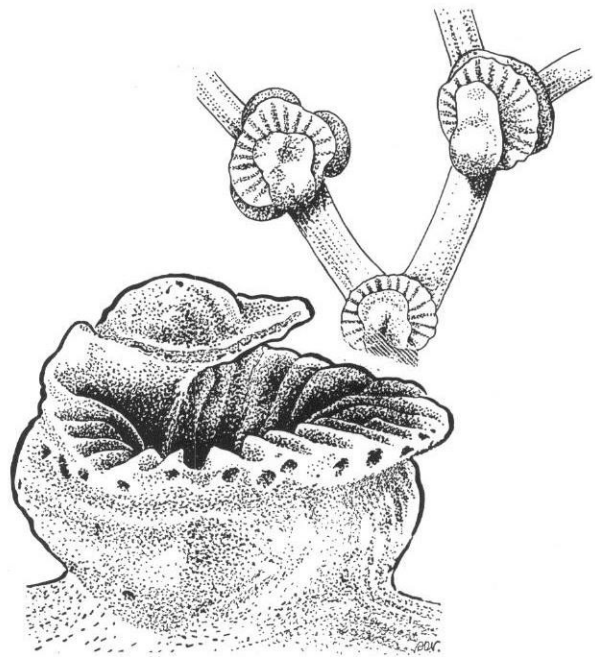


*Revision of the northeast Atlantic
and Mediterranean Stylasteridae
(Cnidaria: Hydrozoa)*



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ABSTRACT

ZIBROWIUS H. & S. D. CAIRNS, 1992. *REVISION OF THE NORTHEAST ATLANTIC AND MEDITERRANEAN STYLASTERIDAE (CNIDARIA: HYDROZOA)*. *Mém. Mus. natn. Hist. nat.*, (A), **153**: 1-136. Paris ISBN: 2-85653-192-X.
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In the northeastern Atlantic, from the Cape Verde Islands to the Mid-Atlantic Ridge at 23°31'N, the Azores, Iceland and northern Scandinavia, 19 species of stylasterids have been recognized, one of which is represented by 3 subspecies. Complementary records extend the study area to Greenland. In addition, 2 species are included from the islands of the Gulf of Guinea, equatorial eastern Atlantic. Of all these species and subspecies, 20 are fully described whereas 3 that are incompletely known, are not yet named. The new taxa are: *Pliobothrus gracilis* n. sp., *Stylaster maroccanus* n. sp., *S. ibericus* n. sp., *S. erubescens groenlandicus* n. ssp., *S. erubescens britannicus* n. ssp., *S. erubescens meteorensis* n. ssp., *Cryptelia medioatlantica* n. sp., and *C. vascomarquesi* n. sp.

Compared with the scleractinian corals present in the same areas, most of the studied stylasterid species appear to have a rather narrow geographical range. Only 3 of the 21 species (15 %) recorded from the

northeastern and equatorial eastern Atlantic are known in the western Atlantic.

Although covering a much wider area, the northeastern Atlantic stylasterid fauna is considerably less diversified than its West Indian counterpart, which comprises about twice as many species in 8 genera. Among the northeastern Atlantic regional faunas, that of the Azores is the richest, with 9 deep-water species. Only one species (*Errina aspera*) occurs in the southwestern Mediterranean.

Although present in the islands of the Gulf of Guinea, shallow-water stylasterids are missing in the northeastern Atlantic and Mediterranean where the shallowest records are from about 100 m. A few records exceed depths of 2000 m.

In the study area various symbionts leave characteristic traces on the stylasterid skeleton or cause modifications: the gastropod genus *Pedicularia* (on 8 species) and polynoid and eunicid polychaetes (each on one species).

The reliable record of fossil stylasterids is scarce in Europe and the Mediterranean basin (as it is elsewhere). It ranges from the Lower Paleocene to the Plio-Pleistocene whereas *Pedicularia*, an obligate symbiont of stylasterids, is known from the Messinian (Upper Miocene) and from the Lower Pleistocene.

RÉSUMÉ

ZIBROWIUS H. & S. D. CAIRNS, 1992. *REVISION OF THE NORTHEAST ATLANTIC AND MEDITERRANEAN STYLASTERIDAE (CNIDARIA: HYDROZOA)*. *Mém. Mus. natn. Hist. nat.*, (A), **153**: 1-136. Paris ISBN: 2-85653-192-X. Publié le 20 Mars 1992.

Révision des Stylasteridae de l'Atlantique nord-oriental et de la Méditerranée. Dans l'Atlantique nord-oriental, des îles du Cap-Vert à la dorsale Médio-Atlantique par 23°31'N, aux Açores, à l'Islande et au nord de la Scandinavie, 19 espèces de Stylasteridae ont été reconnues, dont une représentée par 3 sous-espèces. Des signalisations complémentaires étendent la zone étudiée jusqu'au Groenland. En plus, sont incluses ici 2 espèces des îles du golfe de Guinée, Atlantique équatorial oriental. De toutes ces espèces et sous-espèces, 20 sont décrites en détail tandis que 3 autres, incomplètement connues, n'ont pas encore reçu de nom. Les nouveaux taxa sont: *Pliobothrus gracilis* n. sp., *Stylaster maroccanus* n. sp., *S. ibericus* n. sp., *S. erubescens groenlandicus* n. ssp., *S. erubescens britannicus* n. ssp., *S. erubescens meteorensis* n. ssp., *Cryptohelia medioatlantica* n. sp., *C. vascomarquesi* n. sp.

Les auteurs du 18^e siècle connaissaient trois espèces: deux en provenance des fjords de Norvège, et une obtenue en Méditerranée par les pêcheurs du corail rouge. Avant la fin du 19^e siècle, du matériel de la plupart des espèces avait été récolté, y compris par les expéditions du "Challenger", du "Talisman" et du Prince de Monaco. Mais au-delà de notes dispersées (dont notamment celles de H. BOSCHMA) à propos de quelques espèces, l'ensemble de cette faune n'avait jamais été l'objet d'une synthèse. Trois espèces avaient même été décrites à titre de bryozoaires ("Hornera").

La synthèse présentée ici s'appuie aussi sur de nombreuses campagnes océanographiques plus récentes (y compris des prélèvements par submersibles), telles que les campagnes BIAÇORES, BALGIM, SEAMOUNT 1, HYDROSLAKE et celles de la "Thalassa".

Pour la plupart, les espèces étudiées semblent avoir une répartition géographique assez étroite, comparé à celle des scléractiniaires présents dans les mêmes zones. Seulement 3 espèces sur 21 (15 %) inventoriées dans l'Atlantique nord-oriental et équatorial oriental sont connues aussi dans l'Atlantique occidental. Aucune de ces espèces atlantiques ne semble exister dans les autres océans. Tout comme les scléractiniaires, les Stylasteridae sont absents au-delà de la périphérie du bassin arctique, ce qui contraste avec la diversité des deux groupes dans l'océan Antarctique aux conditions plus stables depuis des millions d'années.

La faune de Stylasteridae de l'Atlantique nord-

oriental est considérablement moins diversifiée que celle de l'Atlantique tropical américain qui comprend environ deux fois plus d'espèces dans 8 genres. Parmi les faunes régionales, celle des Açores est la plus riche, avec 9 espèces de profondeur. Une seule espèce (*Errina aspera*) vit dans la Méditerranée et y est limitée à la partie sud-occidentale. Elle est typique de fonds rocheux exposés à de forts courants (détroit de Messine, détroit de Gibraltar).

Des Stylasteridae littoraux ou de faible profondeur existent aux îles du golfe de Guinée, mais sont absents de l'Atlantique nord-oriental et de la Méditerranée où les signalisations les moins profondes correspondent à environ 100 m de profondeur. De rares récoltes correspondent à des profondeurs dépassant 2000 m, dont une par le submersible "Nautil" sur la dorsale Médio-Atlantique.

Dans la zone étudiée divers symbiontes laissent des traces caractéristiques sur le squelette des Stylasteridae ou causent des modifications: gastropodes prosobranches du genre *Pedicularia* (sur 8 espèces) et polychètes Polynoidae et Eunicidae (chacun sur une espèce). Le contour de la coquille de *Pedicularia* correspond étroitement à la configuration et aux irrégularités de la branche à l'endroit occupé. Après la disparition du symbionte cet emplacement précis reste évident par un dépôt de calcaire. Les galles induites par des Polynoidae, formant des galeries le long des branches et à orifices latérales, sont exceptionnellement rares dans l'Atlantique nord-oriental. *Eunice norvegica*, symbionte d'une espèce de Stylasteridae aux Açores, est le même qu'on trouve dans des colonies de scléractiniaires (*Lophelia*, *Madrepora*, *Solenosmilia*). Son tube souple d'une matière organique est recouvert de la même façon par le sclérenchyme de l'hydrocoralliaire.

Les signalisations fiables de Stylasteridae à l'état fossile pour l'Europe et le bassin méditerranéen sont rares (comme elles le sont aussi ailleurs). Elles vont du Paléocène inférieur au Plio-Pléistocène tandis que *Pedicularia*, symbionte obligatoire de Stylasteridae, est connu dans le Messinien (Miocène supérieur) et dans le Pléistocène inférieur. Les faunes tertiaires comprennent, en plus de genres encore présents dans l'Atlantique nord-oriental, des genres qui font partie de la faune actuelle de l'Atlantique occidental et de l'Indo-Pacifique. *Errina aspera* (accompagnée de *Pedicularia*) vient d'être découvert dans le Plio-Pléistocène de Sicile et de Calabre, dans des conditions sédimentaires analogues à celles de son milieu actuel (détroit de Messina). Cette découverte tardive dans un secteur en principe bien prospecté depuis plus d'un siècle, confirme le peu d'attention porté aux Stylasteridae par les paléontologistes.

INTRODUCTION

The stylasterids, along with the milleporids and scleractinians, are classed as "hard" or "stony" corals, an obviously polyphyletic assemblage including various taxa in two of the three classes of cnidarians. Stylasterids were originally considered as scleractinians and it was only by 1873 that G.O. SARS began to question this relationship. Finally, during the "*Challenger*" expedition (1873-1876) one of the naturalists aboard, H.N. MOSELEY, discovered that stylasterids were highly modified hydroids and thus only distantly related to the anthozoan scleractinians. His results, based on observation of live material carried out during the circumnavigation, were published in a series of preliminary and very elaborate papers (MOSELEY, 1876b, 1877, 1879, 1881).

