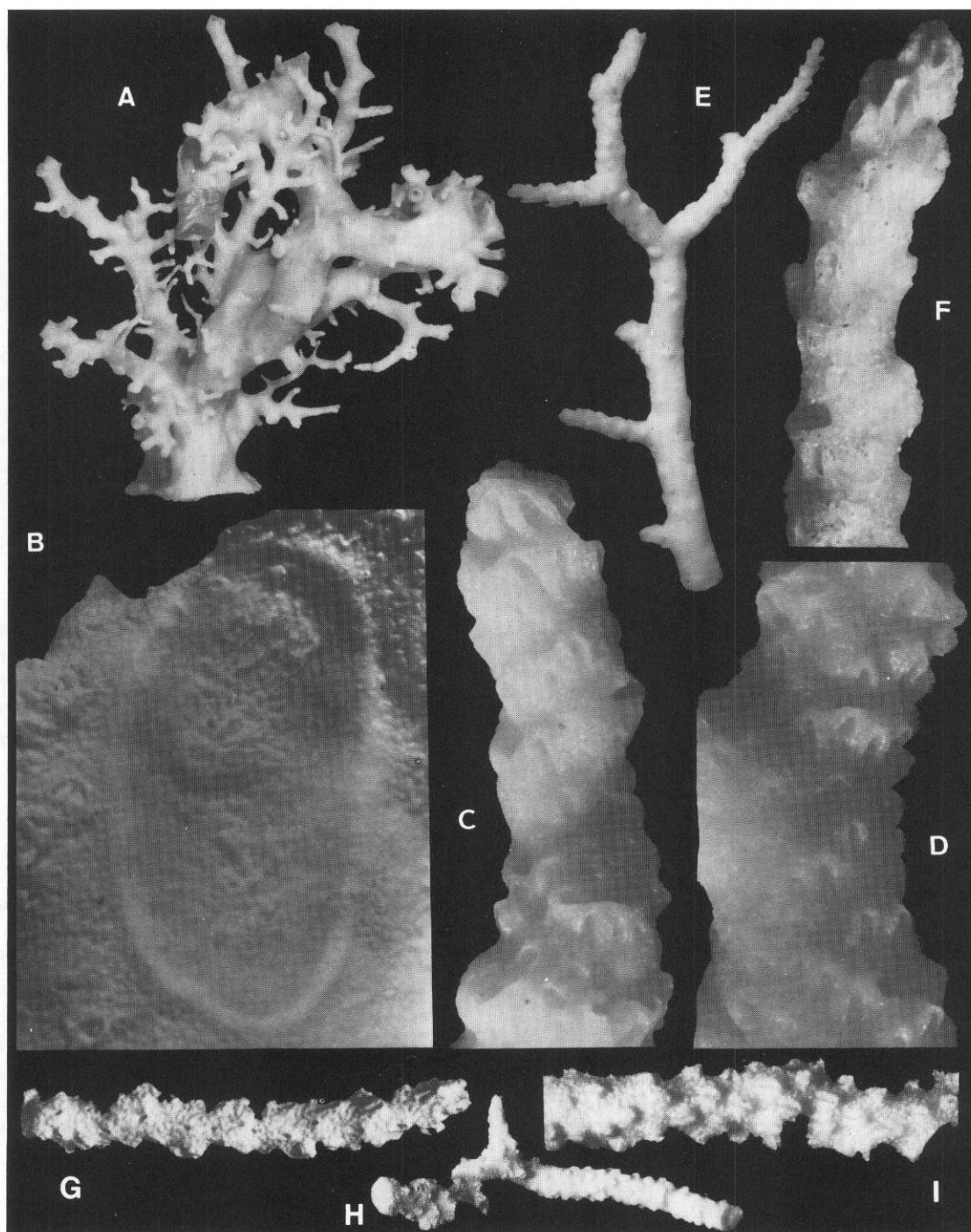


FIG. 14. — *Errina atlantica* (A-D, from “Jean Charcot” 1971, stat 240, MNHN; E-F, syntypes of *E. atlantica*, “Talisman” drag. 128, MNHN): A, bushy colony with incorporated tube of *Eunice norvegica* ($\times 0.8$); B, *Pedicularia* trace ($\times 14$); C-D, branch tip and branch segment illustrating gastro- and dactylopore arrangement (both $\times 18$); E, branch with bulging ampullae ($\times 2.8$); F, branch tip illustrating gastro- and dactylopore arrangement ($\times 8.6$).
Errina atlantica ? (G, from “Noroit” DE-13, MNHN; H-I, from “Noroit” DW-21, MNHN): G, eroded branch ($\times 9.3$); H, small incomplete colony ($\times 4.6$); I, branch ($\times 11$).

large pieces and many branches from at least one big colony (MNHN); stn 212, branch, dead (MNHN); stn 230, central piece of a colony, dead (MNHN); stn 240, several large pieces and many branches of several colonies (most MNHN; USNM 75610).

Gorringe Seamount: Material provisionally included here, identification uncertain (see Comparisons). "Noroit" 1987, cruise SEAMOUNT 1, stn DE-13, 11 fragments, dead (MNHN); stn DW-21, 5 fragments, including 1 live specimen (MNHN).

DESCRIPTION

Colonies bushy and sparsely branched (Fig. 14 A); largest pieces of colonies examined up to 12 cm high and wide, complete colonies apparently considerably larger. Branches cylindrical, gradually tapering to rather thick distal branches 0.8-1.0 mm in diameter. Coenosteum white, reticulate-granular in texture (Fig. 15 C-E). Strips 65-95 μ m wide; granules 10-14 μ m in diameter.

Gastropores circular, 0.22-0.30 mm in diameter, without a proximal lip. Gastropores occur predominantly on anterior face and lateral branch edges but not always in linear sequence as suggested by BOSCHMA (1967). Gastropore tube lacking ring palisade (Fig. 15 G). A slender, sharply pointed gastrostyle occupies lower 50-60 % of gastropore tube. Illustrated style (Fig. 15 G) 0.31 mm tall and 0.093 mm wide (exclusive of projecting spines) for a H:W ratio of 3.3. Two gastrostyles measured by BOSCHMA (1967: 332) had lower ratios of 2.3-2.6. Gastrostyle vertically

ridged and spinose, as in the two previously described species. Dactylopore spines individualized, almost exclusively with groove directed proximally, and occurring primarily on the anterior face and lateral branch edges of distal branches and much less frequently on larger diameter branches. Dactylopore spines quite short, only about 0.14-0.16 mm tall on distal branches and virtually flush with coenosteal surface on larger diameter branches. Width of dactylopore spines 0.25-0.27 mm; width of groove 0.09-0.12 mm, or almost one half width of spine.

Female ampullae hemispherical (Fig. 15 B, F), about 0.70 mm in diameter with a lateral efferent pore about 0.20 mm in diameter. Male ampullae superficial on branch tips, becoming internal on larger diameter branches; mature ampullae about 0.5 mm in diameter, each with 1-3 apical efferent pores 50-60 μ m in diameter.

COMPARISONS

As previously discussed, *E. atlantica* is most similar to *E. aspera* (see Table 1 and *E. aspera*, Comparisons).

Tiny pieces (18 mm maximum length and 1.4 mm maximum diameter) of *Errina* from Gorringe Seamount ("Noroit" 1987, cruise SEAMOUNT 1 stn DE-13, DE-21) are provisionally considered as a delicate form (young stages only ?) of *E. atlantica*. Available material consists of basal parts, unbranched colonies, branched fragments, and elongate straight terminal fragments (Fig. 14 G-I). Compared with Azorean material, the Gorringe specimens have slightly smaller dactylopore dimensions and gastropore diameter, and show no coenosteal luster (presumed to be eroded away). But some typical Azorean *E. atlantica* also have elongate, slender, nonbifurcating branches very similar to the Gorringe specimens.

REMARKS

The original description of *E. atlantica* by HICKSON (1912b) was brief and not illustrated. This description was reproduced by BOSCHMA (1967), who also reexamined part of HICKSON's material and described some additional characters. Having seen original material, BOSCHMA (1967, 1968c) concluded that *E. atlantica* was a typical representative of *Errina* sensu stricto. In previous papers he had referred it, on the basis of HICKSON's description, to *Lepidopora*, then a subgenus of *Errina* but later elevated to generic rank by CAIRNS (1983b).

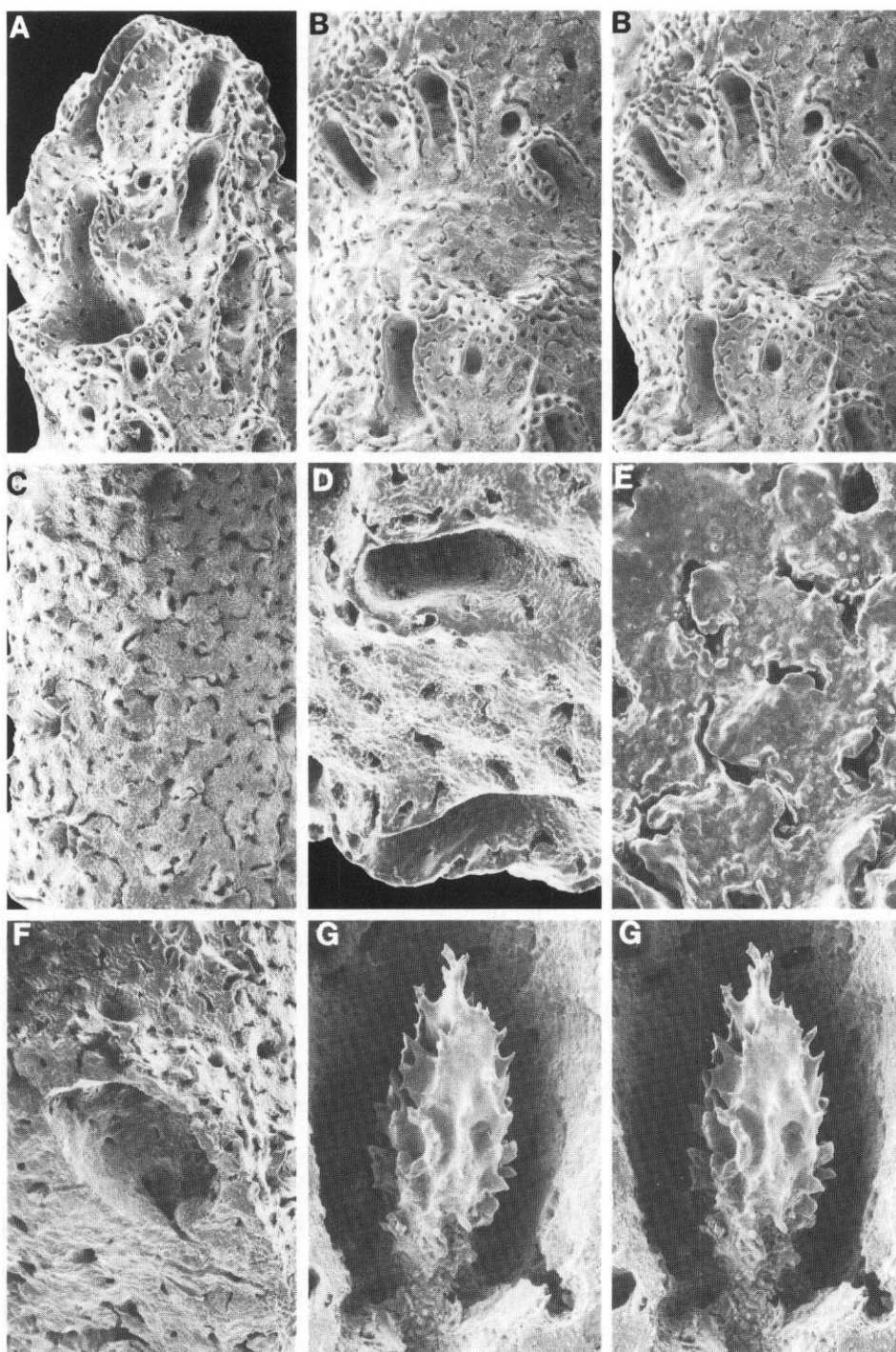


FIG. 15. — *Errina atlantica* (A-G, from "Jean Charcot" 1971, stn 240, female, USNM 75610): A, branch tip with gastropore and several dactylopore spines ($\times 37$); B, female ampullae surrounded by four or five dactylopore spines ($\times 37$, stereo pair); C, E, reticulate-granular branch coenosteum ($\times 35$, $\times 165$, respectively); D, two dactylopore spines ($\times 79$); F, tranverse section of female ampulla ($\times 51$); G, gastrostyle ($\times 158$, stereo pair).

DISTRIBUTION AND ECOLOGY

E. atlantica is known from a few stations in the Azores. The depths of the 4 stations of "Jean Charcot" 1971, cruise BIAÇORES range between 610 m and 825 m; the depths of the type-locality is 983 m, if correctly recorded. Additional live material obtained by the "Talisman" possibly comes from a deeper station (1237 m).

Errina from two stations on Gorringe Seamount, off Portugal (460-480 m, 1110-1180 m), could be the same species.

SYMBIONTS

Larger colonies of *E. atlantica* from the Azores had *Eunice norvegica* (Linnaeus, 1767) as a symbiont ("Jean Charcot" 1971, cruise BIAÇORES stn 197, 230, 240; colony MCM 62). Covered by the coenosteum, the polychaete tube typically extends as an irregular hollow trunk through the greater part of the colony (Fig. 14 A).

Traces of *Pedicularia* (Fig. 14 B) have been found on branches of *E. atlantica* from the Azores, from several stations (colony MCM 62; "Talisman" drag. 128; "Jean Charcot" 1971, cruise BIAÇORES stn 197, 240). Rather large specimens of *Pedicularia* collected at stn 197 and 240 are likely to have been symbionts of *E. atlantica*, on which traces are correspondingly large; at stn 240 one large *Pedicularia* was found still on the coral in the collection.

Genus *STYLASTER* Gray, 1831

Diagnosis. — Gastro- and dactylopores arranged in cyclosystems. Cyclosystems variable in location, ranging from a uniform coverage of all branch surfaces (Group A) to a strictly sympodial arrangement (Group C), with many intermediate arrangements (Group B). Coenosteal colour and texture variable: most common textures reticulate-granular and linear-imbricate. Gastro- and dactylostyles present, the latter robust in Group A and moderate to rudimentary in Groups B and C. Gastrostyles usually ridged and bear long, pointed spines. Ring palisade often present; gastropore inner shelf sometimes present in Group C. Ampullae usually superficial, usually with distinct efferent pores.

Type species: *Madrepora rosea* (Pallas, 1766), from the western Atlantic (a member of Group B).

The 3 groups suggested by CAIRNS (1983b) are terms of convenience, not meant to imply taxonomic categories. CAIRNS (1983b) included *Allopora* Ehrenberg, 1834 (corresponding essentially to his Group A), as a synonym of *Stylaster*.

In the eastern Atlantic, *Stylaster* is represented by 3 species of Group A (*S. norvegicus*, *S. rosaceus*, and *S. blatteus*) and 3 species of Group B (*S. gemmascens*, *S. ibericus*, and *S. erubescens*, the latter with subspecies *groenlandicus* n. ssp., *britannicus* n. ssp., and *meteorensis* n. ssp.). *S. maroccanus* n. sp. is not assigned to a group because so little material was available.

Stylaster norvegicus (Gunnerus, 1768)

Fig. 16 A-G, 17 A-I

Synonymy:

Millepora norvegica Gunnerus, 1768: 64-67, pl. 2, fig. 20-22.

Stylaster (Allopora) norvegicus forma *atlantica* Broch, 1936: 49-52, text-fig. 14, pl. 7, fig. 20-21.

[?] *Allopora oculina* Ehrenberg, 1834: 147.

Chresonymy:

Allopora norvegica — SARS, 1873: 115-118. — STORM, 1882: 26. — HICKSON, 1890: 594. — NORMAN, 1893: 349. — BOSCHMA, 1956b: F100, fig. 80.5; 1957a: 24-26; 1962: 196-203, text-fig. 1d-e, 3a-i, pl. 2, fig. 1-4; 1964e: 109, 115.

Stylaster norvegicus — BROCH, 1914a: 15-19, text-fig. D, pl. 2, fig. 12-15, 18, pl. 3, fig. 23, 27, 31, pl. 4, fig. 35, 37-38, pl. 5, fig. 44-45. — NORDGAARD, 1915: 5. — CAIRNS, 1983b: 429; 1986a: 57.

Stylaster (Allopora) norvegicus — BROCH, 1928: 55, fig. 46c. — DONS, 1939: 197.

Allopora oculina — [?] MILNE EDWARDS & HAIME, 1850: 99, pl. 4, fig. 4; [?] 1857: 132. — DUNCAN, 1870: 290, 295 (part). — MOSELEY, 1879: 480; 1881: 85 (part: Norway).

Stylaster gemmascens — DUNCAN, 1873: 332 (part), pl. 49, fig. 1.