A check list of all stylasterid taxa then known (CAIRNS, 1983b) included 23 genera, 1 subgenus, 184 valid species (20 of them fossil), 11 formae or facies, 42 junior synonyms, 4 nomina nuda, and 4 unnamed "species". Subsequently the number of described species has increased by 35 (CAIRNS, 1985, 1986a, 1986b, 1987, 1988). Furthermore, we are aware of several new genera and many new species yet to be described in rich collections from South Africa, the southwestern Indian Ocean, New Caledonia, and New Zealand. Notwithstanding this expected further increase in number of described taxa, species of stylasterid corals will always remain far less numerous than species of scleractinian corals.

Correspondingly, the literature is less abundant on stylasterids than on scleractinians, and the list of major authors is considerably shorter for stylasterids. Extensive bibliographies compiled by BOSCHMA (1957a) and by VERVOORT & ZIBROWIUS (1981) document the previous literature.

This revision treats mainly the stylasterid fauna of the northeastern Atlantic and the Mediterranean. In the northeastern Atlantic (comprising to the east the coasts of Europe and Africa, and to the west Iceland, the Azores, seamounts southwest and south of the Azores, the Mid-Atlantic Ridge south to 23°31'N, and the Cape Verde Islands) we recognized 19 species, one of which is represented by 3 subspecies. Of all these taxa, 18 are fully described herein, whereas 3 that are known only from poor material are not named. Only one of these Atlantic species also occurs in the southwestern Mediterranean. For comparison, from about the same area, ZIBROWIUS (1980) studied 85 species of scleractinians (which did not represent the entire fauna known at that date); and out of these the Mediterranean scleractinian fauna comprises about 30 species.

In this paper we also include 2 species from the islands of the Gulf of Guinea, equatorial eastern Atlantic (Príncipe, São Tomé). These species are separated by approximately 15° of latitude from the nearest recorded stylasterids in the Cape Verde Islands, and by approximately 34° of latitude from the more diversified South African stylasterid fauna. Both species from the Gulf of Guinea occur in shallow water whereas only deep-water species exist in the Mediterranean and the northeastern Atlantic (shallowest records from about 100 m depth).

ABBREVIATIONS

The following abbreviations are used in the text

— for institutions:

AMNH	American Museum of Natural History, New York
BMNH	The Natural History Museum, London; formerly: British Museum (Natural History)
IMFB	Institut für Meeresforschung, Nordseemuseum, Bremerhaven
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Bruxelles
MCM	Museu Carlos Machado, Ponta Delgada, Azores
MCZ	Museum of Comparative Zoology, Cambridge, Mass.
MHNG	Muséum d'Histoire Naturelle, Genève
MNHN	Muséum national d'Histoire naturelle, Paris
MZUC	Museo Zoologico, Università di Catania
MZUS	Musée Zoologique, Université de Strasbourg
NHMW	Naturhistorisches Museum, Wien
RMNH	Nationaal Natuurhistorisch Museum, Leiden; formerly: Rijksmuseum van Natuurlijke Historie
RSM	Royal Scottish Museum, Edinburgh
SMF	Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt a.M.
SMNH	Naturhistoriska Riksmuseet, Stockholm
UMZC	University Museum of Zoology, Cambridge, U.K.
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C.
VSM	Det Kgl. Norske Videnskabers Selskab Museet, Trondheim
YPM	Yale Peabody Museum, New Haven, Conn.
ZMA	Zoologisch Museum, Amsterdam
ZMB	Museum für Naturkunde, Berlin
ZMUK	Zoologisk Museum, Københavns Universitet
ZMUO	Zoologisk Museum, Universitet i Oslo
ZSM	Zoologische Staatssammlung, München

— for stylasterid morphology:

H:W height to maximum width ratio of gastrostyles

MATERIAL USED FOR THE REVISION

Many samples of stylasterids from various localities throughout the study area were available for this revision. These included types and other samples referred to in the literature, previously unpublished samples in museum collections, abundant new material primarily from French oceanographic cruises since 1958, and a few samples received from individual collectors. For complementary information see also Acknowledgements and List of deep-water stations from oceanographic cruises.

We thus studied stylasterids obtained by various oceanographic expeditions corresponding to more than a century of exploration in the northeastern Atlantic, starting with the "*Challenger*" circumnavigation in 1873. Material collected by submersibles is also included ("*Pisces III*" on Rockall Bank; "*Nautil*" cruise HYDROSLAKE on the Mid-Atlantic Ridge). The most diversified collections, in term of number of species, are those from the "*Talisman*" expedition in 1883, from the Prince of Monaco expeditions (1888 to 1905), and from the "*Jean Charcot*" cruise BIAÇORES in 1971. While the greater part of the "*Talisman*" stylasterids had been published already (but was in great need of a revision), those of the Prince of Monaco expeditions had remained unpublished, except for three mistakenly identified as bryozoans.

Stylasterids from the northeastern Atlantic and the Mediterranean are best represented in museums of Europe, but we also found several samples in American museums. A list of the institutions (with abbreviations used in the text) housing material studied herein is provided above.

One of us (H.Z.) had access (at the RMNH, in 1978 and 1980) to the abundant collections amassed by the late H. BOSCHMA before they were returned to the respective institution of origin. Among these collections originally loaned to BOSCHMA was abundant material from Norway belonging to the ZMUO and VSM, and various samples from the Faroes to Greenland (mainly from the "*Ingolf*" and "*Dana*" expeditions) belonging to the ZMUK.

Other institutions that provided many important samples for our revision were the BMNH, possessing many old samples including types; the MOM, possessing the samples from the Prince of Monaco expeditions; and the MNHN, possessing the greater part of the "*Talisman*" stylasterids and various other old samples including types. Surprisingly, there is only one lot of stylasterid from the "*Travailleur*" expeditions. In addition, the MNHM now houses the abundant material from the French oceanographic cruises in the Atlantic between 1958 and 1988 (some duplicates were given to other institutions) and various samples originally given to H.Z.

ACKNOWLEDGEMENTS

Assistance from many people in the institutions listed above (see Abbreviations) is gratefully acknowledged, their help including guidance in the collections, loan of specimens, and checking various data. Special thanks are extended to W. VERVOORT (retired director, RMNH), G. BEHRMANN (IMFB), C. CARPINE (MOM), P.F.S. CORNELIUS (BMNH), D. KÜHLMANN (ZMB), and M.E. CHRISTIANSEN (ZMUO).

Part of the "*Thalassa*", "*Cryos*" (cruise BALGIM), and "*Noroit*" (cruise SEAMOUNT 1) stylasterids, and the "*Nautile*" (cruise HYDROSLAKE) stylasterids were kindly provided by M. SEGONZAC (Centre de Tri d'Océanographie Biologique, Brest). We further want to thank S. GOFAS and J. LABOREL for specimens collected by diving in the Gulf of Guinea; L. SALDANHA for transmitting samples from the Gulf of Guinea and from off the Azores; J. STIRN for material from Morocco; A. FREIWALD for material from Denmark Strait; J.B. WILSON for material from Rockall and Anton Dohrn Seamount; T.P. SCOFFIN for material from Porcupine Bank; C. ALVAREZ-CLAUDIO for material from the south of the Bay of Biscay; G. BELLAN for material from Hyères Seamount; P. COLANTONI, I. DI GERONIMO and G. FREDJ for specimens from the Straits of Messina and corresponding information; P. BARRIER for the rich fossil stylasterid fauna from Carboneras, southeastern Spain; F. KÉZIRIAN for fossil stylasterids and *Pedicularia* from Sicily; G. HARTMANN-SCHRÖDER for identification of symbiotic polychaetes; and P.M. ARNAUD for information on the symbiotic gastropod genus *Pedicularia*.

H.Z. also acknowledges the opportunity of taking part in cruises that permitted the collection of stylasterids: "*Jean Charcot*" cruise BIAÇORES in 1971 (chief scientist J. FOREST), "*Thalassa*" in 1972 and 1973 (chief scientist L. CABIOCH), "*Cryos*" cruise BALGIM in 1984 and "*Noroit*" cruise SEAMOUNT 1 in 1987 (chief scientist P. BOUCHET).

The scanning electron micrographs were taken by S.D.C. in the s.e.m. Laboratory of the National Museum of Natural History, Smithsonian Institution.

HISTORICAL REVIEW

The first stylasterid species to be described from the study area was *Errina aspera* (Linnaeus, 1767), from the Mediterranean (also reported, by error, from Norway). Next reported were *Stylaster norvegicus* (Gunnerus, 1768) from Norway, and *Stylaster gemmascens* (Esper, 1794), most likely also from Norway although its origin was given as the Indian Ocean.

Allopora oculina Ehrenberg, 1834, was reported from an unknown origin, but most likely was *Stylaster norvegicus* from Norway; the name *A. oculina* was later used again by Norwegian authors for *S. norvegicus*.

In their series of "monographies" and "histoire naturelle des coralliaires", in which MILNE EDWARDS & HAIME (1848-1860) gave a rather complete inventory of the scleractinians then known from the Mediterranean and the northeastern Atlantic, they were less successful with the stylasterids, which at that time were still included in the scleractinian family Oculinidae. From their own experience the authors knew *Stylaster gemmascens* and *Allopora oculina* (probably identical with *Stylaster norvegicus*) and described these in some detail, but they mentioned *Stylaster norvegicus* (under *Allopora norvegica*) as a doubtful species and overlooked *Errina aspera* (MILNE EDWARDS & HAIME, 1850, 1857).

Stenohelia maderensis (Johnson, 1862), originally described from Madeira, was later reported also from the Cape Verde Islands (SAVILLE KENT, 1872; GREEFF, 1884).

Next to be reported, from the Faroes — Hebrides area (DUNCAN, 1870, 1873), was *Pliobothrus symmetricus* Pourtalès, 1868, a species originally described from the western Atlantic.

Errina dabneyi (Portalès, 1871) was the first species to be described from the Azores, an area from which the stylasterid fauna subsequently was found to be more diversified than in the other areas investigated.

Crypthelia pudica Milne Edwards & Haime, 1849, originally described from the Philippines, was mistakenly reported by MOSELEY (1879, 1881) from south of the Canary Islands ("Challenger" expedition), and by FILHOL (1885) without indication of the locality from the "Talisman" expedition. In fact, the "Challenger" stylasterid was *Crypthelia affinis* Moseley, 1879, which had been figured and confusedly named (but not described) under that name, whereas the "Talisman" stylasterid was most likely *Crypthelia tenuiseptata* Cairns, 1986.

Of the two species reported by GREEFF (1884) from the islands of the Gulf of Guinea, one was described as new, *Stylaster rosaceus* (Greeff, 1884), whereas the other was misidentified as the South African *Stylaster subviolaceus* (Saville Kent, 1871) and was much later recognized as a distinct species, *Stylaster blatteus* (Boschma, 1961).

Another exotic species mistakenly reported by THORNELLY (1897) was the southeastern Pacific *Stylaster sanguineus* Milne Edwards & Haime, 1850, which is, in fact, *Stylaster gemmascens* (Esper, 1794) from Rockall Bank.

Lepidopora eburnea (Calvet, 1903) from the Azores was originally described as a bryozoan of the genus *Hornera* (independently described as *Lepidopora hicksoni* Boschma, 1963). In addition, CALVET (1903, 1911) redescribed *Errina dabneyi* and *Pliobothrus symmetricus* (see above) as bryozoans: *Hornera verrucosa* and *Hornera gravieri*, respectively. Two more stylasterid species (*Crypthelia*) have now been discovered in the Prince of Monaco collection, which heretofore had not been the subject of a synthesis.

Errina atlantica Hickson, 1912, was described long after the material had been collected by the "Talisman" expedition in 1883. In the same paper (HICKSON, 1912b) the Philippine *Stenohelia tiliata* Hickson & England, 1905, was mistakenly reported from the Cape Verde Islands (a confusion with *S. maderensis*) and the western Atlantic *Pliobothrus tubulatus* (Pourtalès, 1867) mistakenly reported from the Azores (a confusion with *Lepidopora eburnea*). Altogether HICKSON's (1912b) report on (part of) the stylasterids of the "Talisman" expedition included 6 species (2 of them misidentified) from the Cape Verde Islands and the Azores.

BROCH's (1914a) report on the stylasterids from the "Ingolf" expedition was more exemplary and included 4 species (one misidentified) from high latitudes. He mistakenly reported the West Indian *Stylaster roseus* (Pallas, 1766) from the Greenland – Iceland area; this identification was corrected by BOSCHMA (1955b, 1965c) as *Stylaster erubescens* Pourtalès, 1868, the latter species being previously known only from the western Atlantic. In this paper the North Atlantic *S. erubescens* sensu BOSCHMA is considered as a distinct subspecies, *S. erubescens groenlandicus* n. ssp., differing from the nominotypical West Atlantic *S. erubescens erubescens* (the latter redescribed by CAIRNS, 1986a).

Starting in 1951, BOSCHMA published original data on a greater number of stylasterid species worldwide than any other author before (see VERVOORT & ZIBROWIUS, 1981), including on species from the Mediterranean, the northeastern Atlantic, and the Gulf of Guinea. The analysis of a register and the collections (comprising material sent to him on loan from various museums) found at the RMNH after BOSCHMA's death shows that he had access to 12 out of the 23 species and subspecies revised here. Unfortunately BOSCHMA's observations had not been the subject of a synthesis and his published results on this fauna are dispersed throughout many smaller notes.

In the original description of *Crypthelia tenuiseptata* Cairns, 1986, which was based on western Atlantic material, the distribution was given as amphiatlantic, including the Azores, Hyères Seamount, and Madeira. This indication is here corrected: in the eastern Atlantic *C. tenuiseptata* is known only from the Azores, whereas the *Crypthelia* from Hyères Seamount and Madeira is *C. vascomarquesi* n. sp. (it also occurs in the Azores). The other new species and subspecies described here are *Pliobothrus gracilis* n. sp. from Hyères Seamount, *Stylaster maroccanus* n. sp. from off the Atlantic coast of Morocco, *Stylaster ibericus* n. sp. from off northwest Spain, *Stylaster erubescens groenlandicus* n. ssp. from south and east of Greenland to northwest and southeast of Iceland, *S. erubescens britannicus* n. ssp. from southeast of Iceland to the Celtic Sea, *S. erubescens meteorensis* n. ssp. from the Great Meteor Seamount and southwest of the Azores (imprecise locality), and *Crypthelia medioatlantica* n. sp. from the Azores and the Mid-Atlantic Ridge south of the Azores.

In addition, a flattened form of *Lepidopora* from the Canary Islands collected by the "Challenger" in 1873 (previously unpublished and considered as *Lepidopora* sp. B herein) definitely is a distinct species, whereas a clavate form of *Lepidopora* from off Mauritania collected by the "Talisman" in 1883 (previously identified as *L. eburnea* and considered as *Lepidopora* sp. A herein), remains problematical, but has at least a look distinct of closely related typical *L. eburnea*. There is also a *Stenohelia* from the Azores, unfortunately represented only by a small colony, which differs from *S. maderensis* (considered as *Stenohelia* sp. A herein).

Although most of the 23 species and subspecies studied here had already been collected before the end of the 19th century (3 of which had even been named as early as in the 18th century), the present revision is the first attempt of a representative faunistic study for this area.

BIOGEOGRAPHY

In our analysis of the distribution patterns and affinities of the northeastern Atlantic and Mediterranean stylasterid fauna, the Scleractinia are used as the reference group. These other "hard" or "stony" corals are well known in the investigated area (ZIBROWIUS, 1980) where they are represented by considerably more species than the stylasterids.

The northern limit in the Atlantic of stylasterids (*Stylaster norvegicus*, *S. gemmascens*, *S. erubescens*) roughly coincides with that of the scleractinians. Both groups attain northern Norway, the Faroes, Iceland, and southern Greenland (Denmark Strait), but are absent from the Arctic basin. This is in contrast to the presence of numerous species of both groups in Antarctic waters (CAIRNS, 1982, 1983a) where conditions favorable to benthic life were not largely disrupted during the Pleistocene.

The Mediterranean has only one stylasterid species (*Errina aspera*), which equates to a much lower proportion of the Atlantic species than the approximately 30 species of scleractinians in common to the Mediterranean and the northeastern Atlantic. However, the greater part of the scleractinian species living in the Mediterranean occur in shallow water, whereas the stylasterids from corresponding latitudes in the Atlantic are deep-water species. In terms of number, the shallow-water scleractinians are more successful in the present Mediterranean than the deep-water species, but the latter were more diversified during the Pleistocene when the Mediterranean deep hydrology was more similar to that of the present northeastern Atlantic (ZIBROWIUS, 1980; BARRIER *et al.*, 1989). The deep-water stylasterids may also have been more successful in the Pleistocene Mediterranean, but thus far the fossil records are missing.

Errina aspera is the only stylasterid species living in the Mediterranean, where it appears to be limited to the southwestern part (including the Straits of Messina); it thereby shows a common distribution pattern with some scleractinians.

Concerning rarely collected stylasterids, it may still be premature to compare distribution patterns. Nevertheless, some trends appear sufficiently evident from the available data.

Few of the 23 stylasterid species and subspecies recorded from the northeastern and equatorial eastern Atlantic have a wide latitudinal range, the exceptions (group 1) being: *Stenohelia maderensis* from the Cape Verde Islands through Madeira, Galicia Seamount, and the Bay of Biscay to the Faroes Channel (range 45° of latitude; the northernmost occurrence needing confirmation by new records); *Stylaster erubescens* with three subspecies from Great Meteor Seamount through the Celtic Sea and the Faroes to Iceland and Greenland, Denmark Strait (range 36° of latitude); *Pliobothrus symmetricus* from Madeira and the Azores through the Celtic Sea and the Faroes to southwest of Iceland (range 31° of latitude); *Errina aspera* from the Cape Verde Islands through the Straits of Gibraltar to the Straits of Messina (range 23° of latitude); and *Lepidopora* sp. A from Mauritania through Morocco to Galicia Seamount (range 23° of latitude).

Although they are proportionally rather widespread (compared with group 3 below), some other species (group 2) appear to have a considerably narrower range in latitude. *Stylaster norvegicus* and *S. gemmascens* are known to occur only in high latitudes, from Norway to Iceland and Greenland, respectively, but apparently do not extend south beyond Rockall Bank (at about 58°N). *Crypthelia vascomarquesi* is known from three distant areas (Hyères Seamount, Azores, Madeira Archipelago) that are not widely separated in latitude (range only 7°); this species is perhaps more

widely distributed north and south of Madeira (poorly known representatives of *Crypthelia* from Selvagens Archipelago and Josephine Seamount).

Available data suggest that the remaining species (group 3) occur in a more limited area. Several species are thus far known from the Azores and in part from the Mid-Atlantic ridge to the southwest: *Lepidopora eburnea*, *Errina dabneyi*, *E. atlantica*, *Stenohelia* sp. A, *Crypthelia affinis*, *C. medioatlantica*, and *C. tenuiseptata*. Pending additional records and further investigations, forms similar to *Lepidopora eburnea* and *Errina atlantica* from seamounts between Portugal and Madeira are not formally referred to the Azorean species. *Crypthelia affinis* is provisionally included here; in fact its type locality (given as far southwest of the Canary Islands with the unusual depth of 2790 m) may be incorrect and thus the species is positively known only from the Azores. *Pliobothrus gracilis* was obtained only from Hyères Seamount, *Lepidopora* sp. B from one station off the Canary Islands, *Stylaster maroccanus* only once off Morocco, and *S. ibericus* exclusively northwest of Spain.

The shallow-water species *Stylaster rosaceus* and *S. blatteus* from the islands of the Gulf of Guinea have not been found elsewhere.

With 9 species (*Lepidopora eburnea*, *Pliobothrus symmetricus*, *Errina dabneyi*, *E. atlantica*, *Stenohelia maderensis*, *Crypthelia affinis*, *C. medioatlantica*, *C. vascomarquesi*, *C. tenuiseptata*), the fauna of the Azores is the most diversified. For comparison, the stylasterid faunas of the Cape Verde Islands, the Canary Islands, and the Madeira Archipelago appear poor with one to three species thus far recorded. The situation is similar concerning the deep-water scleractinian fauna of these archipelagos (ZIBROWIUS, 1980). In part this impression may be due to a more intense investigation of the Azores, notably by the "Talisman", the Prince of Monaco expeditions, and "Jean Charcot" cruise BIAÇORES.