NOT *Stylaster (Allopora) norvegicus* — HICKSON, 1915: 544-545, pl. 1, fig. 3 (British Columbia). — BROCH, 1935: 59, fig. 2 (Okhotsk Sea).

NOT *Stylaster (Allopora) norvegicus forma pacifica* Broch, 1936: 52-54, text-fig. 15, pl. 6, fig. 18-19 (Okhotsk Sea, British Columbia)

NOT *Allopora norvegica pacifica* — FISHER, 1938: 522-524, pl. 53, fig. 2-2b, pl. 54, fig. 1, pl. 76, fig. 3-4 (Okhotsk Sea). — EGUCHI, 1941: 1181-1182 (Japan). — BOSCHMA, 1953a: 166, 170-171; 1957a: 26. — NAUMOV, 1960: 533, fig. 417, pl. 25, fig. 3 (Kurile Islands).

TYPES

Millepora norvegica: GUNNERUS' (1768) description was based on specimens from Norway. According to BROCH (1914a: 18), syntypes (number of specimens not given) are present at the vsm. One of these is figured by BROCH (1914a: pl. 2, fig. 12).

Type locality: GUNNERUS' specimens came from Nordmør, west coast of Norway.

Allopora oculina: EHRENBURG's (1834) description was based on a colony (herein considered to be the holotype) of unknown origin at the zmb. This has been redescribed in more detail and figured by MILNE EDWARDS & HAIME (1850). The type could not be found in 1984, and may be lost.

Type locality: Unknown (probably Norway, see Remarks).

Stylaster (Allopora) norvegicus forma atlantica: the original rank of BROCH's (1936) forma *atlantica* (opposed to forma *pacifica*) was clearly meant to be that of a geographical subspecies. However, the North Atlantic subspecies being the nominotypical one, its name must be *S. norvegicus norvegicus*; accordingly, BROCH's naming of forma *atlantica* was an unnecessary taxonomic action.

MATERIAL STUDIED

Denmark Strait: "Ingolf" stn 52, colony (ZMUK). — "Poseidon" stn 12/1, ca. 450 branches + fragments, only one alive (SMF 6470; USNM 88824); stn 14/1, ca. 120 branches + fragments, dead (SMF 6473; USNM 88827).

Iceland or Faroes?: MÜLLER, 28.11.1900, colony (ZMUK).

Faroes: "Dana" stn 6009, small colony (ZMUK). — "Anton Dohrn" 18.11.1973, colony (IMFB). — "Anton Dohrn" 19.11.1973, branch (IMFB).

Between Faroes and Hebrides: "Porcupine" stn 54, 4 branches (BMNH 1880.11.13.4-5/8-9). — "Triton" stn 3, several big colonies + fragments (BMNH 1891.5.7.1, 1889.12.14.1, 1980.1.6.1).

Hebrides: off Butt of Lewis, June 1913, 2 colonies + fragments (RSM 1913.113.2).

Rockall: ca. 165 m, J. CORDEAUX (BMNH 1896.8.3.3-5; USNM 75620).

Norway: abundant samples in ZMUO and vsm, from many localities along the Norwegian coast, Senja, Steinavaer, Lofoten, Røst, Sklinna, Trondheimsfjord (including Agdenes, Brettingnes), Fjellvaerøy, Leksa, Kvalholmen/Hemna, Skredenes/ Sunndalsfjord, Bud, Aukra, Giske/Sunnmøre, Ålesund, Storegga (= Havbroen), Hardangerfjord, etc. — Normans Näsä, NW Storegga, 128-183 m, von YHLEN, colony (SMNH 28). — Storegga (= Havbroen), SARS, small colony (RSM 1884.37.158). — Rodberg, Trondheimsfjord, M. NORMAN, 1893, 1 fragment (BMNH 1922.2.2.6a). — Norwegian Sea, 2 colonies (RMNH Coel 15387). — "? N Atlantic", FRANK, 1897, 4 colonies + fragments (RMNH Coel 15388). — Agdenes, Trondheimsfjord, 60-80m, C. DONS, 23.6.1935, branches (RMNH Coel 15381). —

TABLE 2. — Comparisons of eastern Atlantic

	<i>S. norvegicus</i>	<i>S. rosaceus</i>	<i>S. blatteus</i>	<i>S. maroccanus</i>
cyclosystem orientation (group)	random (group A)	random (group A)	random (group A)	sympodial and anterior face (group ambiguous)
dactylostyle	robust	rudimentary	rudimentary	rudimentary
coenosteal texture; colour	reticulate-granular but smooth; white to off white	reticulate-irregular granular; pink	reticulate-granular (granules irregular); purple	reticulate-granular; white
dactylopores per cyclosystem: range, mean, mode (N)	3-10, 6.33, 6 (500) 5-11, 6.92 7 (738)	5-12, 8.57, 9 (70)	6-12, 8.88, 9 (500)	9-14, 11.77, 11 (27)
cyclosystem shape and size	circular; 0.9-1.1 mm	circular to slightly elliptical; 0.6-0.7 mm	circular to slightly elliptical; 0.8-0.9 mm	circular to elliptical; 1.0-1.4 mm
gastrostyle shape; ridges; H:W ratio	globular to conical; not ridged; 0.9-2.6	elongate-conical; ridged; 3.5	lanceolate; deeply ridged; 2.0-3.9	elongate cylindrical; not ridged; 5.5
ring palisade	absent	well-developed, elements cylindrical	well-developed, elements vertical carinae	well-developed, elements vertical carinae
ampullae: female, male	♀ unknown ♂ internal (0.5-0.6 mm)	♀ superficial (0.7 mm) ♂ unknown	♀ superficial (0.5-0.65 mm) ♂ superficial with apical efferent pores (0.3-0.45 mm)	♀ superficial (0.45 mm × 0.65 mm) ♂ unknown
distribution	Denmark Strait to Rockall and northern Norway, 75-1400 m	Gulf of Guinea: São Tomé, 37 m	Gulf of Guinea: São Tomé and Príncipe, 0-10 m	off Morocco (Atlantic), 1378 m
other diagnostic characters	branch tips robust	isolated dactylopores present; deep slits between coenosteal strips	isolated dactylopores very common; deep slits between coenosteal strips	colonies small and bushy; early sexual maturity

Stylaster and *S. erubescens erubescens*

<i>S. gemmascens</i>	<i>S. ibericus</i>	<i>S. erubescens erubescens</i>	<i>S. erubescens groenlandicus</i>	<i>S. erubescens britannicus</i>	<i>S. erubescens meteorensis</i>
primarily on lateral branch edges but some on anterior and posterior branch faces (group B)	primarily on lateral branch edges but some on anterior and posterior branch faces (group B)	primarily on lateral branch edges but some on anterior and posterior branch faces (group B)	primarily on lateral branch edges but some on anterior and posterior branch faces (group B)	primarily on lateral branch edges but some on anterior and posterior branch faces (group B)	primarily on lateral branch edges but some on anterior and posterior branch faces (group B)
rudimentary	robust	robust	robust	robust	robust
reticulate-granular (rough); white to light yellow	reticulate granular but smooth; glistening white	reticulate-granular (granules irregular in shape); white	reticulate-granular (granules rounded); white	coarse granules (40-60 µm wide); white	reticulate-smooth (strips with numerous symmetrical lateral protuberances), unique; white
7-17, 11.76, 12 (71)	4-11, 7.71, 8 (685)	7-15, 11.45, 11 (350)	5-14, 10.04, 10 (175)	7-12, 9.34, 9 (270)	9-15, 11.98, 11 (206)
circular to quite regular; e.g. 1.3 mm, 1.6 mm × 0.7 mm	circular to slightly elliptical; 0.8-1.1 mm	circular to irregular; 1.3-1.7 mm	circular to slightly elliptical; 1.2-1.4 mm	circular to elliptical; 0.9-1.4 mm	circular to irregular; 0.9-1.2 mm
lanceolate; not ridged; 1.9-4.7	lanceolate, broadest at mid-height; not ridged; 1.3-1.9	squat; not ridged; 0.8-1.4	lanceolate; not ridged but lateral tiers of spines; about 2	lanceolate; broadest at mid-height; not ridged; 1.7-2.0	ovate; unridged, very long spines; 1.1-1.3
diffuse, elements rounded	absent	absent	absent	absent	absent
♀ superficial (0.7-0.8 mm)	♀ very low in relief (0.75-1.0 mm)	♀ superficial, often with efferent tube (1.0 mm)	♀ superficial, large, sometimes with efferent tube, occasionally binary (1.0-1.3 mm)	♀ superficial (1.1 mm)	♀ superficial, often with efferent tube (0.8 mm)
♂ superficial, carinate (0.65-0.75 mm)	♂ internal (0.5 mm)	♂ superficial, with apical efferent pores (0.6 mm)	♂ superficial lateral efferent pore (0.7-0.8 mm)	♂ low, irregular mounds, apical efferent pore (0.6-0.7 mm)	♂ superficial, apical efferent pores (0.6-0.7 mm)
Denmark Strait to Rockall and northern Norway, 40-665 m	off NW Spain, 450-545 m	western Atlantic: off SE U.S.A., 146-530 m	off southern and eastern Greenland to Iceland, 326-713 m	off SE Iceland to Celtic Sea, 350-1080 m	seamounts south/southwest of Azores, 293-500 m
coenosteal papillae not uncommon, especially on or near am-ullae; cyclo-systems rare; efferent pore large	host of <i>Pedicularia</i>	colonies uniplanar, branches often thickened; host of <i>Pedicularia</i> and polynoid polychaete	colonies uniplanar, branches often thickened	colonies uniplanar, branches moderate in thickness; deep coenosteal slits on pseudosepta (Fig. 30 E); host of <i>Pedicularia</i>	colonies bushy, branches slender

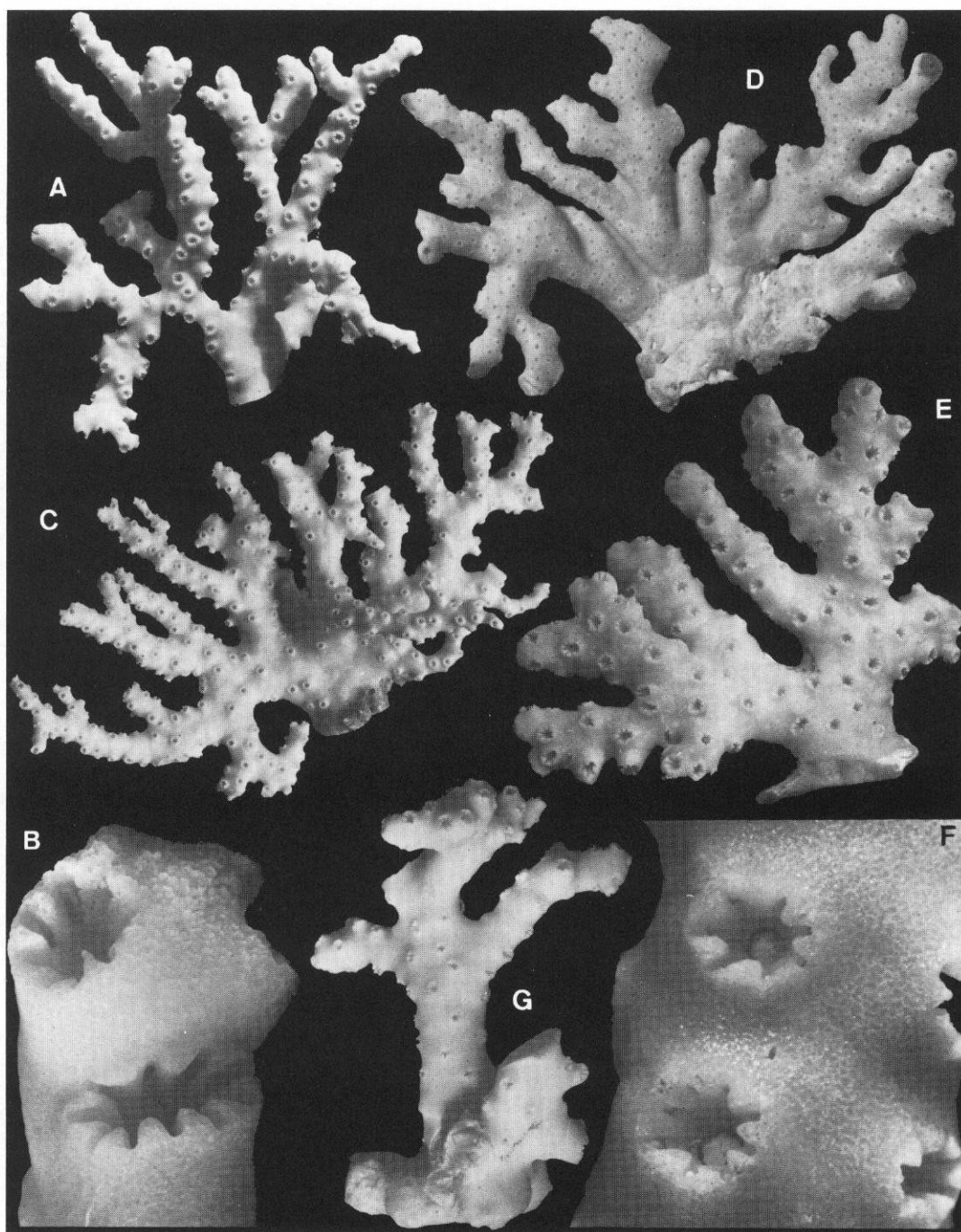


FIG. 16. — *Sylvester norvegicus* (A-B, from Trondheimsfjord, no further details, vsm; C, from Trondheimsfjord, Brettingnes, 100-300 m, coll. C. DONS 4.5.1939, vsm; D, from Hebrides, RSM 1913.113.2; E-F, from Lofoten, Røst, Kunstmalder ESAISSEN, vsm; G, from "Porcupine" stn 54, BMNH 1880.11.12.4-5): A, slightly bushy colony with rather slender cylindrical branches ($\times 1.5$); B, blunt branch tip of A with cyclosystems ($\times 17$); C, larger colony with branches becoming flattened near the base ($\times 1.0$); D, larger uniplanar colony with branches flattened and coalescent near the base ($\times 1.0$); E, colony with blunt branches in uniplanar arrangement ($\times 2.1$); F, branch segment of E, gastrostyles visible in depth of cyclosystems ($\times 17$); G, colony of irregular shape ($\times 2.1$).

Norway, colony received from HICKSON (MNHN). — Norway, colony (NHMW 7970). — Norway, fragment received from G.O. SARS (USNM 6854, erroneously labelled as cotype). — “Anton Dohrn” 10.3.1972, large colony at IMFB known only from photograph.

DESCRIPTION

Colonies mostly uniplanar, up to 10 cm high and 15 cm wide (Fig. 16 A, C-D, F). Branches cylindrical and robust, 2-3 mm in diameter at blunt distal tips. Coenosteum white to off-white and smooth, a result of a reticulate-granular texture with very low relief granules. Figure 17 F shows a transition from an early stage of coenosteal development characterized by irregularly shaped granules to the more advanced, smooth stage in which the granules are united into strips and covered with a smooth coenosteum. Coenosteal strips 45-75 μ m wide. Cyclosystems circular, 0.9-1.1 mm in diameter, occurring with equal frequency on all branch faces. Cyclosystems flush with coenosteum or raised only slightly above coenosteum. According to BOSCHMA's (1962) analysis of 500 cyclosystems, there is a range of 3-10 dactylopores per cyclo-system, mean 6.33, and mode 6. Our analysis of 738 cyclosystems revealed a slightly higher number of dactylopores per cyclosystems: range 5-11, mean 6.92, and mode 7. There are no diastemas.

Gastropore tubes 0.7-2.2 mm long, slightly constricted at level of gastrostyle tip; no ring palisade (Fig. 17 G). Gastrostyle (Fig. 16 F)

occupies a variable percentage of gastropore tube, depending on height of style and length of tube (see BOSCHMA, 1962: fig. 3). Gastrostyle variable in shape, ranging from rotund (wider than high) to conical, with H:W ratios ranging from 0.9-2.6. Tallest known gastrostyle 0.75 mm; widest, 0.52 mm (BOSCHMA, 1962). Gastrostyles covered by extremely long, cylindrical, blunt spines up to 110 μ m long and 15 μ m in diameter, which are sometimes laterally fused into tiers (Fig. 17 H). Ridging of gastrostyle, if present, obscured by tall and abundant gastrostyle spines. Dactylotomes 0.10-0.15 mm wide. Dactylostyles (Fig. 17 C) robust, composed of blunt cylindrical elements much like gastrostyle spines, each element up to 75 μ m tall and about 11 μ m in diameter. Dactylostyles up to 0.6 mm long and 65 μ m wide (4 or 5 elements across width), terminating about 0.2 mm from the tip of dactylopore.

Ampullae (male?) internal to slightly superficial (Fig. 17 E), 0.5-0.6 mm in internal diameter. Efferent pores round, about 0.13 mm in diameter. Female ampullae unknown.

COMPARISONS

S. norvegicus is easily distinguished from the other two eastern Atlantic species of *Stylaster* (Group A), by a large number of characters (Table 2). Within the Atlantic, it is most similar to *S. miniatus* (Pourtales, 1868), known from off the southeast coast of the United States from 146-530 m (CAIRNS, 1986a). Points of similarity include: cyclo-system diameter, gastrostyle ornamentation and H:W ratio, dactylostyle shape, and characteristics of the male ampullae. Nonetheless, *S. norvegicus* can be distinguished by its coenosteal texture and higher number of dactylopores per cyclo-system.

REMARKS

S. norvegicus is recognizable in GUNNERUS' (1768) illustrated description from Norway (as *Millepora*). BROCH (1918) commented upon this description and reproduced some of the figures. Referring to a correspondence he had with LINNAEUS, GUNNERUS (1768: 67) added the erroneous remark that his *Millepora norvegica* was the same as *Millepora aspera* Linnaeus, 1767 (for which the distribution had been given as Mediterranean and Norwegian Sea). This was a misunderstanding (BOSCHMA, 1953a, 1953b, 1965a); in fact, LINNAEUS' coral (now known as *Errina aspera*) is a Mediterranean species and does not occur along the coast of Norway.

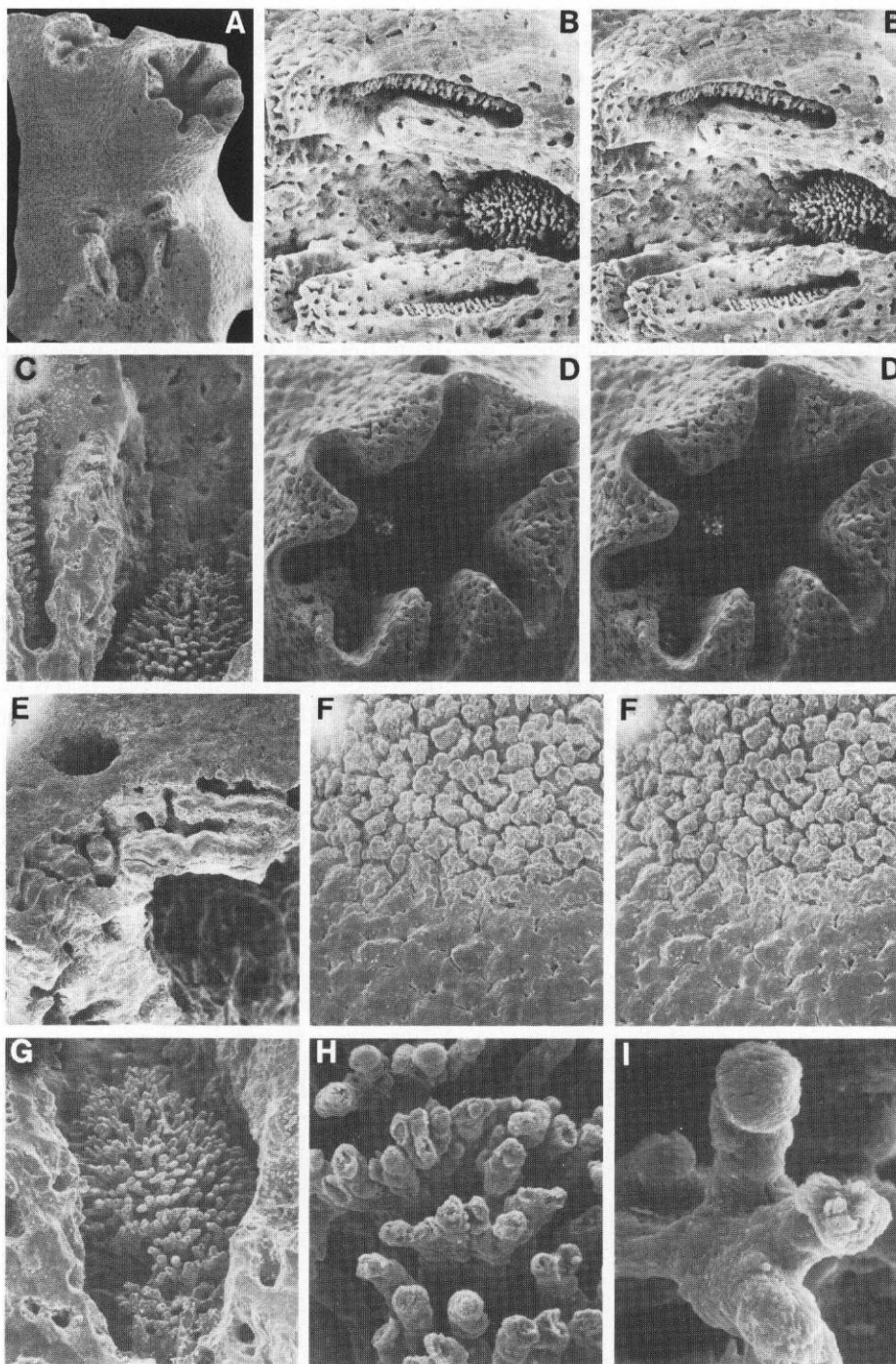


FIG. 17. — *Styaster norvegicus* (A-D, F-I, from Norway, USNM 6854; E, from Rockall, male, BMNH 1896.8.3.3-5): A, branch fragment illustrating two cyclostomes, one of them longitudinally fractured ($\times 13$); B, longitudinally fractured cyclostome illustrating gastrostyle and dactylostyles ($\times 32$, stereo pair); C, tip of gastrostyle and dactylostyle ($\times 60$); D, cyclostome ($\times 42$, stereo pair); E, fracture through internal male ampulla, efferent pore at coenosteal surface ($\times 65$); F, transitional coenosteal texture ($\times 85$, stereo pair); G, gastrostyle ($\times 81$); H-I, transversely fused gastrostyle spines ($\times 300$, $\times 1560$, respectively).

BROCH (1936) erroneously included *Allopora miniata* Pourtalès, 1868, in the synonymy of *S. norvegicus*. As BOSCHMA (1962) had already argued, BROCH's reference specimens were not authentic western Atlantic *A. miniata*, but mislabeled northeastern Atlantic *S. norvegicus*; in fact, BROCH had not seen the single authentic small branch of *A. miniata* in the ZMUO. Typical *A. miniata* (redescribed by CAIRNS, 1986a, as *Stylaster miniatus*) differs from *S. norvegicus* in various aspects, such as surface structure, depth of gastropores, higher number of dactylopores (see Comparisons).

Allopora oculina Ehrenberg, 1834, of unknown origin, is most likely a synonym of *S. norvegicus*. The original description and a redescription by MILNE EDWARDS & HAIME (1850) may apply to the Norwegian stylasterid, which was easily available to the older authors. *A. oculina*, as repeatedly reported from Norway in the 19th century, should be referred to *Stylaster norvegicus*. *A. oculina* sensu STUDER (1878), from South Africa (ZMB 1654), is very different, close to *Stylaster bithalamus* Broch, 1936.

The first adequate description of *S. norvegicus*, according to modern standards, was given by BROCH (1914a) from Norwegian and other northern Atlantic material (including GUNNERUS' types). Norwegian material was again analyzed in detail by BROCH (1936) and BOSCHMA (1962).

S. norvegicus, often attributed to the genus *Allopora*, is mentioned in various publications on the fauna of Norway, where *S. norvegicus* and *S. gemmascens* frequently occur together but have not always been distinguished; many lots in museum collections under one or the other name have proved to be a mixture of both species.

S. norvegicus is one of four species reported by DUNCAN from between the Faroes and the Hebrides, first (1870) as *Allopora oculina*, then (1873) as *Stylaster gemmascens* (the other species are *S. gemmascens*, *S. erubescens britannicus*, and *Stenohelia maderensis*).

Stylasterids from the northern Pacific (Japan to British Columbia) have occasionally been referred to *Stylaster* (or *Allopora*) *norvegicus*, mostly as a distinct form or subspecies *pacifica* as opposed to *atlantica* (HICKSON, 1915; BROCH, 1935, 1936; FISHER, 1938; EGUCHI, 1941; NAUMOV, 1960). One of these records (British Columbia) was subsequently reidentified as *Stylaster verrillii* Dall, 1884 (FISHER, 1938: 524; BROCH, 1942: 6). Likewise, CAIRNS (1983b: 429) tentatively included *Allopora norvegica pacifica* Broch, 1936, in the synonymy of *S. verrillii*.

DISTRIBUTION AND ECOLOGY

S. norvegicus is known from many stations in a wide area of the North Atlantic: from Denmark Strait, the northwest, southwest, and southeast of Iceland, Faroes and Hebrides, Rockall, and along the coast of Norway. Its occurrence in Icelandic waters, already reported by BROCH (1914a), is here confirmed. The northernmost records are 66°18'N in Denmark Strait, and 69°14'N off Norway.

In Norway the species is common in depths of 80-300 m, frequently found together with the bank-forming scleractinian *Lophelia pertusa*. Elsewhere, the shallowest record is from 75 m in the Faroes. In the Iceland - Faroes area the species has been obtained as deep as 1040 m and 1400 m.

No symbionts are known.

Stylaster rosaceus (Greeff, 1886)

Fig. 18 A-H

Synonymy:

Allopora rosacea Greeff, 1886: 19-20.

Chresonymy:

Allopora rosacea — BROCH, 1914b: 38-40, text-fig. 12, pl.1, fig.4-5. — BOSCHMA, 1957a: 27; 1961: 219-220.
Stylaster rosaceus — CAIRNS, 1983b: 429.

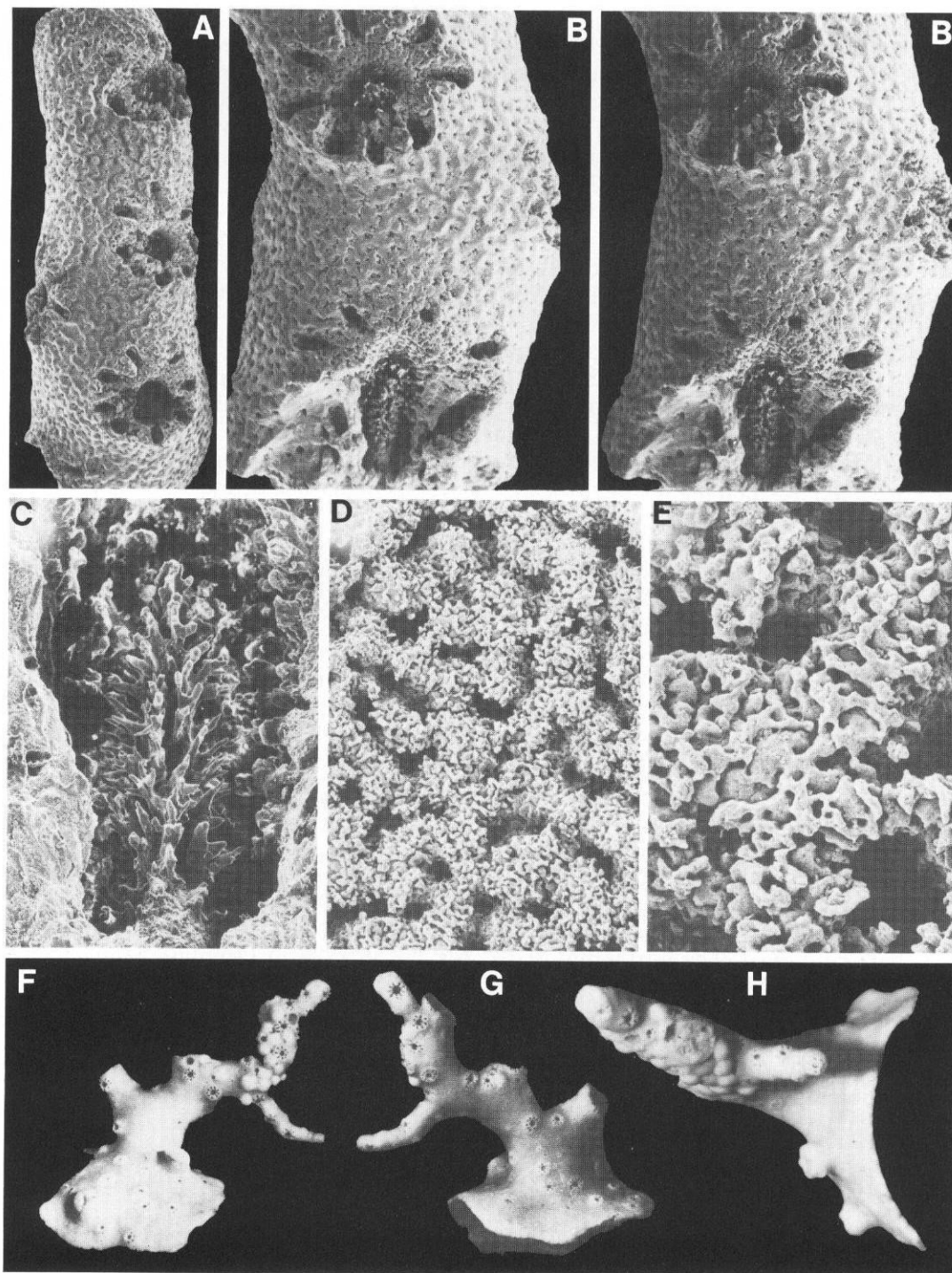


FIG. 18. — *Stylaster rosaceus* (A-H, female syntype, ZMB 4725): A, branch fragment bearing three cyclostomes ($\times 24$); B, branch segment bearing two cyclostomes, lowermost fractured revealing gastrostyle ($\times 36$, stereo pair); C, gastrostyle and ring palisade ($\times 142$); D-E, coenosteal texture ($\times 128$, $\times 359$, respectively); F-G, opposite faces of colony, one with clustered female ampullae (both $\times 3.5$); H, edge view of colony ($\times 5.3$).

TYPES

Allopora rosacea: In the original unillustrated description, GREEFF (1886) mentioned several small colonies up to 35 mm high. Having not been given a precise type status, they are considered as syntypes. After GREEFF's death at least part of his collections were transferred from the Zoological Institute, Marburg, to the Zoological Museum, Hamburg, where BROCH (1914b) was able to study one of the syntypes. This specimen was lost when the museum burnt in 1943. Another smaller female syntype (12 mm tall, 13 mm broad) exists at the ZMB (4725), probably deposited there by GREEFF himself. This is the only specimen known to be preserved (Fig. 18 F-H).

Type locality: Passage between São Tomé and Ilha das Rolas, Gulf of Guinea, depth ca. 37 m (R. GREEFF, 1880, dredge).

MATERIAL STUDIED

São Tomé: 1 syntype (ZMB 4725).

DESCRIPTION

The only specimen available (Fig. 18 F-H) is a slender incomplete colony (most branch tips broken), 12 mm tall, uniplanar, with a thin encrusting concave base about 8 mm wide, the latter originally encrusting a cylindrical substrate. On the same base, next to the main stem, two smaller branches are broken away. Branches cylindrical, gradually tapering to slender branch tips the diameter of a cyclosystem. Coenosteum pink, mature (female) ampullae less pigmented to whitish; branch tips may also be of lighter colour. Coenosteum reticulate, strips 55-80 µm wide, but not granular, rather covered with irregularly shaped elongate carinae about 30 µm long and 7 µm wide (Fig. 18 D-E).

Cyclosystems occur on all branch surfaces; they are circular to slightly elliptical, 0.6-0.7 mm in diameter, almost flush with coenosteum. No diastemas observed. Based on 70 cyclosystems from encrusting base and branches, the range is 5-12 dactylopores per cyclosystem, mean 8.57, and mode 9.

Gastropore about 0.2 mm in diameter, with a robust ring palisade (Fig. 18 C) composed of cylindrical elements about 25 µm in height and diameter, not vertical carinae. Gastrostyles elongate-conical (Fig. 18 C), about 0.35 mm tall and 0.10 mm in diameter (H:W = 3.6), occupying basal half of gastropore tube. Gastrostyles vertically ridged, each ridge bearing slender elongate spines up to 41 µm long and 8 µm in diameter. Dactylotomes about 70 µm wide, separated by low pseudosepta 1-1.5 times width of dactylotomes; no diastemas. Dactylotomes open apically, rarely directly into gastropore chamber. Isolated dactylopores present but sparse. Dactylostyles not examined.

Female ampullae superficial hemispheres about 0.70 mm in diameter, clustered on both anterior and posterior faces. Efferent pore about 0.15 mm in diameter. Male ampullae unknown.

COMPARISONS

Based on the single preserved syntype, *S. rosaceus* differs from the better known sympatric *S. blatteus* in the following characters: colour pink versus purple; slender branches; smaller cyclosystem diameter; cyclosystems flush and widely spaced versus slightly exsert and denser; dactylotomes open apically versus opening into gastropore tube; diastema absent versus occasionally present; ring palisade consisting of cylindrical elements versus vertical carinae; gastrostyle spines tall and slender (e.g. 41 x 7 µm) versus short and blunt (e.g. 25 x 12 µm).