Three of the 21 stylasterid species (15 %) recorded from the northeastern and equatorial eastern Atlantic also occur in the western Atlantic (CAIRNS, 1986a). Among these, *Pliobothrus symmetricus* and *Stylaster erubescens* (with distinct subspecies) range from the West Indies to the eastern margin of the Atlantic and attain high latitudes, whereas *Crypthelia tenuiseptata* is known only from the West Indies and the Azores. None of the specifically northeastern Atlantic stylasterids is known from any other area. Furthermore, there are no species in common with the South African fauna or that of the Indo-Pacific. Proportionally more deep-water scleractinians have amphiatlantic distributions (CAIRNS, 1979; ZIBROWIUS, 1980), and some species have even wider geographic ranges extending into the Indo-Pacific.

With 21 species in 6 genera, the stylasterid fauna of the northeastern Atlantic (to which are herein annexed the 2 species of the Gulf of Guinea) is considerably less diversified than the geographically nearest stylasterid fauna of the West Indies, which comprises 42 species in 8 genera (CAIRNS, 1986a). The genera *Lepidothea* and *Distichopora* are not represented in the northeastern Atlantic. In the northwestern Atlantic no stylasterids are thus far recorded from between North Carolina and Greenland, whereas in the northeastern Atlantic no similar gap of recorded distribution exists.

The West Indian stylasterid fauna has only one shallow-water species (*Stylaster roseus*); likewise, shallow-water species occur in the eastern Atlantic in the Gulf of Guinea (*Stylaster rosaceus*, *S. blatteus*). However, shallow-water stylasterids are not confined to tropical areas; some do exist on the coast of South Africa and in the fjords of New Zealand. A preliminary study (H.Z.) of the South African stylasterid fauna, largely based on the collections of the South African Museum, Cape Town, shows that, in a smaller geographical area this fauna is about as diversified in term of number of species as the northeastern Atlantic stylasterid fauna.

SYMBIOTIC ASSOCIATIONS

Attention has been focused by ZIBROWIUS (1981) on the diversity of symbiotic associations involving stylasterid corals and other organisms. That preliminary inventory, which was worldwide and based on records from the literature and on new observations, listed the following symbionts adapted to life on a stylasterid host (simple epibionts on dead parts of skeleton excluded):

- a nemertean coiled around tops of branches and causing an unusual structure of the irritated zone;
- a species of *Polydora* (spionid polychaete) perforating living branches;
- a species of *Autolytus* (syllid polychaete) living in blister-like galls;
- various species of polynoid polychaetes causing gallery-like gall-tubes with lateral openings along stems and branches (a particular new case reported by CAIRNS, 1987);
- gastropods of the prosobranch genus *Pedicularia* having their shell contour adapted to the precise place where they settled on the coral branch;
- tiny pycnogonid larvae found inside gastrozooids (larger pycnogonid larvae inside the gastropore tube have been found subsequently by H.Z. on material from New Zealand);
- siphonostomatoid copepods which cause galls each of which envelop a cyclosystem;
- a thoracic cirriped largely overgrown by its host coral;
- an acrothoracic cirriped perforating live branches; and
- aplacophoran molluscs coiled around stylasterid branches or inside polynoid gall-tubes have recently been reported by CAIRNS (1986b, 1987).

When the northeastern Atlantic and Mediterranean stylasterid fauna was investigated in detail, symbiotic associations were especially noted and three types were found, one of them here reported for the first time.

1) *Eunice norvegica* (Linnaeus, 1767) (identified by G. HARTMANN-SCHRÖDER), an eunicid polychaete, lives in colonies of *Errina atlantica* from the Azores. The rather large worm (several cm long) builds its own tube of a soft organic material which, providing an additional substrate for the coral, is subsequently covered by the coenosteum. The worm tube thus influences the shape of the colony by inducing growth along a preferential axis. Covered by the coral skeleton, the tube becomes equivalent to a strong trunk of the colony (Fig. 14 A).

Previously, *Eunice norvegica* was known as a symbiont of three colonial deep-water scleractinian corals (ZIBROWIUS, 1980), all of which cover the worm tube as described above for the stylasterid: *Madrepora oculata* Linnaeus, 1758; *Lophelia pertusa* (Linnaeus, 1758); and *Solenosmilia variabilis* Duncan, 1873.

2) Although polynoid polychaetes are probably the most widely distributed type of stylasterid symbiont, they are poorly represented in the northeastern Atlantic stylasterids. Only one colony of *Stenohelia* sp. A from an unknown station in the Azores shows an irregular growth caused by the presence of a gall-tube inhabited by *Harmothoe* sp. (identified by G. HARTMANN-SCHRÖDER; Fig. 35 G). The infested colony is not flabellate as normal *Stenohelia* colonies. For comparison, in the western Atlantic several species of stylasterids have a polynoid symbiont (CAIRNS, 1986a). In the case of the polynoid — stylasterid association, the polychaete does not produce its own tube of organic material which is subsequently covered by the coral. Instead, the gall-tube is entirely an induced production of the coral.

3) The prosobranch gastropod *Pedicularia* causes a characteristic, very localized modification of the stylasterid branch surface. It deposits a layer of lime under which the sealed off skeleton cannot grow in thickness, unlike the surrounding skeletal areas. This may result in a slight depression, the contour of which fits that of the shell. Generally the crust of lime deposited by the snail (apparently by its foot) comprises conspicuous prominent crests which considerably enlarge the crust surface and on which the foot of the snail adheres more efficiently. These elongate subelliptical or more irregular *Pedicularia* traces (Fig. 1 C, 2 C, 5 C, 9 G, 11 H, 14 B, 25 A, D, E, 33 C) are easily recognizable and provide information on the occurrence of the snail, even when the latter had been lost, or when the stylasterid was already dead when collected.

Pedicularia gastropods are the most common symbionts of the northeastern Atlantic and Mediterranean stylasterids. Their characteristic traces, if not the molluscs themselves, have been found on 8 species and subspecies: *Lepidopora eburnea*, *Pliobothrus symmetricus*, *Errina aspera*, *E. dabneyi*, *E. atlantica*, *Stylaster ibericus*, *S. erubescens britannicus*, and *Stenohelia maderensis*. In the investigated area the *Pedicularia* – stylasterid association has thus been recognized in the Azores, Madeira Archipelago, Canary Islands (only isolated disassociated *Pedicularia* collected here), Cape Verde Islands, Celtic Sea, off northwestern Spain, Atlantic coast of Morocco, Straits of Gibraltar, and Straits of Messina. Indirect records of *Pedicularia* (traces on *Pliobothrus symmetricus* and *Stylaster erubescens britannicus*) from the Celtic Sea at 48°37.0'N to 48°38.2'N are the northernmost ones known worldwide.

Pedicularia from the northeastern Atlantic area have been reported in the malacological literature (BELLON-HUMBERT & GOFAS, 1977; DAUTZENBERG, 1889, 1927; LOCARD, 1897; etc.) under various specific names: *P. sicula* Swainson, 1840; *P. decussata* Gould, 1855; *P. decurvata* Locard, 1897; and *P. sicula* var. *sublaevigata* Locard, 1897. BOUCHET & WAREN (1992) synonymize all these under *P. sicula*.

The incidence of *Pedicularia* on the northeastern Atlantic and Mediterranean stylasterid fauna is considerably higher than on that of the western Atlantic. In the western Atlantic, *Pedicularia* traces are rare (not mentioned by CAIRNS, 1986a) and are known only from 4 species: *Stylaster complanatus* Pourtalès, 1867, from Cuba near Havana; *Stylaster erubescens* Pourtalès, 1867, from the Blake Plateau; *Conopora* sp. from northwestern Brazil; and *Crypthelia peircei* Pourtalès, 1867, from Guadeloupe and St. Vincent. Apparently no specimen of western Atlantic *Pedicularia* has yet been seen on its host coral.

RECORDS OF FOSSIL STYLASTERIDS FROM EUROPE

Records of fossil stylasterids are worldwide but comparatively rare. In emerged areas neighbouring the Mediterranean and the northeastern Atlantic, fossil stylasterids are thus far known only from Europe.

The geologically oldest record, from the Maastrichtian (uppermost Cretaceous) of Denmark, is only briefly mentioned by FLORIS (1979) in a paper dealing mainly with scleractinians. Alluding to previous records from the Danian (lowermost Paleocene, see below), FLORIS indicated that "rare finds of stylasterine have now also been made in the Maastrichtian"; however, these stylasterids from the Maastrichtian are not even tentatively referred to genera.

NIELSEN (1919) distinguished 8 new species from the Danian of Fakse (= Faxe), Denmark, originally considered as uppermost Cretaceous but now known to be Lower Paleocene: *Sporadopora faxensis*, *Pliobothrus dispergens*, *P. laevis*, *Spinipora irregularis*, *Labiopora lobata*, *Congregopora nasiformis*, *Astylus crassus*, and *Conopora arborescens*. BOSCHMA (1951a) reproduced the description and figures of *Congregopora nasiformis* and discussed the affinities of this form. NIELSEN's 8 species, with subsequent citations by other authors (no original new data) are listed by BOSCHMA (1957a), who also transferred 3 of them into different genera: *Spinipora irregularis* and *Labiopora lobata* into the genus *Errina*, *Astylus crassus* into the genus *Astya*. CAIRNS (1983b) followed BOSCHMA, except for transferring *Labiopora lobata* into the genus *Errinopora* (not *Errina*) and considered most species (except *Errina irregularis*, formerly under *Spinipora*) as of uncertain generic placement, or *incertae sedis*. Some of NIELSEN's species have been reported again from Fakse by BERNECKER & WEIDLICH (1990).

Distichopora antiqua DeFrance, 1826, from the Eocene of the Paris basin (list of references in BOSCHMA, 1957a) is a typical representative of the genus *Distichopora* (specimen at MNHN labelled "calcaire grossier de Chaumont").

Allopora compressa (Römer, 1863), as revised by BOSCHMA (1951b) (detailed synonymy also in BOSCHMA, 1957a), has been described from the Oligocene of Lattorf near Kassel, Germany, under various names: *Dendracis compressa* Römer, 1863; *D. multipora* Römer, 1863; *D. pygmaea* Römer, 1863; *D. tuberculata* Römer, 1863; and *Cryptaxis alloporeoides* Reuss, 1865. CAIRNS (1983b) included this species in *Stylaster* (Group A).

Stylaster priscus Reuss, 1872, has been described and figured in some detail from material from the Miocene of Porzteich near Nikolsburg (now Mikulov), Moravia, Central Czecho-Slovakia. BOSCHMA (1951b, 1957a) listed it as *Allopora prisca*. CAIRNS (1983b) included this species in *Stylaster* (Group B).