Coenosteal texture, gastrostyle, and range, mean and mode of dactylopores per cyclosystem are not significantly different in the two species. However, the impression of a similar coenosteal texture is based on only a very small piece of the basal encrustation of *S. rosaceus* used for SEM study.

GREEFF's syntypes of *S. rosaceus* (only one of which is preserved) are the only pink stylasterids from the Gulf of Guinea, thereby strangely contrasting with the many specimens of *S. blatteus* (types included) available for the present study, all of which have the purple colour described by BOSCHMA (1961). If pink *S. rosaceus* and purple *S. blatteus* are just colour variations of one species, they would be expected to occur together, but this apparently is not the case. Some other stylasterid species do show colour variations, generally even among material from one station, e.g. the South African *Errina diffusa* Boschma, 1963b, which may be either white or pink.

The occurrence of *S. rosaceus* at a depth of about 37 m may also point to a specific difference from *S. blatteus*, which is always collected from infralittoral rocks at depths not exceeding 10 m.

REMARKS

Specimens corresponding to the pink *S. rosaceus* as described by GREEFF (1886, under *Allopora*) have never been subsequently collected. BROCH (1914b) reproduced GREEFF's description and added a few details on the surface structure and on the shape of the cyclosystems. In order to preserve the single available syntype undamaged, he forsook any detailed study that required dissection.

According to GREEFF (1886), the main characters distinguishing *S. rosaceus* from *S. blatteus* are the colour (pink in *rosaceus*, deep violet or wine-red in *blatteus*) and the absence of isolated dactylopores between the cyclosystems. GREEFF was wrong on the second point: we found isolated dactylopores on the only preserved syntype. BROCH (1914b) mentioned a difference of the surface structure: in *S. rosaceus* roughly reticulate, the small "fields" being separated by "stripes" of lighter colour; in *S. blatteus* with a fine punctuation (but most specimens of the latter were beach worn). Indications on the cyclosystems by both authors (width, number of dactylopores) are apparently based on a rough comparison and only a few countings. Cyclosystems of *S. rosaceus* are said to be less regularly circular, occasionally also deformed by adjacent ampullae. There are in fact some less regular cyclosystems on the remaining syntype, but this should not be considered significant; irregularities are also observed in *S. blatteus*.

DISTRIBUTION AND ECOLOGY

S. rosaceus is known only from one record at São Tomé (type locality), depth ca. 37 m. No symbionts are known.

Stylaster blatteus (Boschma, 1961)

Fig. 19 A-J, 20 A-F

Synonymy:

Allopora blattea Boschma, 1961: 210-221, pl. 3-6.

Chresonymy:

Allopora subviolacea — GREEFF, 1886: (11-13)16-19. — BROCH, 1914b: 40-41, pl. 1, fig. 6-7. — BOSCHMA, 1957a: 28-89 (part).

Allopora blattea — VERVOORT & ZIBROWIUS, 1981: 27.

Stylaster blatteus — CAIRNS, 1983b: 429.

TYPES

Allopora blattea: The original description by BOSCHMA (1961) was based on many specimens from several localities at Principe and São Tomé, islands in the Gulf of Guinea. One of these colonies ("Calypso" 1956, stn 70, São Tomé) was designated by BOSCHMA (pl. 3, fig. 1-2) as holotype, all other colonies from the same and other localities ("Calypso" 1956, stn T-25, stn 67, stn 74, stn 111; São Tomé, I. MARCHE-MARCHAD, 1956) as paratypes (pl. 4-6, and other unfigured specimens). Holotype and most paratypes at MNHN. Additional paratypes at RMNH ("Calypso" 1956, stn T-25,

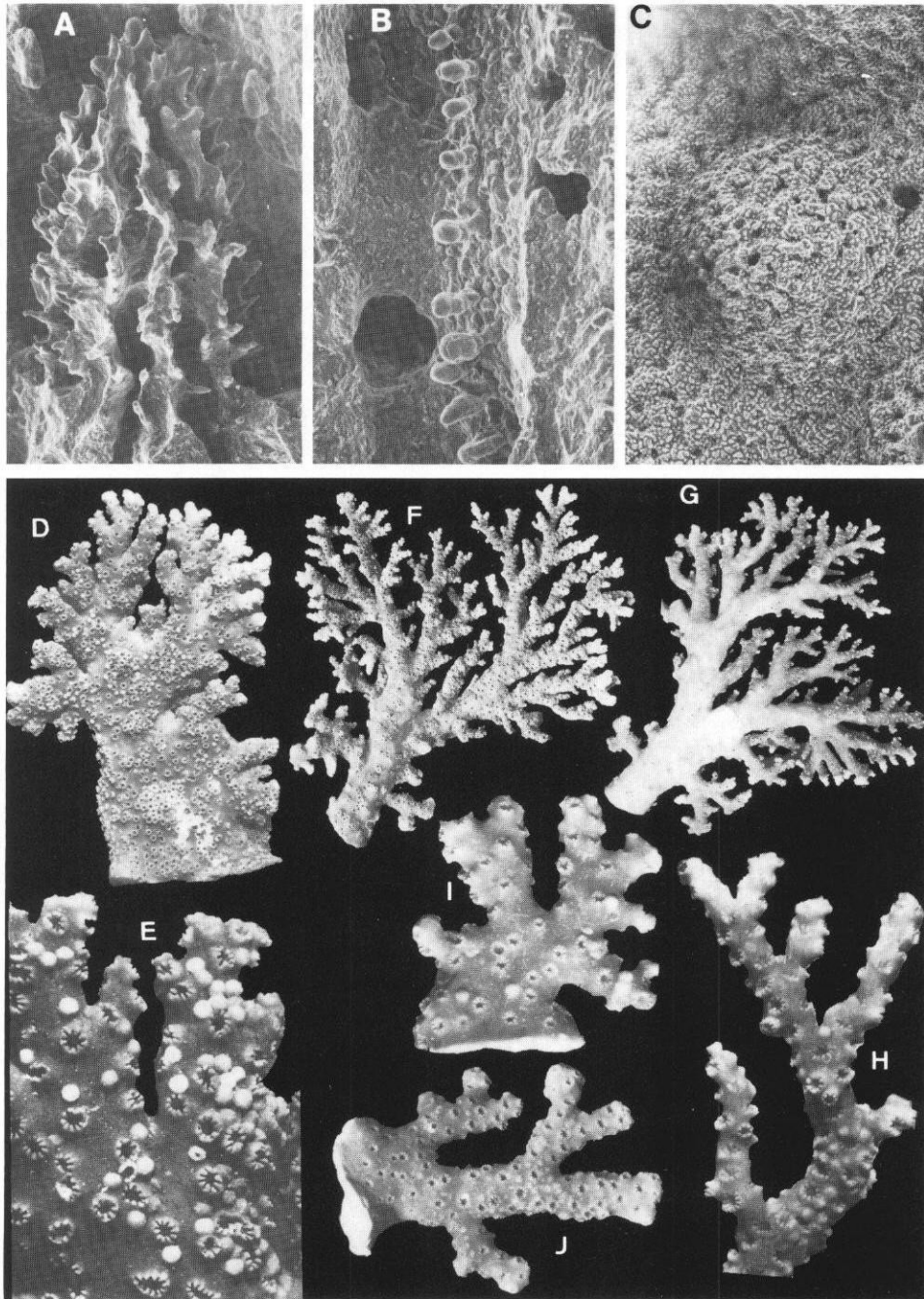


FIG. 19. — *Stylaster blatteus* (A-C, from Praia das Conchas, São Tomé, male, USNM 75614; F-H, same locality, MNHN; D-E, from São Tomé, coll. CPAS, MNHN; I-J, from Príncipe, Ilheu dos Mosteiros, coll. J. LABOREL, MNHN); A, gastrostyle and ring palisade ($\times 169$); B, dactylostyle ($\times 253$); C, male ampulla with apical efferent pore ($\times 63$); D, robust colony with short stout branches ($\times 1.2$); E, detail of D illustrating cyclosystems and ampullae ($\times 4.3$); F-G, anterior and posterior face of colony with rather slender branches (both $\times 0.6$); H, slender branch of another colony ($\times 4.4$); I-J, young colonies ($\times 2.9$, $\times 2.0$, respectively).

dry colony Coel 13750A, alcohol preserved material Coel 13750B; São Tomé, I. MARCHE-MARCHAD, 1956, 2 colonies Coel 13902) and USNM ("Calypso" 1956, stn T-25, 2 fragments 75613). In addition, the RMNH has fragments from "Calypso" 1956, stn T-25 and stn 70 that have been used by BOSCHMA to make preparations, but were not given type status (VERVOORT & ZIBROWIUS, 1981: 27).

Type locality: Holotype (and several, but not all paratypes) from "Calypso" 1956, stn 70, 19.6.1956. Praia Santa Catarina on the west coast of São Tomé, 3-10 m.

MATERIAL STUDIED

All specimens listed by BOSCHMA (1961) from the "Calypso" cruise in 1956 to the islands in the Gulf of Guinea (see Types), and additional more recently collected specimens.

Príncipe: "Calypso" 1956, stn 111, 7.7.1956, Ilheu dos Mosteiros, 3-10 m, 8 colonies (paratypes). — Ilheu dos Mosteiros, overhang 4-6 m, 18 small colonies, J. LABOREL, Jan. 1971 (most MNHN; USNM 77124).

São Tomé: "Calypso" 1956, stn T-25, 15.6.1956, Punta Furada, 3-8 m, 4 colonies + several fragments (paratypes); stn 67, 18.6.1956, Punta Diogo Vaz, 6-10 m, 3 colonies (paratypes); stn 70, 19.6.1956, Praia Santa Catarina, 3-10 m, 8 colonies + several fragments (holotype + paratypes); stn 74, 21.6.1956, São Miguel bay, 6-10 m, 2 colonies (paratypes); same cruise, precise locality not given, I. MARCHE-MARCHAD, several small branches + fragments (paratypes); same cruise, northwestern coast of São Tomé, branch. — São Tomé, without further details, colony collected by divers of Centro Portugues de Actividades Subaquaticas [= CPAS], transmitted by L. SALDANHA. — Praia das Conchas, Guadalupe, 10 m, S. GOFAS, Nov. 1983, 7 colonies (most MNHN; USNM 75614; BMNH).

DESCRIPTION

Colonies robust and primarily uniplanar (Fig. 19 D, F-G): holotype 10.7 cm high and 10.5 cm wide, with a massive basal branch and encrusting base. Branches cylindrical, their distal part following last ramification still rather stout before tapering to tip the diameter of a cyclosystem. Coenosteum purple, reticulate in texture, the strips 35-55 μ m wide and separated by deep slits up to 11 μ m wide. Strips covered with irregularly shaped pointed granules and short carinae; the granules as small as 10 μ m in diameter, the carinae up to 25 μ m long and about 7 μ m wide (Fig. 20 B).

Cyclosystems occur on all branch surfaces. They are round to slightly elliptical, 0.8-0.9 mm in diameter, rather exsert on their proximal margin and occasionally develop a narrow diastema (Fig. 20 A). Based on 500 cyclosystems, BOSCHMA (1961) found a range of 6-12 dactylopores per cyclosystem, mean 8.88, and mode 9.

Gastropore about 0.3 mm in diameter and 0.65-1.55 mm deep, with a well-defined ring palisade at level of gastrostyle tip. Ring palisade composed of 12-15 vertical carinae (Fig. 20 E-F) up to 80 μ m long and 15 μ m wide arranged parallel to one another. Gastrostyles 0.30-0.65

mm tall and 0.13-0.24 mm wide (H:W = 2.0-3.9), occupying basal 40-60 % of gastropore. Gastrostyle deeply ridged, bearing short, blunt spines about 25 μ m long and 12 μ m in diameter. Well developed high dactylotomes about 73 μ m wide, opening straight into steep-walled dactylopore tube devoid of shelf; pseudosepta one to four times width of dactylotomes. Narrow distal diastemas occasionally present, especially on large diameter branches. Circular to irregularly shaped isolated dactylopores very common (Fig. 20 C), 60-90 μ m in diameter. Dactylostyles rudimentary (Fig. 20 B), composed of a single line of well-spaced cylindrical to clavate elements, each up to 35 μ m tall and about 12 μ m in diameter. Isolated dactylopores do not have dactylostyles.

Female ampullae (Fig. 20 C-D) smooth, superficial hemispheres 0.50-0.65 mm in diameter, each with an efferent pore about 0.11 mm in diameter. Male ampullae (Fig. 19 C) also superficial, 0.30-0.45 mm in diameter, with 1-3 apical efferent pores, each about 22 μ m in diameter. Ampullae of both sexes often clustered (Fig. 19 E, H, 20 D) on both anterior and posterior faces.

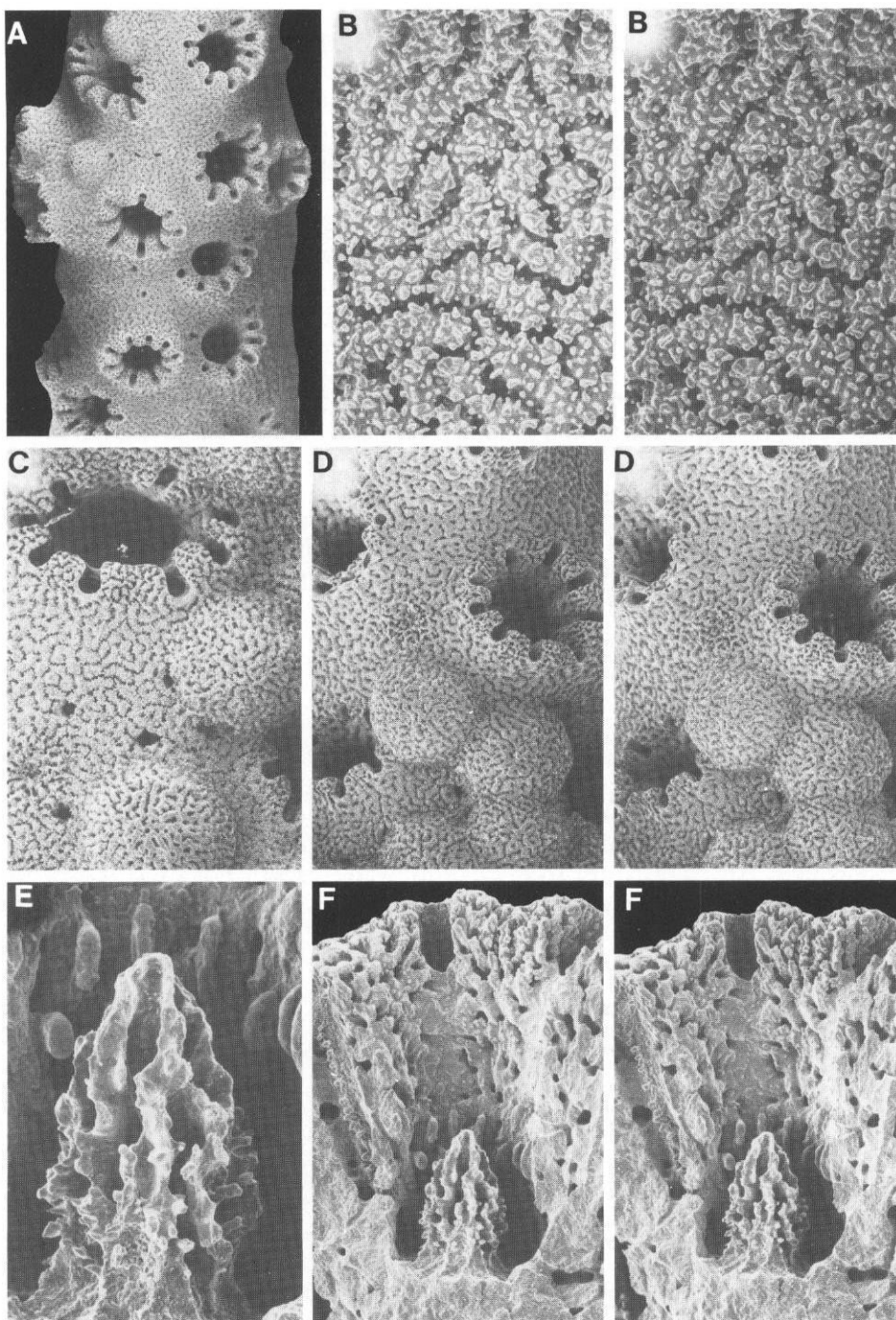


FIG. 20. — *Stylaster blatteus* (A, B-F, from Praia das Conchas, São Tomé, male and female, respectively, USNM 75614): A, branch segment showing cyclosystems and isolated dactylopores ($\times 14$); B, coenosteal texture ($\times 128$, stereo pair); C-D, coenosteum illustrating cyclosystems, female ampullae, and isolated dactylopores ($\times 32$, $\times 24$, respectively; D being a stereo pair); E-F, gastrostyle and ring palisade ($\times 164$, $\times 64$, respectively, F being a stereo pair).