Stylaster antiquus Michelotti in Sismonda, 1871, was summarily described (not figured) from material from Sassello near Savona, Liguria, northwestern Italy. Originally referred to the Lower Miocene, it has later been considered as from the Oligocene. This species was also mentioned by DE ANGELIS (1895) and BOSCHMA (1951a, 1957a). CAIRNS (1983b) included this species in *Stylaster* (Group C).

GIGNOUX (1913: 650) mentioned *Distichopora* sp. from what he considered as upper Pliocene (now identified as Lower Pleistocene) at Musalà near Villa San Giovanni, Calabria, southern Italy. MIRIGLIANO (1949) also mentioned *Distichopora* sp. in the species list of a Plio-Pleistocene fauna from the province of Salerno, southern Italy. No further information was provided, and the corresponding

material could not be located at Naples (university and museum) where MIRIGLIANO carried out his study (I. DI GERONIMO, *in litt.* 1979).

Heretofore unreported fossil stylasterids include the following new geographic records from the Mediterranean basin.

A remarkably rich fauna (in fact the most diversified assemblage of fossil stylasterids presently known) was discovered in 1989 by P. BARRIER in the "red breccia" of Messinian age (Upper Miocene) at Carboneras, southeastern Spain (BARRIER *et al.*, 1992). It comprises at least 14 species in at least 8 genera: *Calyptopora*, *Conopora*, *Crypthelia*, *Distichopora*, *Lepidopora*, *Pliobothrus*, *Stenohelia*, *Stylaster* (Groups A, C, sensu CAIRNS, 1983b). In addition, one shell of the gastropod *Pedicularia*, an obligate symbiont of stylasterids, was found with that fauna; this is the oldest record of *Pedicularia* known.

Ironically, *Errina aspera*, the only stylasterid species now living in the Mediterranean and occurring abundantly in the Straits of Messina, had previously not been reported as a fossil from this area rich in Plio-Pleistocene fossiliferous deposits. According to MONTENAT & BARRIER (1985) and BARRIER, DI GERONIMO & MONTENAT (1988), a narrow passageway similar to the present Straits of Messina in canalizing strong tidal currents, already existed in the Plio-Pleistocene. Most likely, ideal conditions for *E. aspera* occurred there in the past as they do at present.

Although *E. aspera* was heretofore missing from the faunal lists of the Plio-Pleistocene, the obligate symbiont of stylasterids, *Pedicularia*, was already known as a fossil from Sicily: SEGUENZA (1865) described *P. deshayesiana* from what he considered as Miocene (in fact, Plio-Pleistocene) of Rometta near Messina. A few years ago, a second fossil specimen of *Pedicularia* was obtained by I. DI GERONIMO (pers. comm.) from the Lower Pleistocene near Capo dell'Armi, Calabria (locality Canale).

Specially searched for, *E. aspera* has finally been obtained (in 1990; most specimens by F. KÉZIRIAN) on both sides of the Straits of Messina: in Calabria from the Lower Pleistocene near Capo dell'Armi (same locality Canale as for *Pedicularia*; see above); in Sicily (province of Messina) from the Upper Pliocene at Salice, and from the Lower Pleistocene at Giampilieri and at Casino di Falcone (together with *Pedicularia*). In addition, when studying fossil scleractinians (H.Z.) from Sicily described by SEGUENZA (1864) and donated by him to the Wien museum, one small colony of *E. aspera* was recently discovered attached to a fragment of *Lophelia defrancei* sensu SEGUENZA (NHMW 1864/XXI/242). This sample, with SEGUENZA's original label indicating "dintorni di Messina", should be considered as of imprecise origin (Messina area) and of Plio-Pleistocene age although a later museum label refers it to SEGUENZA's "Miocene" of St. Filippo near Messina.

The Lower Pleistocene deposit at Casino di Falcone (Sicily; see above) also contains a second species of stylasterid of which only a tiny fragment is presently known: it is a typical *Stenohelia*, probably referable to *S. maderensis*, a species still living in the north-eastern Atlantic.

The records of fossil stylasterids from Europe are too scarce to permit an analysis of how the stylasterid fauna of European seas evolved since the late Cretaceous. The generic attribution of most of the Lower Paleocene stylasterids from Denmark remains questionable due to incomplete conservation of essential structures. Two of the genera possibly represented in the Fakse fauna do still exist in European seas: *Pliobothrus* and *Errina*. A few representatives of the large genus *Stylaster* (Groups A, B, C, sensu CAIRNS, 1983b) are well documented in the Oligocene and Miocene of central Germany, Central Czecho-Slovakia (Moravia), northwestern Italy, and southeastern Spain. Related forms of *Stylaster* (Groups A, B) still live in European seas.

In addition to genera still represented in European seas (*Crypthelia*, *Lepidopora*, *Pliobothrus*, *Stenohelia*, *Stylaster*), the rich Messinian fauna of Carboneras comprises genera that no longer occur there. *Calyptopora* is known only in the Indo-Pacific and *Conopora* is widespread throughout the Indo-Pacific and in Antarctic and Sub-Antarctic waters, the nearest location to Europe being off Brazil.

The genus *Distichopora* deserves special attention. In the Indo-Pacific it is now represented by several shallow- and deep-water species (BOSCHMA, 1959), and in the western Atlantic (Caribbean) by several deep-water species (CAIRNS, 1986a). It is absent from the northeastern Atlantic and

adjacent waters. The Eocene *D. antiqua* from the Paris basin and the unnamed *Distichopora* from the Messinian of Carboneras are authentic *Distichopora*, whereas we may doubt the correct generic identification of GIGNOUX's (1913) and MIRIGLIANO's (1949) *Distichopora* sp. from the Plio-Pleistocene of southern Italy (specimens unavailable). Although *Distichopora* is easily recognizable among all other stylasterids, GIGNOUX and MIRIGLIANO were surely not experts on this group. A confusion with morphologically convergent bryozoan colonies is most probable, especially since "transphyletic" confusions have happened to trained bryozoan and coral workers (see ZIBROWIUS, 1982, and CAIRNS, 1983b: 441, for examples).

TAXONOMICAL REVISION

The 21 species included in this revision belong to 6 genera. Because CAIRNS (1983b) has already published a generic revision, general information on these genera is kept to minimum.

The presentation of each species (and subspecies) entails the following arrangement: valid name followed by author and date, synonymy and chresonymy (see SMITH & SMITH, 1972), types, material studied, description, comparisons, remarks, distribution and ecology, and symbionts. Under "types", information is provided on all nominal species subsequently synonymized. Under "material studied" only cursory data are given for deep-water stations from oceanographic expeditions; detailed station data for all expeditions are compiled in a general station list. The passage "remarks" includes historical comments (see also under types) and rectification of misidentifications in the previous literature.

The morphological terminology used in the descriptions is that reviewed, augmented and illustrated by CAIRNS (1983b, 1985, 1986a, 1986b); however an additional new term is introduced here. A binary ampulla is a large female ampulla, usually elongate in shape, with two efferent pores on opposite vertices and, presumably, two planulae within (see *Stenohelia maderensis*).

Key to the genera of Stylasteridae from the study area

- | | |
|---|--------------------|
| 1a Gastro- and dactylopores not arranged in cyclo systems..... | 2 |
| 1b Gastro- and dactylopores arranged in cyclo systems | 4 |
| 2a Gastropore without gastrostyle..... | <i>Pliobothrus</i> |
| 2b Gastropore with gastrostyle..... | 3 |
| 3a Dactylopores are (low) apically perforate cones..... | <i>Lepidopora</i> |
| 3b Dactylopores are U-shaped spines with slit..... | <i>Errina</i> |
| 4a Cyclo system (partially) covered by lid;
gastropore tube double-chambered;
gastro- and dactylostyles absent..... | <i>Crypthelia</i> |
| 4b Cyclo system without lid;
gastropore tube cylindrical;
gastro- and dactylostyles present..... | 5 |
| 5a Cyclo systems unifacially arranged;
gastropore tube long and curved;
ampullae usually clustered near cyclo systems..... | <i>Stenohelia</i> |
| 5b Cyclo systems randomly or sympodially arranged;
gastropore tube (usually) short and (nearly) straight;
ampullae scattered randomly over coenosteum | <i>Stylaster</i> |

Genus *LEPIDOPORA* Pourtalès, 1871

Diagnosis. — Coordination of gastro- and dactylopores usually random; however, in some species dactylopores serially arranged on branch edges, and gastropores serially arranged on anterior or anterolateral branch faces. Coenosteal texture quite variable. Gastropores often bordered by proximal lip; gastro- and dactylopore tubes long. Gastrostyles usually not ridged; H:W ratio high. Dactylopores apically perforate mounds; no dactylostyles.

Type species: *Errina glabra* Pourtalès, 1867, from the western Atlantic.

Lepidopora was formerly considered as a subgenus of *Errina* Gray, 1835. *Lepidopora* is represented in the study area by one well known species from the Azores, *L. eburnea* (Calvet, 1903), and two unnamed forms. Under *Lepidopora* sp. A, we provisionally group problematical material (in part poorly preserved) close to *L. eburnea*, from Mauritania, Morocco, and Seine, Gorringer and Galicia Seamounts. In contrast, *Lepidopora* sp. B, known only from one well preserved but incomplete specimen from the Canary Islands, definitely is a distinct species.

Lepidopora eburnea (Calvet, 1903)

Fig. 1 A-F, 2 A-J

Synonymy:

Hornera eburnea Calvet, 1903: 162, pl. 18, fig. 5a-c.

Errina (Lepidopora) hicksoni Boschma, 1963a: 339-342, text-fig. 1, pl. 1, fig. 1-3.

Chresonymy:

Hornera eburnea — CALVET, 1906: 479 (part, NOT “*Talisman*” drag. 96, Mauritania); 1931: 45. — BORG, 1944: 203. — BELLOC, 1960: 12.

Errina (Lepidopora) eburnea — ZIBROWIUS, 1981: 982 (part, NOT “*Talisman*” drag. 96, Mauritania).

Errina (Lepidopora) hicksoni — BOSCHMA, 1963b: 395-396; 1964a: 61; 1967: 335-336; 1968c: 207. — VERVOORT & ZIBROWIUS, 1981: 27.

Lepidopora hicksoni — CAIRNS, 1983b: 428.

Pliobothrus tubulatus — HICKSON, 1912b: 465, pl. 8, upper fig.