COMPARISONS

BOSCHMA (1961), who knew *S. rosaceus* only from the literature, questioned whether GREEFF's (1886) pink *S. rosaceus* and the sympatric purple *S. blatteus* were distinct species.

We conclude that these forms are different species: *S. blatteus* has purple coenosteum; stouter distal branches; and more densely crowded and exert larger cyclosystems with higher dactylotomes. Other structures of both species are similar, such as coenosteal texture and gastrostyle, as well as range, mean and mode of dactylopores per cyclosystem.

Young colonies of *S. blatteus* (Fig. 19 I-J) similar in size to the only preserved syntype of *S. rosaceus* are different in aspect, being stouter with more crowded cyclosystems.

REMARKS

GREEFF (1886), the first collector of the purple stylasterid from the Gulf of Guinea, mistakenly referred it to *Allopora subviolacea* Saville Kent, 1871, at that time known only from the type from unknown origin. BROCH (1914b), who reexamined part of GREEFF's specimens (beach worn pieces only), had little to add to the previous description.

BOSCHMA (1961) finally had access to abundant new material from the Gulf of Guinea and described it as *Allopora blattea* (the name meaning purple), while his student GOEDBLOED (1962a, b) studied the dactylozooids and gonophores of this species. BOSCHMA (1966) also examined the type of *A. subviolacea* and redescribed this species from new material from South Africa. Having seen all samples studied by BOSCHMA, as well as additional specimens from the Gulf of Guinea and South Africa, we confirm BOSCHMA's conclusion on the obvious difference of the two species (now absorbed into the genus *Stylaster*).

DISTRIBUTION AND ECOLOGY

S. blatteus is known only from the two central islands in the Gulf of Guinea, Principe and São Tomé. The presence of the stylasterid is best documented for São Tomé, which has been more intensively investigated. All records are from shallow water (depth not exceeding 10 m), especially from steep cliffs, under overhangs, and in vertical fissures of zones exposed to strong currents (FOREST, 1959: 10).

No symbionts are known.

Stylaster maroccanus new species

Fig. 21 A-D, 22 A-G

TYPES

Type lot comprising 8 specimens collected dead, 3 of them representing lower parts of colonies with the preserved base, the other 5 being colonies without base or detached branches. Holotype largest specimen, colony about 8 mm high, without base, with 8 cyclosystems (Fig. 21 A-B). The other 7 specimens are paratypes. Holotype and most paratypes at MNHN; 1 paratype at USNM (77125).

Type locality: "Cryos" cruise BALGIM, stn CP-95, 8.6.1984, 34°24.7'N, 7°39.3'W, 1378 m. Off Atlantic coast of Morocco.

MATERIAL STUDIED

Morocco: holotype and paratypes (see above).

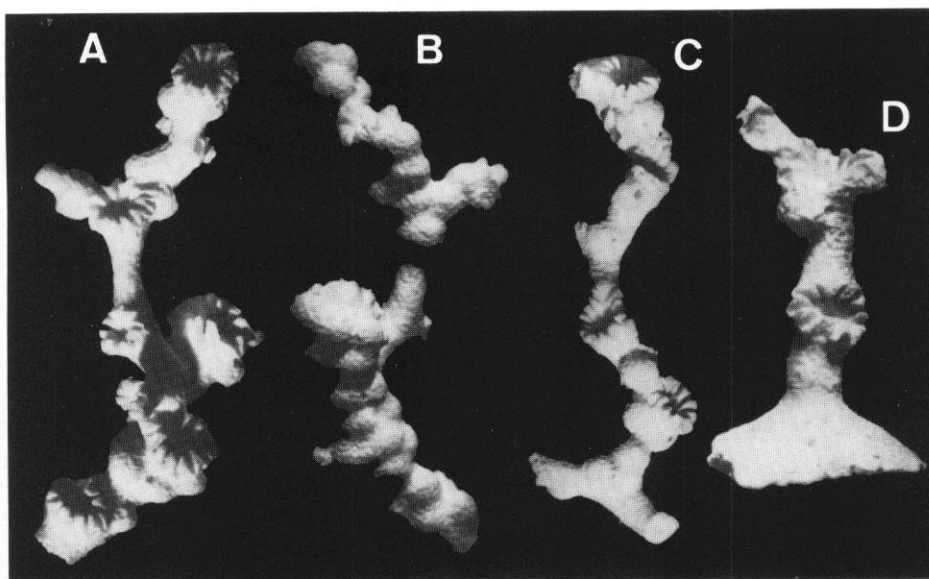


FIG. 21. — *Stylaster maroccanus* (A-D, from "Cryos" CP-95, MNHN): A-B, opposite views of female holotype illustrating clustering of ampullae on posterior face (both $\times 9.0$); C-D, paratypes ($\times 9.0$, $\times 13$, respectively).

DESCRIPTION

The few fragmentary specimens available suggest a delicate, bushy corallum. Largest available specimen has only 8 cyclosystems. Branches cylindrical; 0.5-0.7 mm in diameter. All specimens were dead when collected, with poorly preserved coenosteum, some specimens apparently suffering from bioerosion. Coenosteum white and reticulate-granular in texture (Fig. 22 F), the strips about 70 μm wide. No nematopores or isolated dactylopores apparent.

Cyclosystems sympodially arranged on some branches or parts of branches and restricted to anterior face of other branches. Cyclosystems circular to slightly elliptical in shape, 1.0-1.4 mm in diameter. Based on 27 cyclosystems (all available), there is a range of 9-14 dactylopores per cyclosystem, mean 11.77, and mode 11. Some cyclosystems have a narrow diastema.

Only one poorly preserved gastrostyle was examined (Fig. 22 C): it is 0.40 mm high and

0.073 mm wide ($H:W = 5.47$) and not ridged. Little more detail is known of the gastrostyle; however, the ring palisade is well developed. Elongate elements up to 0.1 mm long, 30 μm wide, and 30 μm high encircle upper third of gastrostyle (Fig. 22 G). Gastrostyle tip extends slightly beyond the ring palisade zone into the slightly expanded upper gastropore chamber. Dactylotomes about 65 μm wide; pseudosepta 1-3 times width of dactylotomes and often slightly concave, especially on their outer edges. Dactylostyle rudimentary, composed of a single line of cylindrical elements.

Female ampullae (Fig. 22 A, D) elliptical in outline, about 0.65 \times 0.45 mm, the circular lateral efferent pore at one of the vertices of ellipse. Female efferent pore 0.12 mm in diameter. Male ampullae unknown. Mature female ampullae present on very small branches, indicative of early maturation and/or small colony size.

COMPARISONS

S. maroccanus is a very distinctive species among the eastern Atlantic *Stylaster* (Table 2) based on its cyclosystem orientation, elongate gastrostyles, and very small corallum size. It is perhaps most similar to *S. blatteus*, both having similar dactylostyle and ring palisade morphology; however, it is

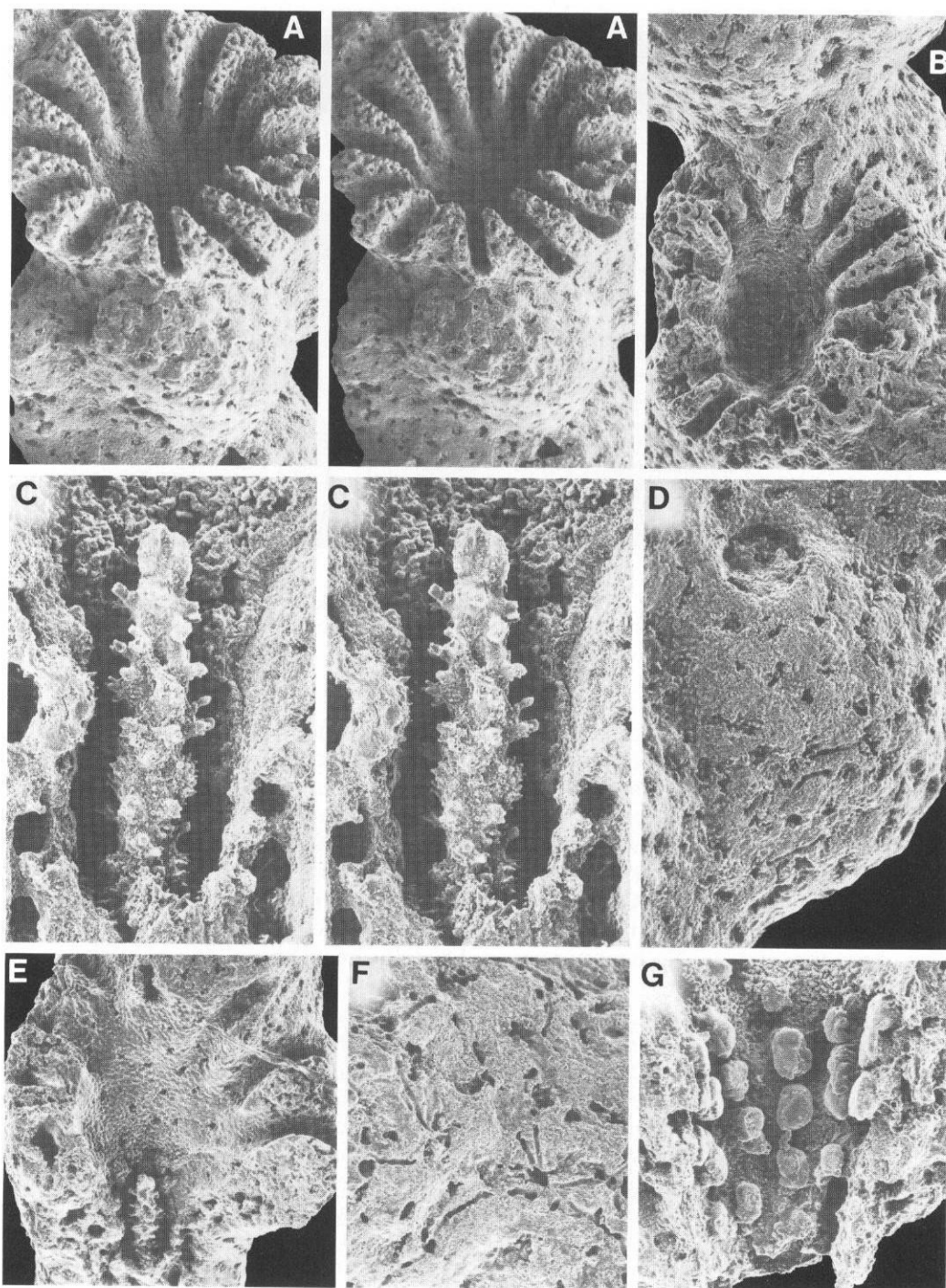


FIG. 22. — *Stylaster maroccanus* (A-G, paratype from "Cryos" CP-95, female, USNM 77125): A, cyclosystem surrounded by several ampullae ($\times 40$, stereo pair); B, top view of cyclosystem that has calcified lower gastropore tube, female ampullae and efferent pore above cyclosystem ($\times 46$); C, poorly preserved gastrostyle and ring palisade ($\times 146$, stereo pair); D, female ampulla and efferent pore ($\times 87$); E, longitudinal fracture of cyclosystem revealing gastrostyle of C ($\times 50$); F, poorly preserved coenosteum showing bioerosion (?) ($\times 123$); G, well-developed ring palisade, gastrostyle removed ($\times 113$).

easily distinguished by its coenosteal color, larger cyclo systems, and greater average number of dactylo pores per cyclo system, as well as by a very different depth and geographic range.

REMARKS

The specific name given to the new species refers to its geographic distribution.

DISTRIBUTION AND ECOLOGY

Species known from one station only (type locality), off the Atlantic coast of Morocco, depth 1378 m.

No symbionts are known.

Stylaster gemmascens (Esper, 1794)

Fig. 23 A-H, 24 A-F

Synonymy:

Madrepora gemmascens Esper, 1790: pl. 55, fig. 1-2; corresponding text 1794: 60.

Chresonymy:

Madrepora virginea — GUNNERUS, 1768: 56, pl. 8, fig. 2-4.

Oculina gemmascens — EHRENBURG, 1834: 303.

Allopora gemmascens — DANA, 1848: 696.

Stylaster gemmascens: MILNE EDWARDS & HAIME, 1850: 98; 1857: 130-131. — SAVILLE KENT, 1871: 281. — SARS, 1873: 115. — DUNCAN, 1873: 332 (part), pl. 49, fig. 4-7. — STORM, 1879: 24; 1882: 25-26. — MOSELEY, 1879: 480; 1881: 86. — NORMAN, 1893: 349. — THOMSON, 1910: 61. — RITCHIE, 1912: 281. — NORDGAARD, 1912: 7. — ARNDT, 1913: 122. — BROCH, 1914a: 8-12, text-fig. C, pl. 1, fig. 4-7, pl. 2, fig. 16, pl. 3, fig. 21, 24-26, 30-31, pl. 4, fig. 32-33, pl. 5, fig. 46, 49-50; 1918: 9, fig. C. — DONS, 1932: 15. — BOSCHMA, 1955a: 22-31, text-fig. 1-3, pl. 1-2; 1956b: F98; 1957a: 10-11; 1958: 71-72. — BOURDON-JONES & TAMBS-LYCHE, 1960: 7. — CAIRNS, 1983b: 430.

Stylaster (Eustylaster) gemmascens — DONS, 1939: 197.

Allopora oculina — DUNCAN, 1870: 290, 295 (part).

Stylaster sanguineus — THORNELLY, 1897: 81.

NOT *Stylaster gemmascens* — HICKSON & ENGLAND, 1905: 12 (Sulu Islands).

NOT *Stylaster* cf. *gemmascens* — EGUCHI, 1941: 1176 (Japan).

NOT *Stylaster gemmascens alaskanus* Fisher, 1938: 500-501, pl. 47, pl. 54, fig. 2 (Aleutian Islands). — BOSCHMA, 1953a: 166; 1957a: 11. — NAUMOV, 1960: 534, fig. 430-431 (Kurile Islands).

TYPES

Madrepora gemmascens: As shown by GRASSHOFF & SCHEER (1991) ESPER's description (1794) was published after the illustration (1790), but opinion No. 574(3b) of the International Commission on Zoological Nomenclature (1959) had already rejected all uses of the binomen *Madrepora gemmascens* prior to ESPER (1794). It was based on presumably only one specimen. BOSCHMA (1955a) described and figured in detail the specimen found in ESPER's collection and regarded it as the "type"; this colony is massive, 10 cm high, 8.5 cm wide, 1.7 cm basal branch diameter (Fig. 23 C-D) and is a male, not a female as suggested by BOSCHMA. In a later publication (BOSCHMA, 1958) it was referred to as the "holotype" and also "selected as the lectotype". It is now deposited at the SMF, where it had been transferred from Erlangen (VERVOORT & ZIBROWIUS, 1981: 10).

Type locality: According to ESPER (1794), his material came from the East Indian Sea, information which was reiterated by, among others, MILNE EDWARDS & HAIME (1850, 1857). The origin given by ESPER was certainly incorrect: the species is known only from the North Atlantic. Most likely, ESPER's type came from Norway, where the species occurs in relatively shallow water, and where it was already known to GUNNERUS (1768). Accordingly, Norway should be considered as the type locality.