TYPES

Hornera eburnea: In the original description, CALVET (1903) mentioned “a beautiful sample” from the Azores (Prince of Monaco stn 229), apparently the figured colony (40 mm high, 35 mm wide). Being the only specimen mentioned, it must be considered the holotype. Its depository is unknown. The MOM possesses 3 smaller topotypic specimens (stn 229) not specially mentioned by CALVET (lower part of 2 colonies and 1 slender distal branch; part of them figured herein, Fig. 1 D-E).

Type locality: Prince of Monaco stn 229, 16.8.1888, 38°22'N, 28°14'24"W, 736 m. Azores.

Errina (Lepidopora) hicksoni: In the original description, BOSCHMA (1963a) designated the holotype and a paratype: as holotype the colony figured by HICKSON (1912b, pl. 8, upper figure with the explanation “*Pliobothrus tubulatus*, Azores, 56 meters”), and as paratype a colony figured in his own paper (pl. 1, fig. 3), also part of the material previously referred to *P. tubulatus*. The holotype was known to BOSCHMA only from HICKSON's paper and was presumed to be deposited at the MNHN; in fact, this specimen had been retained by HICKSON and later transferred to the BMNH (1964.9.17.11). The specimen designated paratype had also been retained by HICKSON and deposited at the Manchester museum (from where BOSCHMA had it on loan and to where he returned it in 1969,

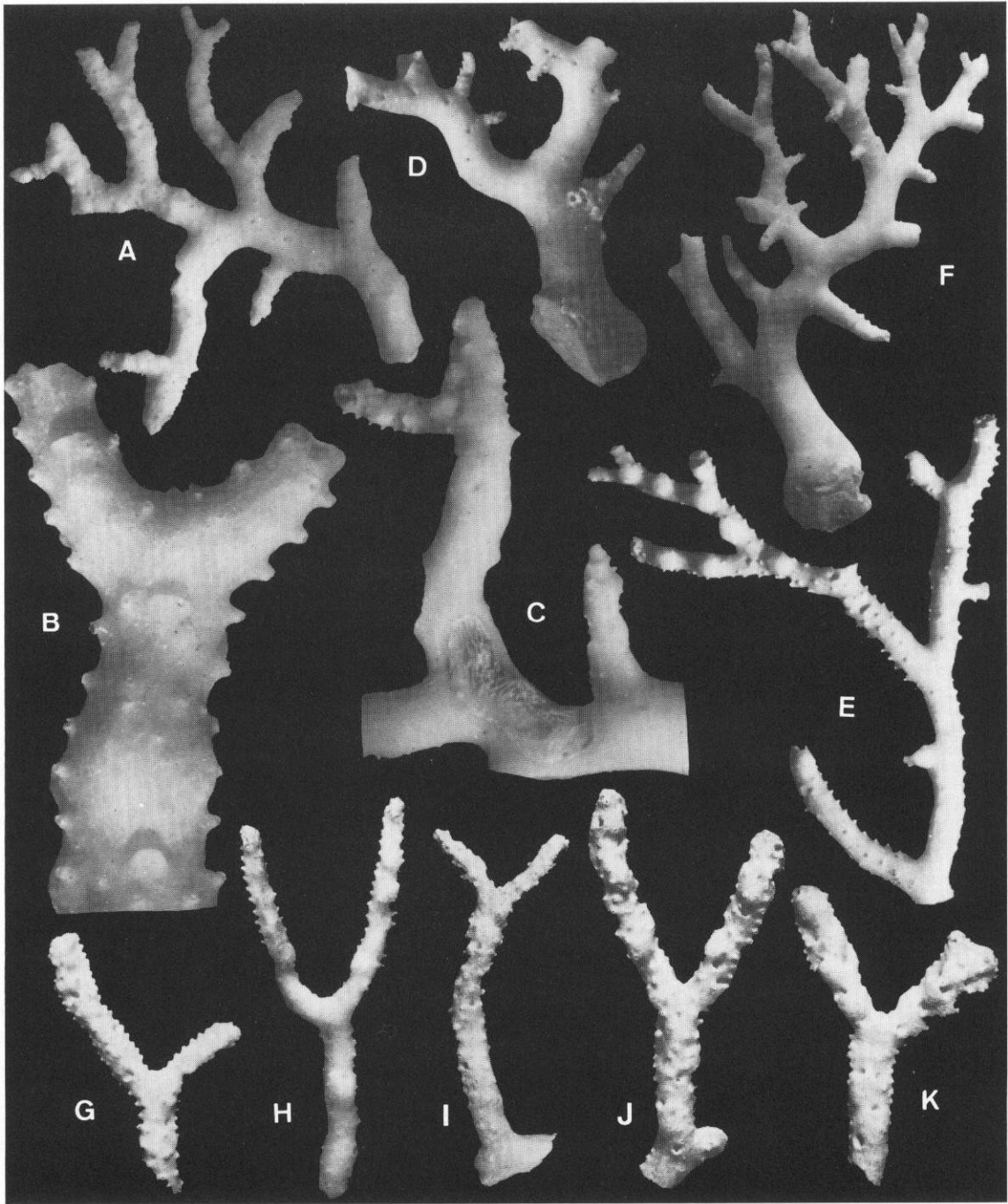


FIG. 1. — *Lepidopora eburnea* (A-C, from "Talisman" drag. 123, MNHN; D-E, topotypes of *Hornera eburnea*, MOM; F, from "Jean Charcot" 1971, stn 161, MNHN): A, colony ($\times 3.0$); B, detail of A showing gastro- and dactylopore arrangement, gastropore lips ($\times 18$); C, detail of A, opposite face showing *Pedicularia* trace ($\times 5.9$); D, colony ($\times 3.1$); E, slender colony with bulging female ampullae ($\times 4.6$); F, colony ($\times 3.3$).

Lepidopora sp. A, branched specimens close to *L. eburnea* (G-H, from "Noroit" DW-21, MNHN; I-K, from "Noroit" DW-78, MNHN): G, branched distal fragment showing gastro- and dactylopore arrangement ($\times 3.8$); H, nearly complete bifurcate colony showing bulging ampullae ($\times 4.1$); I, colony bifurcate in upper part ($\times 4.1$); J, repeatedly branched specimen showing gastro- and dactylopore arrangement and bulging ampullae ($\times 4.1$); K, branched distal fragment, like J ($\times 4.1$).

according to his annotations preserved at the RMNH). Additional topotypic specimens are at the BMNH (1977.8.2.1, 3 colonies) and at the MNHN (10 colonies, branches and minor fragments).

Type locality: Given by BOSCHMA (1963a) as "Talisman" expedition dredging no. 120, Azores, 560 m. The data available to BOSCHMA were incomplete and partly incorrect. The correct data are: "Talisman" drag. 123, 13.8.1883, 38°23'N, 28°49'45"W, 560 m. Azores.

MATERIAL STUDIED

Azores: Prince of Monaco stn 229, 2 small colonies + branch, topotypes of *Hornera eburnea* (MOM); stn 597 (?), 3 small branches, labeled [by CALVET ?] *Hornera eburnea* (MOM). — "Talisman" drag. 123, about 15 colonies, branches and fragments including holotype of *E. (L.) hicksoni* (BMNH 1964.9.17.11, 1977.8.2.1; MNHN); drag. 128, 3 small branches (MNHN). — "Jean Charcot" 1971, stn 159, 3 colonies (MNHN); stn 161, 2 colonies (MNHN); stn 213, 4 colonies (MNHN); stn 229, 3 small colonies + branch (MNHN); unknown station, about 60 colonies, branches and fragments (most MNHN; USNM 75600). — "Bartlett" 1975, stn 2, branch (ZMUK); stn 4, branch (ZMUK).

DESCRIPTION

Colonies uniplanar, with regular dichotomous branching forming V-shaped to U-shaped axils (Fig. 1 A-E, 2 A). Examined specimens up to 25 mm high and 35 mm wide; holotype of *Hornera eburnea* slightly taller (40 mm). Branches circular in cross section, tapering to slender tips about 0.45 mm in diameter. Coenosteum white and linear-imbricate (Fig. 2 F-G), composed of well-ordered parallel strips each 0.11-0.12 mm wide. Strips not well defined, bordered by an alignment of narrow coenosteal pores 20-30 μ m long. Platelets irregular in width but rarely extend across entire strip.

Gastropores occur primarily on anterior face, each about 0.25 mm in diameter and often bordered by a small proximal lip. Gastropore lip does not actually cover any of gastropore (Fig. 1 B) but, rather, gives anterior directionality to gastrozoid. Illustrated gastrostyle (Fig. 2 J) 0.50 mm tall and 0.16 mm in basal diameter (H:W = 3.13); gastrostyles measured by BOSCHMA (1963a) slightly more slender (H:W = 3.75). Gastrostyle unridged and acutely conical with a pointed tip. Extremely large spines cover gastrostyle in a

random arrangement; spines up to 68 μ m long and 10 μ m in diameter. Gastropore tube smooth; no ring palisade. According to BOSCHMA (1963a), gastrostyles occupy only lower one-sixth of gastropore tube.

Mound shaped dactylopores (Fig. 1 B, 2 D) occur mainly on anterior branch faces and lateral branch edges. Dactylopores often linearly arranged on branch edges in series of 5-9 but randomly arranged on branch faces. Dactylopores 50-70 μ m in diameter, quite short (rarely more than 60 μ m tall), and projecting perpendicularly to slightly anteriorly from branch.

Female ampullae massive, superficial, elliptical mounds (Fig. 1 E, 2 H) about 0.9-1.1 mm in diameter, the greater axis aligned with branch axis. When mature, female efferent pore located at distal vertex of ellipse, a concavity about 0.16 mm in diameter. Female ampullae occur on both branch faces and often in series of two or three. Male ampullae smaller, about 0.7 x 0.5 mm in diameter, superficial on branch tip but internal in larger diameter branches.