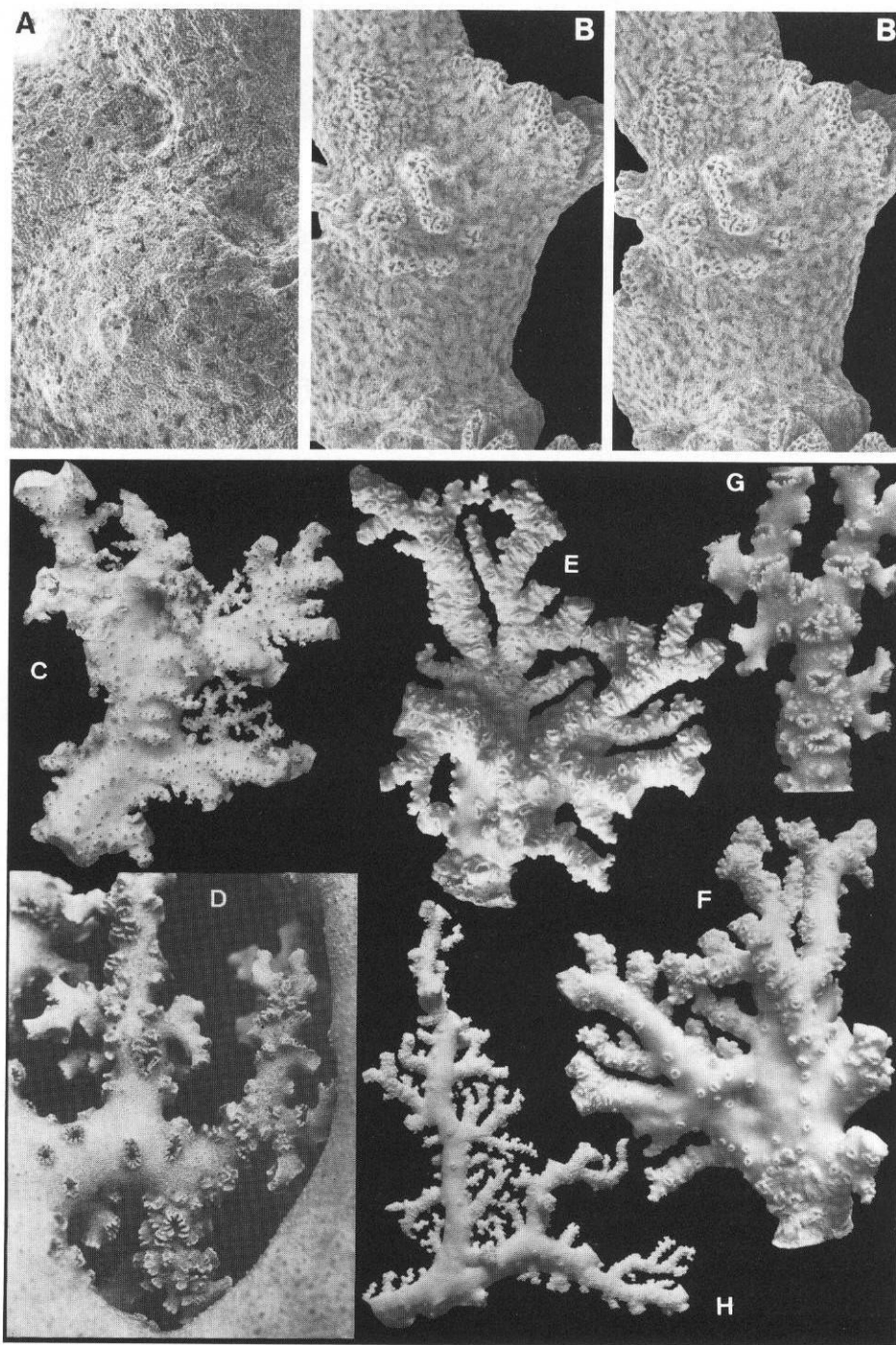


FIG. 23. — *Stylaster gemmascens* (A, from unknown locality, female, USNM 52229; B, from Hardangerfjord, male, USNM 75618; C-D, male holotype, SMF; E-F, from Trondheimsfjord, NHRM 33; G, from Bud, RMNH Coel 15338; H, from Faroes, RSM 1909.191.13): A, female ampulla with efferent pore ($\times 37$); B, male ampulla ($\times 25$, stereo pair); C, massive male colony ($\times 0.6$); D, detail from C illustrating cyclosystem shape and male ampullae covered by papillae ($\times 3.0$); E-F, anterior and posterior faces of colony with crowded stout branches and mostly compressed cyclosystems (both $\times 1.1$); G, branch segment illustrating cyclosystems and male ampullae covered with papillae ($\times 3.0$); H, slender colony ($\times 1.8$).

MATERIAL STUDIED

Denmark Strait: "Ingolf" stn 94, many small branches + fragments, dead (ZMUK). — "Poseidon" stn 12/1, ca. 430 branches + fragments, dead (SMF 6471; USNM 88825); stn 14/1, ca. 70 branches + fragments, dead (SMF 6474; USNM 88828).

Faroës: off Faroës, taken by fishing boat, colony + fragment (RSM 1909.191.3). — "Michael Sars" 1902, stn 43, long line fishing, branch (ZMUK). — "Dana" stn 5835, 3 colonies on pebbles (ZMUK); stn 6005, branch (ZMUK). — "Ingolf" stn 1, 2 branches (ZMUK); stn 2, 2 branches (ZMUK).

Between Faroës and Hebrides: "Porcupine" 1869, stn 54, 4 branches (BMNH 1880.11.13.1-3/7).

Rockall: "Granuaile" 1896, branch + fragment (= *Stylaster sanguineus* sensu THORNELY, 1897; BMNH 1898.6.6.1). — J. CORDEAUX, 2 colonies (BMNH 1898.8.25.1). — "Pisces III" dive 73-5, fragment of a big photographed colony.

Norway: Various old museum specimens of confused origin are likely to come from Norway. Holotype of *Madrepora gemmascens* (SMF). — Colony labeled "Mer des Indes" (MNHN). — Colony labeled "Océan Indien" (RMNH Coel 15806). — Abundant samples in ZMUO and VSM, from many localities along the Norwegian coast, Hjelmsøystauren, Malangen, Steinavaer, Brettesnes/Lofoten, Sklinna, Rodøy, Trondheimsfjord (including Brettingnes, Hysnes, Røberg, Storneset, Tømmerdalen), Mefjordsgrunnen/Beian, Sunde/Trondelag, Kristiansund, Skredness/Sunddalsfjord, Bud, Giske/Sunnmøre, etc. — Trondheimsfjord, KRØYER, colony (NHRM 33). — Rodberg, Trondheimsfjord, ca. 300 m, T. MORTENSEN, 27.7.1911, colonies (ZMUK). — Trondheimsfjord, 40-170 m, 31.8.1961, 10 colonies + branches (RMNH Coel 17414). — Rodberg, Trondheimsfjord, 150-300 m, "Gunnerus", 16.3.1926 (RMNH Coel 15335). — Bud, 200 m, "Gunnerus" 6.7.1931, 3 branches + fragments (RMNH Coel 15338). — Norway, deep water, colony (BMNH 1896.7.31.1). — Trondheimsfjord, 457 m, C. BOVALLIUS, several colonies + branches (BMNH 1891.5.11.1-3). — Rodberg, Trondheimsfjord, A.M. NORMAN, 1893, several colonies (BMNH 1898.5.7.15). — Rodberg, Trondheimsfjord, A.M. NORMAN, 1893 (BMNH 1922.2.2.6b). — Hardangerfjord, A.M. NORMAN, 1879, ca. 20 colonies on pebbles + branches (most BMNH 1910.10.1.71, 1912.11.30.4-6; USNM 75618). — Norway, colony + 2 branches from Univ. Copenhagen (YPM 1358). — Norway, 2 colonies (USNM 15275). — No locality, female colony (USNM 52229).

DESCRIPTION

Colonies uniplanar to slightly bushy (Fig. 23 C, E-F, H), up to at least 11 cm high and wide. Branches cylindrical; branch tips are diameter of terminal cyclosystems. Coenosteum white to light yellow, reticulate-granular in texture (Fig. 24 C-E). Coenosteal strips uniformly 75-85 µm wide and covered with granules irregular in size and shape, producing a rough texture. Coenosteal papillae (specialized nematocyst structures?) common on some specimens, particularly around ampullae (Fig. 23 B, G). Papillae cylindrical or carinate: up to 0.8 mm long, 0.2-0.4 mm high, and about 0.10 mm wide.

Cyclosystems occur primarily on lateral edges of distal branches in a sympodial manner, but on larger diameter branches they occur with greater frequency on anterior and posterior branch faces (Fig. 23 C-F). Cyclosystems circular to irregular in shape, some quite compressed: circular cyclosystems about 1.3 mm in diameter; a compressed

cyclosystem might measure 1.6 x 0.7 mm. Proximal dactylopores of cyclosystem project up to 0.8 mm, whereas distal dactylopores usually flush with coenosteum, tending to give the cyclosystem a proximal orientation. Based on 100 cyclosystems examined from the holotype, BOSCHMA (1955) found a range of 6-15 dactylopores per cyclosystem, mean 10.19, and mode 10. Based on 71 cyclosystems examined from five other localities, we found a range of 7-17 dactylopores per cyclosystem, mean 11.76, and mode 12. BOSCHMA's slightly lower average and range may be attributable to his counting cyclosystems in which the distal dactylopores had become obsolete (diastema).

Lower gastropore chamber narrow and cylindrical, about 0.30 mm in diameter, which gives the cyclosystem a flared aspect. Diffuse ring

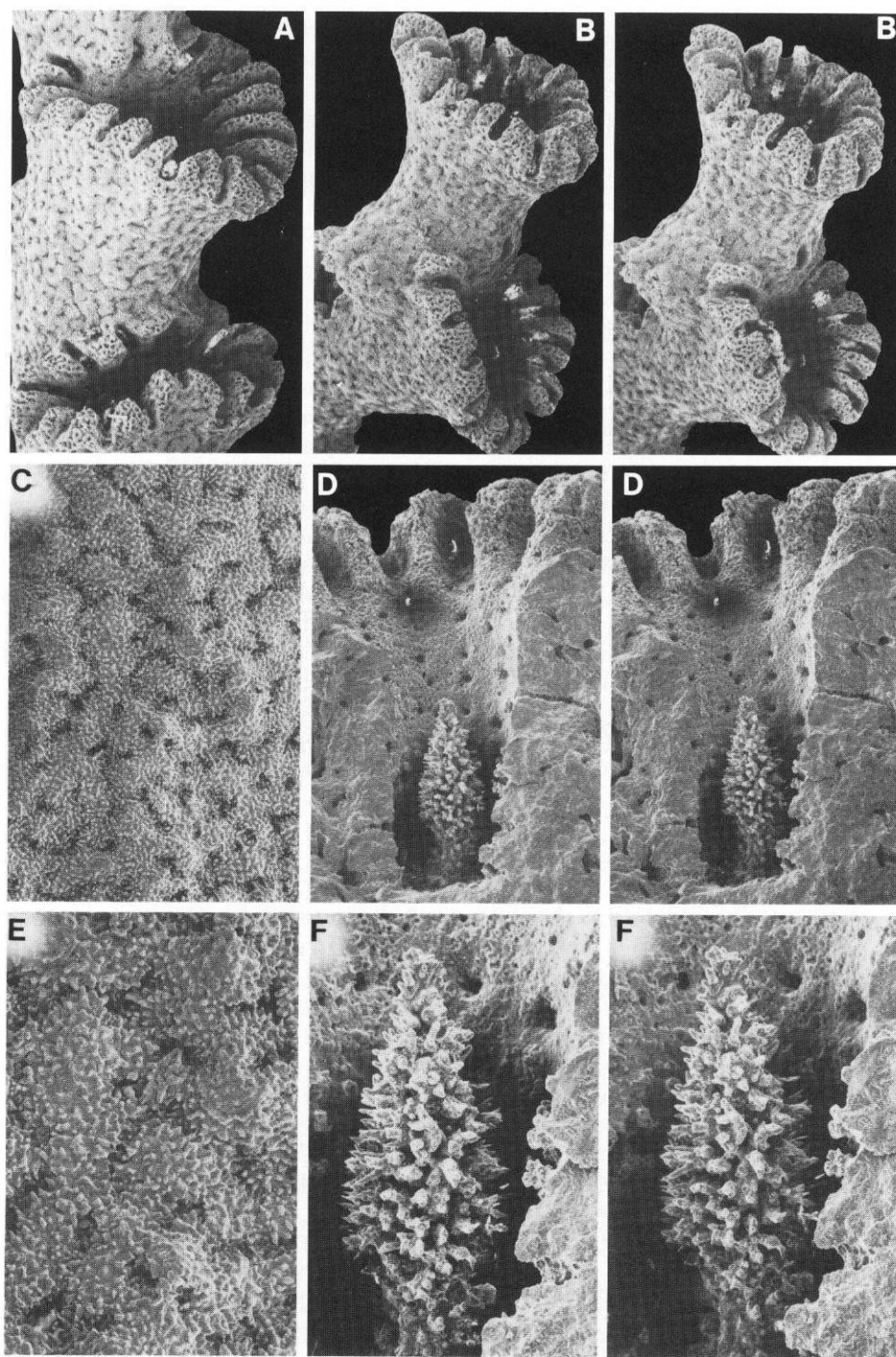


FIG. 24. — *Styaster gemmascens* (A-C, E, from Hardangerfjord, male, USNM 75618; D, F, from unknown locality, female, USNM 52229): A-B, cyclosystems ($\times 24$, $\times 21$, respectively, B being a stereo pair); C, E, coenosteal texture ($\times 65$, $\times 128$, respectively); D, F, gastropore tube and ring palisade ($\times 45$, $\times 112$, respectively, both being stereo pairs).

palisade present at mid-gastrostyle level, composed of elements about 30 μm in height and diameter. Gastrostyle lanceolate; figured style (Fig. 24 D-E) 0.56 mm high and 0.15 mm in diameter (H:W = 3.7). BOSCHMA (1955) illustrated 15 gastrostyles with H:W ratios ranging from 1.9 to 4.7. Gastrostyles not ridged but bear sharply pointed spines up to 42 μm long. Dactylostyles about 84 μm wide; pseudosepta one to three times width of dactylostome. Dactylostyle

rudimentary, composed of a single line of blunt cylindrical elements up to 57 μm high and 11 μm in diameter.

Female ampullae superficial hemispheres (Fig. 24 A) 0.7-0.9 mm in diameter, each with a large efferent pore about 0.24 mm in diameter. Male ampullae also superficial, 0.65-0.75 mm in diameter, often covered by 1-5 papillae or carinae (Fig. 24 B). Male efferent pore not observed.

COMPARISONS

S. gemmascens is one of the most easily distinguished eastern Atlantic *Stylaster*, characterized by a rough coenosteal texture, flared cyclostyles, narrow gastropore tubes, and carinate male ampullae (Table 2).

REMARKS

As pointed out by BROCH (1918), *S. gemmascens* had been well characterized by GUNNERUS (1768) from material from Norway but had been referred to the scleractinian *Madrepora virginea* (Linnaeus, 1758). Figures from GUNNERUS were reproduced by BROCH (1918). The same stylasterid species was again recognizably figured and described by ESPER (1790/1794) as *Madrepora gemmascens* from material said to come from the East Indian Sea (description and figures reproduced by BOSCHMA, 1955a). *S. gemmascens* was then reported from the North Atlantic, starting with SAVILLE KENT (1871), DUNCAN (1873), and SARS (1873). It was often mentioned in papers on the fauna of Norway. Although ESPER's name *gemmascens* was thus in common use for the North Atlantic stylasterid, it became available only by suppression of the senior homonym, *Madrepora gemmascens* Wilkens, 1787, for a scleractinian (BOSCHMA, 1955a, 1958; International commission on zoological nomenclature, 1959: opinion No. 574).

In the northern Atlantic, *S. gemmascens* has occasionally been confused with other species. Material from between the Faroes and the Hebrides reported by DUNCAN, first (1870) as *Allopora oculina*, and later (1873) as *Stylaster gemmascens*, proved to be a mixture of 4 species: *S. gemmascens*, *S. norvegicus*, *S. erubescens britannicus*, and *Stenohelia maderensis*. *Stylaster sanguineus* sensu THORNELY (1897), from Rockall Bank, proved to be *S. gemmascens*; the true *S. sanguineus* Milne Edwards & Haime, 1850, with a pink skeleton, is confined to the southwestern Pacific (ZIBROWIUS, 1981).

S. gemmascens and *S. norvegicus* frequently occur together and have not always been properly distinguished; many lots in museum collections under one or the other name have proved to be a mixture of both species.

The fact that *S. gemmascens* had been reported, first (mistakenly) from the East Indian Sea and then recognized in the northern Atlantic, encouraged other authors to accept its wide geographic range, and to uncritically refer somewhat similar forms from other areas to the same species.

The North Pacific *S. gemmascens alaskanus* Fisher, 1938, first reported from the Aleutian and subsequently from the Kurile Islands (NAUMOV, 1960), should not be considered as *S. gemmascens*. CAIRNS (1983b: 430) listed it as a distinct species, *S. alakanus*, in Group C (and not Group B) within the genus *Stylaster*.

S. gemmascens sensu HICKSON & ENGLAND (1905), from the Sulu Islands (southern Philippines), is also different (ZMA Coel 7386). The insufficiently known *S. cf. gemmascens* sensu EGUCHI (1941) from Japan is also undoubtedly misidentified.

DISTRIBUTION AND ECOLOGY

S. gemmascens is known from a wide area in the North Atlantic, from Denmark Strait east of Greenland (off Angmagssalik) and northwest of Iceland through the Faroes – Hebrides area to Norway and Rockall. The occurrence in Icelandic waters is here reported based on BROCH (1914a); from all other areas material was available for the present study. The species is new for eastern Greenland. The northernmost records are 66°18'N in Denmark Strait, and 71°07'N in Finmark, Norway.

Along the Norwegian coast the species is common in depths of about 40 m to 400 m, frequently found together with the bankforming scleractinian *Lophelia pertusa*. Elsewhere, the species has been collected down to 621 m northwest of Iceland, and at 665 m between the Faroes and Hebrides. On Rockall Bank large colonies have been photographed and collected by the submersible “*Pisces III*” in depths of 160-190 m.

No symbionts are known.