COMPARISONS

Eleven valid species of *Lepidopora* (13, counting the 2 unnamed species included herein) have been described: 6 from the Atlantic, 2 from the Subantarctic off South America, 1 from South Africa, and 2 from New Zealand (CAIRNS, 1983b, 1985, 1986a). *L. eburnea* can be distinguished from all congeners by its dactylopore arrangement: short rows on lateral branch edges in addition to dactylopores randomly scattered on anterior face. It is also characterized by having very short

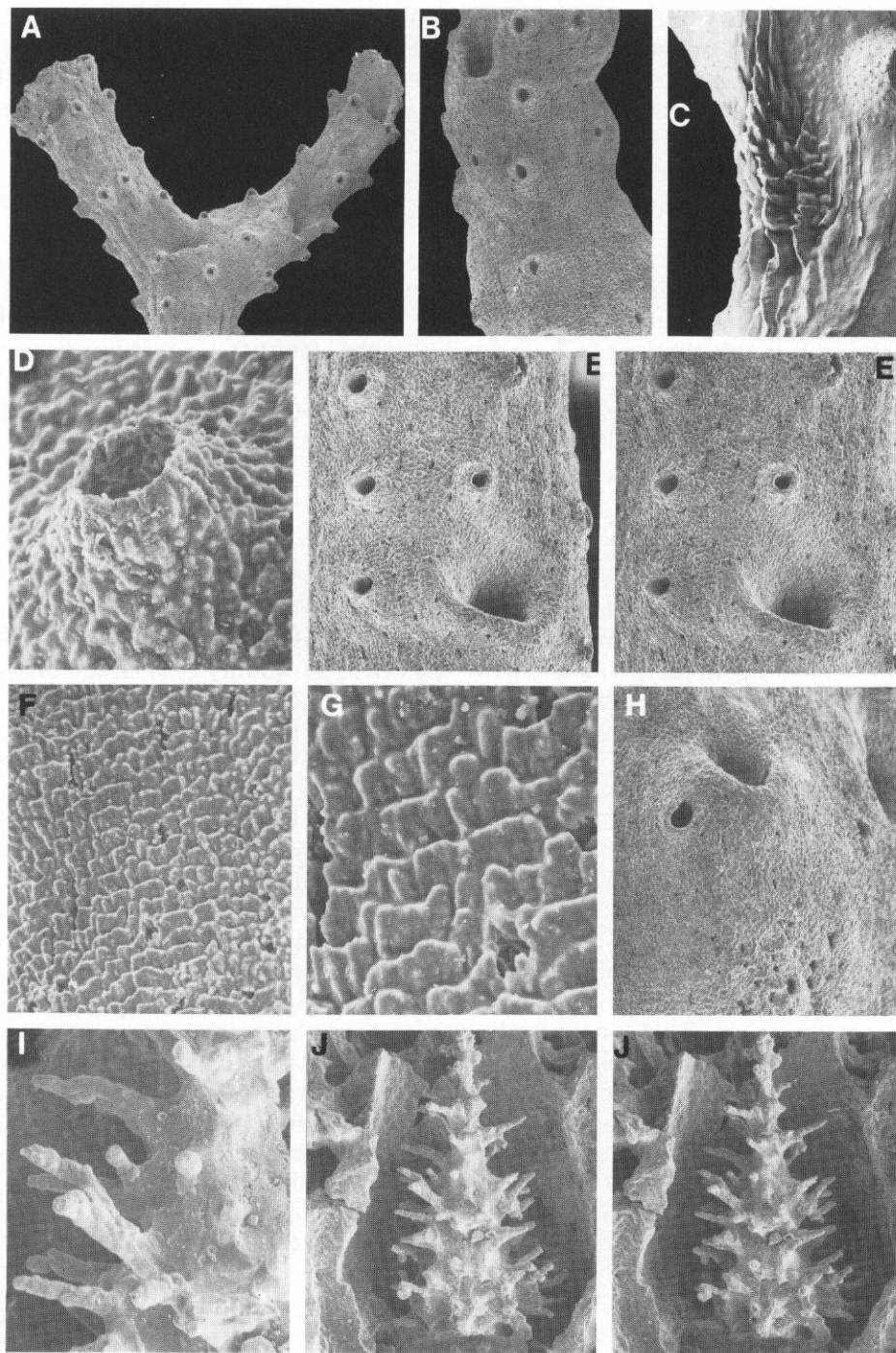


FIG. 2. — *Lepidopora eburnea* (A-B, D, F, G, from “*Talisman*” drag, 123, BMNH 1977.8.2.1; C, E, H-J, from “*Jean Charcot*” 1971, unknown station, Azores, female, USNM 75600): A, distal branch showing arrangement of gastro- and dactylopores ($\times 18$); B, branch edge illustrating a row of dactylopores ($\times 29$); C, *Pedicularia* trace ($\times 17$); D, conical dactylopore ($\times 252$); E, detail of branch surface showing gastropore, several aligned dactylopores, and coenosteal texture ($\times 33$, stereopair); F-G, coenosteal texture ($\times 121$, $\times 300$, respectively); H, female ampulla ($\times 41$); I, gastrostyle spines ($\times 289$); J, gastrostyle ($\times 97$ stereo pair).

dactylopore spines and a relatively low gastrostyle H:W ratio. Only one other species of *Lepidopora* is known to have linear-imbricate coenosteal texture, the western Atlantic *L. carinata* (Pourtalès, 1867), which can be distinguished by its distinctively shaped, ridged dactylopore spines; ring palisade; and complete absence of gastropore lips. Comparisons of *L. eburnea* to the 2 unnamed species (*Lepidopora* sp. A and sp. B) are made in the accounts of the latter.

REMARKS

L. eburnea was considered at first as a bryozoan and described as *Hornera eburnea* by CALVET (1903). CALVET (1906) also recognized *H. eburnea* in the "Talisman" collection, still considering it as bryozoan. We agree that his material from "Talisman" drag. 128 (Azores) is typical *L. eburnea*, but we consider the stylasterid from "Talisman" drag. 96 (Mauritania) to be problematical, possibly a distinct species (see *Lepidopora* sp. A). Only much later CALVET became aware that his *Hornera eburnea*, as well as two other supposed bryozoans described by him (*H. verrucosa* and *H. gravieri* — see *Errina dabneyi* and *Pliobothrus symmetricus*), were stylasterid hydrocorals (CALVET, 1931: 45-46). This rectification had been reiterated in the bryozoan literature by BORG (1944: 203) and COOK (1968: 238).

HICKSON (1912b) erroneously referred specimens from the Azores ("Talisman") to *Pliobothrus tubulatus* (Pourtalès, 1867), a species known only from the western Atlantic (CAIRNS, 1986a). Intending to correct this confusion, and being unaware of CALVET's *Hornera eburnea*, BOSCHMA (1963a) erected a new species, *Errina (Lepidopora) hicksoni*, which he mentioned again in later papers. It lists as *Lepidopora hicksoni* in CAIRNS' (1983b) check list, in which the former subgenus *Lepidopora* had been elevated to generic rank. The "transphyletic" synonymy of BOSCHMA's stylasterid with CALVET's bryozoan was noted by ZIBROWIUS (1981).

DISTRIBUTION AND ECOLOGY

The typical branched form of *L. eburnea* is known from about 10 stations in the Azores at depths ranging from 480 m to 983 m.

Some branched colonies of *Lepidopora* from Seine Seamount (235 m) and Gorringe Seamount (460-545 m) between Madeira and Portugal resemble the Azorean *L. eburnea* (see *Lepidopora* sp. A).

SYMBIONTS

In the Azores, *L. eburnea* is frequently inhabited by *Pedicularia*. Two small specimens of this gastropod have been obtained from branches from an unknown station ("Jean Charcot" 1971, cruise BIAÇORES) and the characteristic traces (Fig. 1 C, 2 C) have also been found on material from several other stations ("Talisman" drag. 123; "Jean Charcot" 1971, cruise BIAÇORES, stn 161, 213, 229; "Bartlett" 1975, stn 2, 4). Material with *Pedicularia* traces includes the holotype, paratype, and topotypic specimens of *Errina (Lepidopora) hicksoni*; the trace on the paratype is obvious on two illustrations published by BOSCHMA (1963a, pl. 1, fig. 2-3).

Lepidopora sp. A

Fig. 1G-K, 3 A-U, 4 A-E

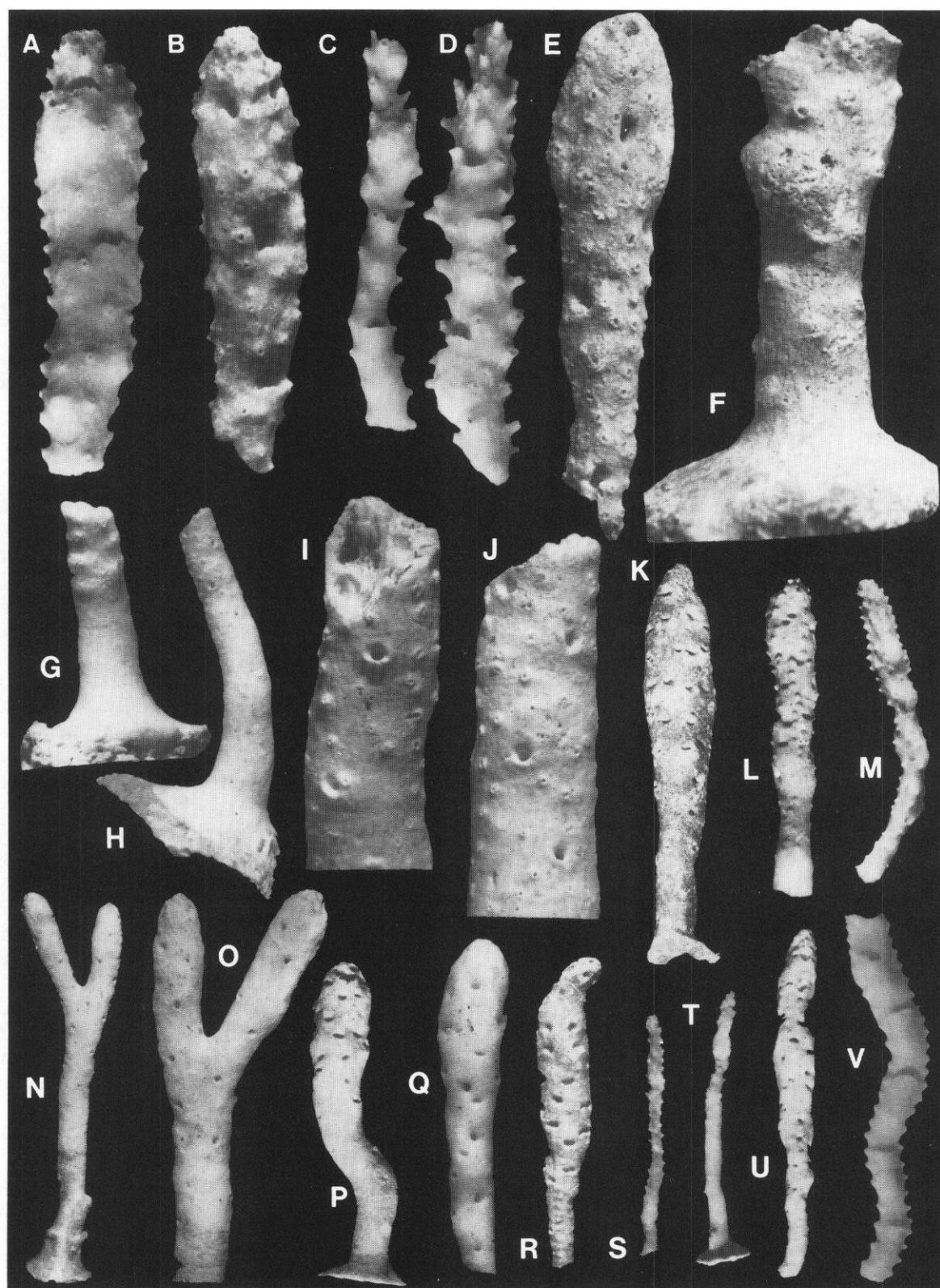
Chresonymy:

Hornera eburnea — CALVET, 1906: 479 (part, "Talisman" drag. 96, Mauritania).