Stylaster ibericus new species

Fig. 25 A-O, 26 A-G

TYPES

All available specimens from seven closely adjacent stations of northwestern Spain are given type status: “*Thalassa*” stn U-807, 2 colonies fused at the base; stn Y-428, 4 encrusting bases of colonies; stn Y-430, 21 colonies + 10 branches + fragments; stn Y-431, branch; stn Y-432, colony + 3 branches; stn Y-438, dead branch; stn Y-440, 28 colonies, branches, fragments, mostly dead. A rather complete fan-shaped colony 30 mm high and 42 mm wide from stn Y-430 is designated holotype (Fig. 25 H), all other specimens from stn Y-430 and the other stations paratypes. Holotype and most paratypes at MNHN, 4 paratypes from stn Y-430 at USNM (75619).

Type locality: “*Thalassa*” stn Y-430, 4.9.1972, 44°1.6'N, 8°40.6'W, 500 m. Off northwestern Spain.

MATERIAL STUDIED

NW Spain: Holotype and paratypes (see above).

DESCRIPTION

Colonies uniplanar, up to 40 mm high and wide (Fig. 25 F-H, L-O). Branches cylindrical, about 1.5 mm in distal branch diameter. Coenosteum glistening white. Coenosteal texture smooth, resulting from a reticulate-granular coenosteum with very few low granules, each about 11 μ m in diameter. As in *S. norvegicus*, some colonies show a transition of coenosteal textures from coarse, disjointed granules (Fig. 26 D) to a smooth, almost porcelaneous coenosteum (Fig. 26 C). Coenosteal strips 45-95 μ m wide.

Cyclosystems circular to slightly elliptical, 0.8-1.1 mm in diameter, occurring primarily on lateral to anterolateral branch edges. Occasionally some cyclosystems occur on anterior face

and, more rarely, posterior face. Cyclosystems all slightly exsert, extending about 0.4 mm above coenosteum. Based on 685 cyclosystems, there is a range of 4-11 dactylopores per cyclosystem, mean 7.71, and mode 8. These data include the single branch from stn Y-438 which has many cyclosystems with a low number of dactylopores: based on 70 cyclosystems, its range is 4-8, mean 6.00, and mode 6. There are no diastemas.

Gastrostyle occupies lower half of gastropore chamber, which is constricted at level of gastrostyle tip (Fig. 26 E). Gastrostyle ovate and sharply pointed, its widest section being at mid-height, caused by the perpendicular projection of very long spines. Illustrated style (Fig. 26

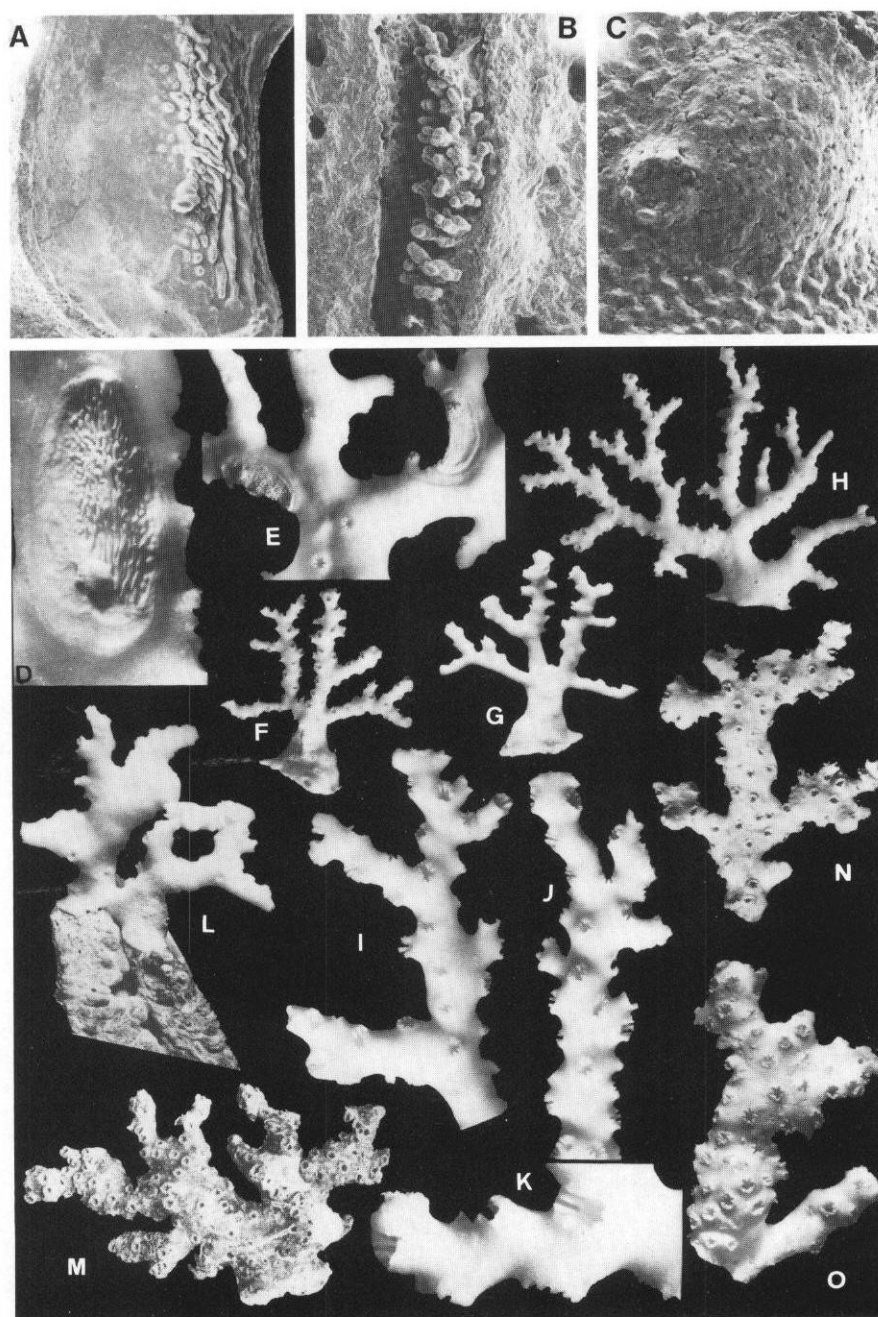


FIG. 25. — *Stylaster ibericus* (A-B, paratype from "Thalassa" Y-430, male, USNM 75619; C, paratype from "Thalassa" Y-440, female, MNHN; D-K, from "Thalassa" Y-430, MNHN; L, from "Thalassa" U-807, MNHN; M-N, from "Thalassa" Y-440, MNHN; O, from "Thalassa" Y-438, MNHN): A, *Pedicularia* trace ($\times 13$); B, dactylostyle ($\times 125$); C, female ampulla and efferent pore ($\times 39$); D, *Pedicularia* trace ($\times 6.8$); E, detail of paratype with two *Pedicularia* traces ($\times 2.5$); F-G, opposite views of paratype, *Pedicularia* trace near the base (both $\times 1.1$); H, holotype ($\times 1.1$); I-K, branches of holotype showing sympodial arrangement of cyclosystems ($\times 3.0$, $\times 3.1$, $\times 4.9$ respectively); L, two paratypes on cirriped shell, next to base of right colony some very young stages consisting of a single cyclosystem ($\times 1.9$); M-N, stouter dead paratype ($\times 1.3$, $\times 1.5$, respectively); O, stouter dead paratype characterized by cyclosystems with low dactylopore number ($\times 2.1$).

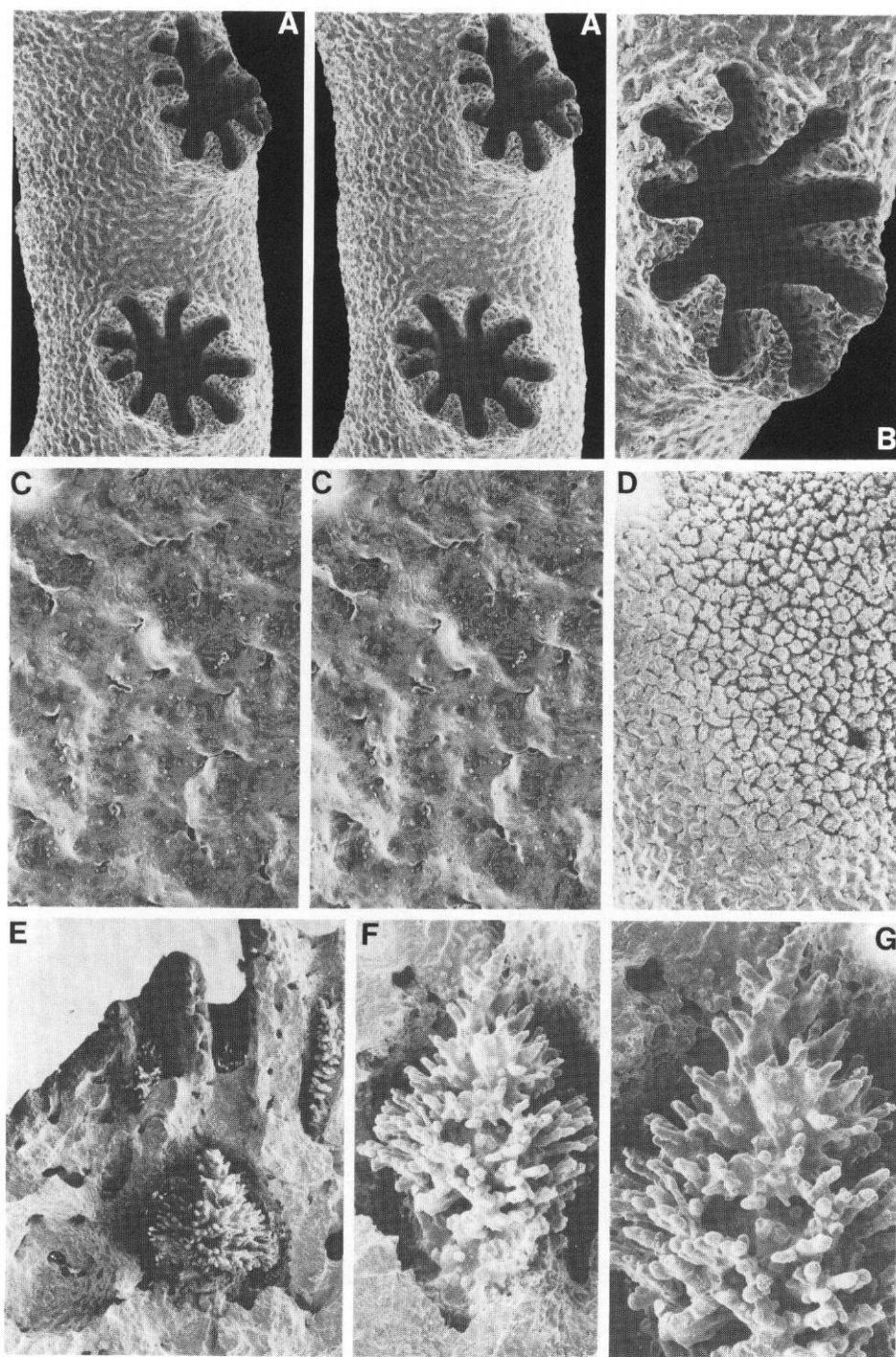


FIG. 26. — *Styaster ibericus* (A-G, paratype from "Thalassa" Y-430, male, USNM 75619): A, branch segment with two cyclosystems ($\times 21$); B, cyclosystem ($\times 43$); C, coenosteal texture ($\times 141$, stereo pair); D, transitional coenosteal texture ($\times 30$); E, fractured cyclosystem revealing gastrostyle, dactylostyle, and internal male ampulla ($\times 54$); F-G, gastrostyle ($\times 106$, $\times 165$, respectively).

F-G) 0.46 mm high and 0.24 mm in diameter (H:W = 1.9); another style with H:W = 1.3. Gastrostyle spines cylindrical and blunt, up to 60 μ m long and 11 μ m in diameter. Spines often laterally fused into transverse or oblique tiers. Gastrostyle not ridged. Dactylotomes about 0.12 mm wide. Dactylostyles robust, composed of blunt, cylindrical elements up to 50 μ m tall and 15 μ m in diameter. Dactylostyle elements basally

fused and occur 3 or 4 across the width of dactylostyle (Fig. 26 B).

Male ampullae internal, about 0.5 mm in internal diameter. Male efferent pores small concavities about 0.15 mm in diameter. Female ampullae elongate and very low in relief (0.75-1.0 mm in diameter and about 0.25 mm tall); efferent pore about 0.18 mm in diameter, lateral in position but inclined upward (Fig. 25 B).

COMPARISONS

S. ibericus is similar to *S. erubescens britannicus*, particularly regarding cyclosystem diameter, gastro- and dactylostyle morphology, and internal male ampullae. These are the only two eastern Atlantic taxa of *Stylaster* known to have internal male ampullae. *S. ibericus* is distinguished by its smooth, porcellaneous coenosteum; higher average number of dactylopores per cyclosystem (9.34 versus 7.71), and normally shaped pseudosepta (Table 2).

REMARKS

The specific name given to the new species refers to its geographic distribution.

DISTRIBUTION AND ECOLOGY

S. ibericus is known from 7 closely adjacent dredging stations in the La Coruña area, northwestern Spain. The species lives solidly attached to big boulders apparently exposed to bottom currents (no sediment in dredge).

SYMBIONTS

Specimens of *Pedicularia* have been found on live colonies of *S. ibericus* from 2 stations ("Thalassa" stn Y-430, Y-432). Dead branches from a third station (Y-440) also show typical *Pedicularia* traces (Fig. 25 D, 26 D).

Stylaster erubescens Pourtalès, 1868

Material from the study area identified as *S. erubescens* differs in several aspects from specimens of the nominotypical western Atlantic form (north to North Carolina) previously described by CAIRNS (1986a). Largely a matter of degree, these differences appear insufficient to justify the description of distinct species; accordingly, these geographically nonoverlapping forms are presented here as subspecies of *S. erubescens*: *groenlandicus* n. ssp., *britannicus* n. ssp., and *meteorensis* n. ssp., the western Atlantic nominotypical subspecies being *S. erubescens erubescens*.

Stylaster erubescens erubescens Pourtalès, 1868

Synonymy:

Stylaster erubescens Pourtalès, 1868: 135-136.

Chresonymy:

Stylaster erubescens: POURTALÈS, 1871: 34, pl. 4, fig. 10-11; 1878: 210. — BROCH, 1914a: 12 (only in synonymy of *Stylaster roseus*). — BOSCHMA, 1955b: 135-138 (part: NOT North Atlantic); 1957a: 8 (part: NOT

North Atlantic); 1965c: 235-236, 245-247, pl. 4, fig. 1-4 (part: NOT North Atlantic). — ZIBROWIUS & CAIRNS, 1982: 210, 212 (part: NOT East and North Atlantic). — CAIRNS, 1983b: 430; 1986a: 58-61, fig. 26A-H (part: NOT Northeast Atlantic).

TYPES

Stylaster erubescens: In the original description (POURTALES, 1868) the species is qualified as "rather common between 120 and 324 fathoms [220-592 m] off the Florida reef" (area known as Pourtales Terrace); this information was reiterated in a later publication (POURTALES, 1871). Types were not specially designated. According to CAIRNS (1986a), there is only one larger syntype (fan-shaped colony about 80 mm high, 117 mm wide) at the MCZ, with data corresponding to the 1868 description (Florida, 120-324 fathoms). He also recognized additional syntype branches at USNM (71822), YPM, and RMNH. Five branches at BMNH (1869.10.25.11, 1891.2.4.15, 1894.12.22.6) also deserve syntype status.

Type locality: Pourtales Terrace (Florida), 220-592 m.

MATERIAL STUDIED

For western Atlantic material north to North Carolina see CAIRNS (1986a).

DESCRIPTION

See CAIRNS (1986a), description based on the western Atlantic nominotypical subspecies.

COMPARISONS

See Table 2 and Comparisons of the 3 new subspecies.

REMARKS

BROCH (1914a) incorrectly included *S. erubescens* as a synonym of *S. roseus* (Pallas, 1766). As already demonstrated by BOSCHMA (1955b, 1957a, 1965c), *S. erubescens* and *S. roseus* are distinct species. The latter (redescribed by CAIRNS, 1986a), is primarily a shallow-water species widespread throughout the Caribbean and ranging south to Brazil.

S. erubescens has been mistakenly reported by early authors from beyond the confirmed range of its four subspecies presently known in the northwestern and northeastern Atlantic: by MOSELEY (1876b: 94) from "Challenger" stn 320 in the southwestern Atlantic (subsequently described as a distinct species, *S. densicaulis* Moseley, 1879; redescribed by CAIRNS, 1983a; types BMNH 1880.11.25.175/199); by THOMSON (1877: vol. 2, 267) from "Challenger" stn 344 off Ascension Island (mentioned by MOSELEY, 1879: 450; 1881: 58) as *S. granulata* (*nomen nudum*; material not at BMNH); and by MOSELEY (1881: 81) from "Challenger" stn 170 off the Kermadec Islands (in reality *Conopora verrucosa* (Studer, 1878), BMNH 1880.11.25.178).

DISTRIBUTION AND ECOLOGY

S. erubescens (nominotypical subspecies *erubescens*) was known to POURTALES (1868, 1871, 1878) exclusively from off southeastern Florida. CAIRNS (1986a) provided a station list for this form that he qualified as the most commonly collected stylasterid of the western Atlantic. The distribution was given as comprising the continental shelf and slope of the southeastern United States, from the Blake Plateau off South Carolina to off southwestern Florida, and extending to Little Bahama Bank, Cay Sal Bank, and Arrowsmith Bank off Yucatan Peninsula, depth 146-965 m, but most common at 650-850 m.

SYMBIONTS

In the western Atlantic *S. erubescens erubescens* is one of the rare stylasterids known as the host of *Pedicularia*; traces have been found on material from one of the northern localities ("Albatross" stn 2416, off Georgia, 505 m; USNM 10542).

In the western Atlantic, CAIRNS (1986a) found about half of the colonies with gall-tubes induced by a polynoid polychaete, an association first noticed by POURTALES (1869).

Stylaster erubescens groenlandicus new subspecies

Fig. 27 A-H, 28 A-H

Chresonymy:

Stylaster roseus — BROCH, 1914a: 12-15, pl. 1, fig. 8-9, pl. 2, fig. 10, 11, 17, pl. 3, fig. 22, pl. 4, fig. 36, 39, pl. 5, fig. 43, 47-48 (part); 1936: 15.

Stylaster erubescens — BOSCHMA, 1955b: 135-138 (part: North Atlantic); 1957a: 8 (part: North Atlantic); 1965c: 236, 246 (part: North Atlantic). — ZIBROWIUS & CAIRNS, 1982: 212 (part: East and North Atlantic). — CAIRNS, 1986a: 61 (part: Northeast Atlantic).

TYPES

Most available material from Greenland through Denmark Strait ("Poseidon" excepted) to southeast of Iceland is given type status: a male colony 61 mm high and 40 mm wide from "Ingolf" stn 15 is designated holotype (Fig. 27 C), all other specimens from "Ingolf" stn 15 and various other stations paratypes (see Material studied). Holotype deposited at ZMUK, together with most paratypes from type locality.

Type locality: "Ingolf" stn 15, 4.6.1895, 66°18'N, 25°59'W, 621m. Denmark Strait, northwest of Iceland.

MATERIAL STUDIED

Denmark Strait and Greenland: "Ingolf" stn 15, 18 colonies + 26 branches + numerous fragments (holotype + paratypes, ZMUK, USNM 77123); stn 16, 2 branches (paratypes ZMUK). — East Greenland Expedition 1900, off Angmagssalik, 263 m, 5 colonies + 2 branches (paratypes, ZMUK, USNM 77122). — "Walther Herwig" stn 538-24, 2 male branches (paratypes, IMFB). "Vema" stn v17/RD-29, 7 colonies + 5 branches + fragments, male + female (paratypes, USNM 60004). — "Poseidon" stn 12/1, ca. 260 branches + fragments, most dead, only one alive (SMF 6472; USNM 88826); stn 14/1, ca. 50 branches + fragments, dead (SMF 6475; USNM 88829).

Iceland: "Ingolf" stn 7, 2 colonies + 7 branches (paratypes, ZMUK); stn 52, 16 branches (paratypes, ZMUK). — "Bartlett" 1975, stn 52C-5, male branch (paratype, USNM 60005).

DESCRIPTION

Colonies uniplanar (Fig. 27 A, C), up to 80 mm high with a basal diameter of 7 mm (East Greenland expd. specimens); branches sometimes thickened (Fig. 27 C) as in nominotypical subspecies but evidence of polynoid symbiont not observed. Coenosteum white and reticulate-granular in texture (Fig. 28 D). Strips 70-90 μ m wide and fairly continuous, covered with small rounded granules 8-10 μ m in diameter.

Cyclosystems primarily on lateral and antero-

lateral branch edges but some occasionally on anterior and posterior branch faces. Cyclosystems circular to slightly elliptical in shape, 1.2-1.4 mm in diameter (Fig. 28 A-B). Based on 175 cyclosystems, there is a range of 5-15 dactylopores per cyclosystem, mean 10.15, and mode 10.

Gastrostyle conical (Fig. 28 E-F), about 0.50 mm tall and 0.25 mm wide in greatest width, with H:W ratios around 2. Style covered with blunt, cylindrical spines about 40 μ m long and 15

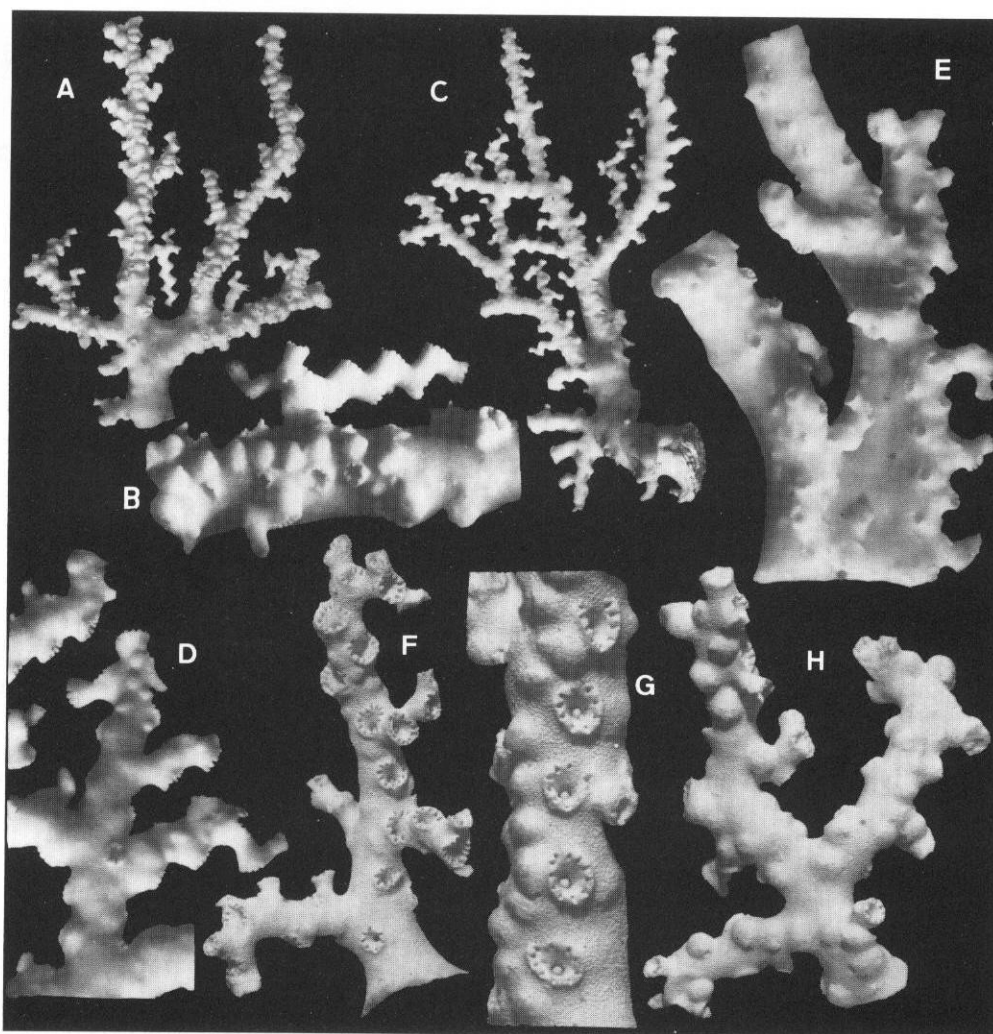


FIG. 27. — *Styaster erubescens groenlandicus* (A-D, from "Ingolf" stn 15, ZMUK; E, from "Bartlett" 1975, 52C-5, USNM 60005; F-H, from "Vema" v17/RD-29, USNM 60004): A, female paratype with abundant clustered ampullae ($\times 1.0$); B, detail of A illustrating large female ampullae ($\times 3.2$); C, male holotype ($\times 1.0$); D, detail of holotype illustrating small male ampullae ($\times 3.2$); E, male paratype with particularly thickened branches ($\times 2.1$); F, male paratype ($\times 2.9$); G, detail of female paratype illustrating large ampullae and gastrostyles in depth of cyclosystems ($\times 4.3$); H, female paratype with large ampullae ($\times 3.0$).

μm in diameter, the bases of which are fused into transverse or oblique tiers as in *S. norvegicus* and *S. ibericus*. Dactylotomes about 0.12 mm wide; dactylostyles robust. Pseudosepta usually equal to dactylotomes width (Fig. 28 G). Diastemas present on cyclosystems positioned at branch axils (Fig. 28 C) and on larger diameter branches.

Female ampullae large superficial hemispheres (Fig. 27 B, 28 C) 1.0-1.3 mm in diameter, sometimes with a short lateral efferent tube.

Female efferent pore about 0.20-0.25 mm in diameter; binary ampullae sometimes present. Male ampullae (Fig. 27 D, 28 H) superficial mounds 0.7-0.8 mm in diameter, becoming internal on large diameter branches. Male efferent pore circular, 80-90 μm in diameter, and located laterally (Fig. 27 D, 28 H), not apically. Both genders of ampullae often densely clustered, especially the males, on anterior and posterior branch faces (Fig. 27 A-H).

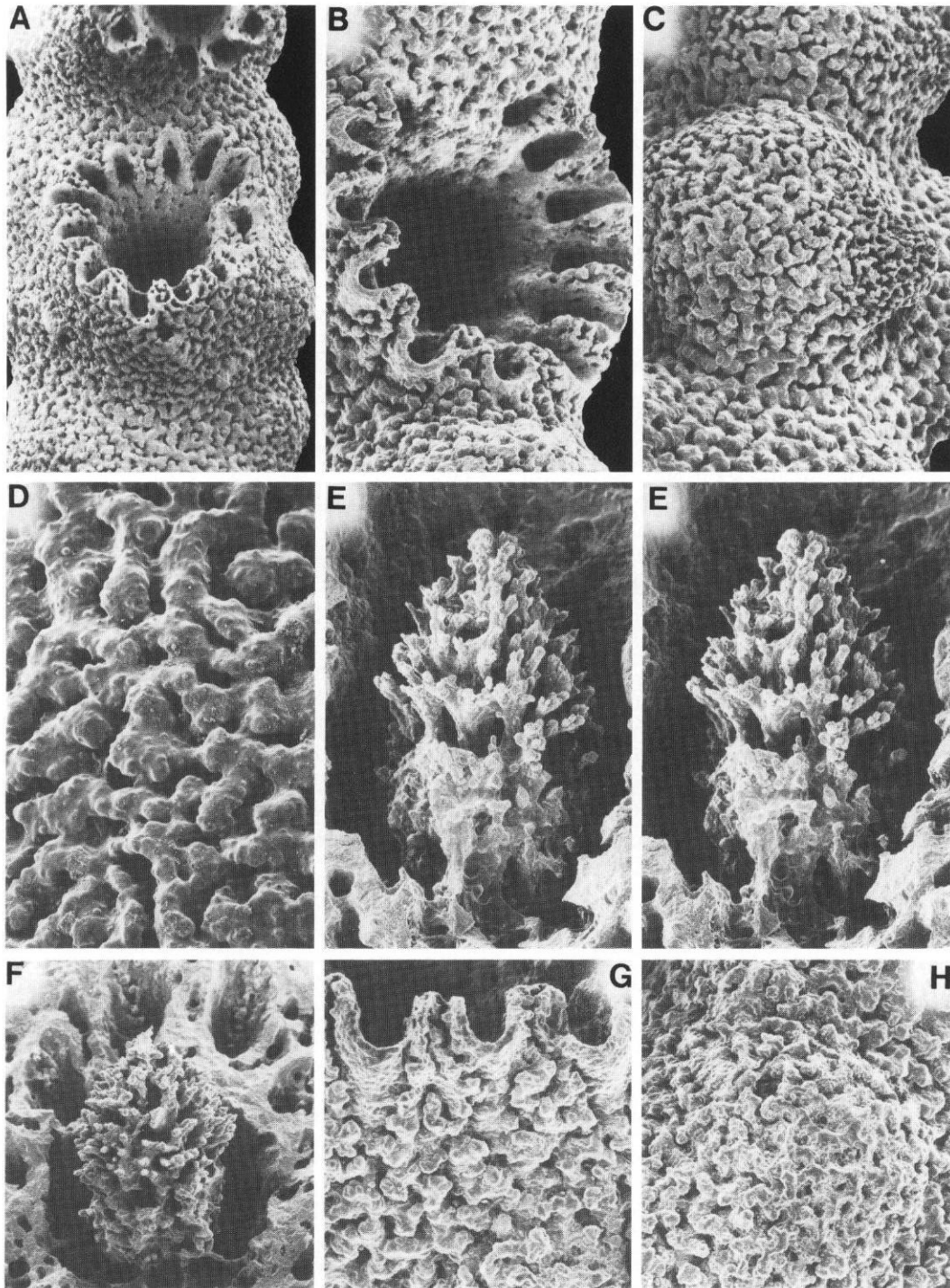


FIG. 28. — *Stylaster erubescens groenlandicus* (A-B, E-H, male paratype from "Ingolf" stn 15, ZMUK; C-D, female paratype from "Ingolf" stn 15, ZMUK): A-B, cyclosystem ($\times 24$, $\times 41$, respectively); C, female ampulla and efferent tube ($\times 33$); D, coenosteal texture ($\times 92$); E, gastrostyle ($\times 116$, stereo pair); F, gastrostyle surrounded by damaged dactylostyles ($\times 69$); G, outer edges of pseudosepta, coenosteal texture ($\times 56$); H, male ampulla with efferent pore ($\times 56$).

COMPARISONS

S. erubescens groenlandicus is clearly most similar to the nominotypical subspecies, both having the same coenosteal texture, thickened branches, and relatively large cyclosystems (Table 2). Their differences are largely a matter of degree: *S. erubescens groenlandicus* has a slightly lower average number of dactylopores per cyclosystem, a higher gastrostyle H:W ratio, and larger ampullae of both sexes. One qualitative difference concerns the male efferent pores, which are lateral in *S. erubescens groenlandicus* and apical in *S. erubescens erubescens*.

S. erubescens groenlandicus can be distinguished from the other two subspecies on the basis of coenosteal texture, cyclosystem diameter, gastrostyle shape, and ampullar position and size (Table 2).

REMARKS

The name given to the new subspecies refers to its geographic distribution.

BROCH (1914a) was the first to report corals referable to *S. erubescens groenlandicus* from the northern Atlantic (specimens from 3 stations figured), but he incorrectly included *S. erubescens* as a synonym of *S. roseus* (Pallas, 1766). BOSCHMA (1955b, 1957a, 1965c) corrected this identification to *S. erubescens*, but did not examine BROCH's material.

Material mentioned by BROCH (1914a) from 3 stations between Greenland and Iceland ("Ingolf" stn 17, 94; "Thor" 1904) was not available for the present study; most likely this was ssp. *groenlandicus*, also obtained from other stations in the same area.

DISTRIBUTION AND ECOLOGY

S. erubescens groenlandicus is separated from the nominotypical subspecies by a broad geographic hiatus extending from South Carolina (32°24'N) to Greenland (60°27'N). It is geographically nearest to *S. erubescens britannicus* which extends north to southeast of Iceland.

BROCH (1914a) reported *S. erubescens groenlandicus* (misidentified as *S. roseus*) from 7 stations (mainly "Ingolf") in the North Atlantic, from east of Greenland to northwest and southeast of Iceland, all north of 60°N. We have seen additional material of the same form from 6 stations. BROCH's data combined with ours cover a depth range from 263 m to 1440 m. The northernmost record is 66°18'N in Denmark Strait, northwest of Iceland.

No symbionts are known.

Stylaster erubescens britannicus new subspecies

Fig. 29 A-G, 30 A-G

Chresonymy:

Allopora oculina — DUNCAN, 1870: 90, 95 (part).

Stylaster gemmascens — DUNCAN, 1873: 322 (part), pl. 49, fig. 8-10.

Stylaster erubescens — WILSON, 1979: 157. — ZIBROWIUS & CAIRNS, 1982: 212 (part: East and North Atlantic). — CAIRNS, 1986a: 61 (part: Northeast Atlantic).

TYPES

All available material (except "Dana" stn 6001) from southeast of Iceland through Rockall Trough to the Celtic Sea is given type status: a female specimen (17 mm high, 24 mm wide) collected by C. WANDEL, SE Iceland, is designated holotype (Fig. 29 A), all other specimens from the same and various other stations paratypes (see material studied). Holotype deposited at ZMUK, together with most paratypes from type locality.

Type locality: 64°16'N, 11°15'W, 350 m, C. WANDEL, 19.9.1891. Southeast of Iceland.