Errina (Lepidopora) eburnea — ZIBROWIUS, 1981: 982 (part: "Talisman" drag. 96, Mauritania).

FIG. 3. — *Lepidopora* sp. A (A-E, from "Talisman" drag. 96, MNHN; F, from "Cryos" CP-95, MNHN; G-J, from "Calypso" 1958, SME-1277, MNHN; K-M, from "Noroit" DE-10, MNHN; N-O, from "Noroit" CP-12, MNHN; P, from "Noroit" CP-11, MNHN; Q-S, from "Noroit" DE-13, MNHN; T-U, from "Noroit" DW-108, MNHN): A, clavate form, same specimen as FIG. 4 A, opposite face illustrating gastro- and dactylopore arrangement ($\times 11$); B, clavate form, more eroded specimen with less regular gastro- and dactylopore arrangement ($\times 11$); C-D, slender form, distal branch fragments showing gastro- and dactylopores ($\times 11$); E, clavate form, larger eroded specimen ($\times 8.3$); F, lower part of colony with bulging ampulla and eroded surface ($\times 14$); G-H, lower part of colonies ($\times 9.1$, $\times 3.8$, respectively); I-J, two faces of distal end of H showing gastro- and dactylopore arrangement, I also showing internal ampullae ($\times 9.8$); K, eroded strongly clavate colony showing gastropores and large efferent pores of internal ampullae ($\times 3.5$); L, nearly complete slightly clavate colony showing gastro- and dactylopore arrangement ($\times 4.1$); M, nearly cylindrical curved colony showing bulging ampullae and distal dactylopores arranged in several ridges ($\times 4.1$); N, cylindrical colony dichotomous in distal part ($\times 2.8$); O, distal part of N, opposite face ($\times 4.6$); P, eroded clavate colony showing gastropores and large efferent pores of internal ampullae ($\times 4.1$); Q, incomplete clavate, like P ($\times 4.1$); R, eroded clavate colony, incomplete, showing many large efferent pores of internal ampullae ($\times 4.1$); S-T, slender cylindrical colonies ($\times 4.1$); U, eroded clavate colony showing gastro- and dactylopores and large efferent pores of internal ampullae ($\times 4.1$).

Lepidopora sp. B (V, from "Challenger", stn 85, BMNH 1890.4.11.24): V, unique specimen, branch face illustrating gastro- and dactylopore arrangement ($\times 5.7$).



MATERIAL STUDIED

Galicia, Gorrige and Seine Seamounts: "Calypso" 1958, stn SME-1277, 5 incomplete colonies, dead (MNHN). — "Noroit" 1987, cruise SEAMOUNT 1, stn DW-8, 6 specimens, basis or lower part of colonies (MNHN); stn DE-10, 9 specimens, mostly fragments, lower or upper parts (MNHN); stn CP-11, 18 specimens, including bases, incomplete and complete unbranched colonies, dead (MNHN); stn CP-12, 17 specimens, including lower and distal parts, unbranched colonies (MNHN); stn DE-13, ca. 70 specimens including bases and nearly complete unbranched colonies (MNHN); stn DW-21, 45 specimens, including bases, various fragments and incomplete colonies, many pieces branched (MNHN); stn CP-30, 3 specimens, including complete unbranched colony (MNHN); stn DW-78, 45 specimens including bases, lower parts and various fragments, many pieces branched (MNHN); stn DW-108, 13 specimens including various fragments, from base to nearly complete unbranched colony (MNHN); stn DW-111, 2 incomplete unbranched colonies (MNHN); stn DW-116, lower part of colony (MNHN).

Morocco: "Cryos" 1984, cruise BALGIM, stn CP-95, incomplete colony, dead (MNHN).

Mauritania: "Talisman" drag. 96, 12 colonies, some of them incomplete or in two pieces (MNHN).

DESCRIPTION

The first samples of *Lepidopora* obtained from Gorrige Seamount ("Calypso" 1958, stn SME-1277) comprise the lower part of 5 colonies (part of them considerably corroded). They are unbranched, up to 12 mm high, cylindrical, and decrease in diameter to the distal fracture (Fig. 3 G-J). Gastropores and dactylopores occur on all sides. Ampullae are internal.

Further material obtained from Gorrige Seamount ("Noroit" 1987, cruise SEAMOUNT 1, stn DW-8, DE-10, CP-11, CP-12, DE-13, DW-21, CP-30) is morphologically variable (Fig. 2 G-H, 3 K-S), but includes many tiny fragments, often in poor condition. Many pieces, including complete colonies, are similar to the earlier "Calypso" material: cylindrical and unbranched, up to 15 mm high and 1.5-3.3 mm in diameter. Ampullae internal to slightly bulging near distal end. Other unbranched specimens of similar size (up to 18 mm high) tend to a clavate shape, with intermediates from almost cylindrical to considerably widened in the upper part. Ampullae typically bulging, even vaguely packed into four straight lines in some specimens. A large transverse orifice up to twice as wide as a gastropore can be found in the distal part of bulging ampullae, but may be obstructed by calcareous deposit (Fig. 3 K, P, Q, R, U).

In addition to the unbranched, either slender cylindrical or clavate specimens, some lots from Gorrige Seamount (stn DW-10, CP-12, DW-21) comprise branched fragments or incomplete co-

lonies, with either internal or bulging ampullae. The better preserved bifurcating specimen from stn DE-10 is 7.5 mm high and its terminal branches are slightly clavate with distinct bulging ampullae (Fig. 3 N-O). The unique bifurcating colony from stn CP-12 is 22.5 mm high and cylindrical all along, with an average diameter of 2.4 mm. It bifurcates only in the upper third. Ampullae are not evident externally. Most pieces of the large lot from stn DW-21, up to 18 mm high and 3 mm in diameter, are branched (occasionally more than once) and show distinct ampullae.

Material from Seine Seamount (stn DW-78, Fig. 1 I-K) consists of one larger lot of mostly branched (and corroded) specimens similar to those from Gorrige Seamount (stn DW-21, Fig. 1 G-H). A few slender cylindrical unbranched specimens are also present, but no clavate ones.

Material from Galicia Seamount (stn DW-108, DW-111, DW-116) includes subcylindrical to clavate unbranched specimens (maximum size 15.5 mm, Fig. 3 T-U). A poorly preserved specimen looks branched, unless it results from specimens being attached one on the other.

All well preserved *Lepidopora* from the three seamounts resemble the Azorean *L. eburnea* by having white, linear-imbricate coenosteum composed of parallel strips. Gastropores may have distinct proximal lip. Gastrostyles are similar to those of *L. eburnea*, as are the dactylopores.

The unique specimen from Morocco ("Cryos" 1984, cruise BALGIM, stn CP-95), in very bad condition, is the lower part (6.5 mm high) of a small mature colony (ampullae present) (Fig. 3 F). Its diameter increases from the narrowest zone just above the encrusting base to the distal fracture and thereby is similar to clavate specimens from Gorringe Seamount and Mauritania.

Material from Mauritania ("Talisman" drag. 96) first mentioned by CALVET (1906) comprises 15 small unbranched pieces in poor condition. Some of these, belonging together, can be recombined into more complete colonies. Two forms can be distinguished on the basis of their general aspect.

The slender form (Fig. 3 C-D, 4 C-D) is slightly sinuous, thin, subcircular in cross section, and of rather uniform diameter. It is represented by 3 specimens, the largest of which (incomplete, base missing) is 7 mm high and up to 1.8 mm wide. The clavate form (Fig. 3 A-B, D, 4 A-B) is rather massive, straight, subcircular to slightly flattened in cross section, and notably wider in the upper part (Fig. 4 A). It is represented by 12 pieces, corresponding to

9 colonies, the largest of which (incomplete, base missing), is 10 mm high and up to 2.5 mm wide in the upper part. Distal branch tip of this form about 1.6 mm in diameter.

Both forms have white, linear-imbricate coenosteum composed of parallel strips about 0.15 mm wide. Their platelet structure (Fig. 4 C), although worn in all specimens, is very similar to that of *L. eburnea*.

Gastropores 0.32-0.44 mm in diameter, each bordered by a proximal lip, which is slightly more prominent in several of the clavate specimens (Fig. 4 A-B, 4 D-E). Gastrostyles could not be examined.

Conical to tubular dactylopore spines occur in lines on lateral branch edges as well as sparsely scattered on branch faces (Fig. 4 A-B, 4 D-E). Dactylopores 67-80 μ m in diameter and up to 0.25 mm tall, directed perpendicular to branch surface. Dactylopore centers about 0.37 mm apart.

Ampullae (female ?) superficial, about 0.55 mm in diameter. No efferent pores noted.

COMPARISONS

The northeastern Atlantic stylasterids here provisionally grouped under *Lepidopora* sp. A appear to reflect a disconcerting range of colony shape. Although we can see differences especially between the end points, i.e. the typical Azorean *L. eburnea* and the distinctive clavate form from Gorringe Seamount and Mauritania, we hesitate to draw a line. All these forms are clearly similar in coenosteal texture; dactylopore arrangement; gastropore lips; female ampullar size, location, and efferent pore location; and gastrostyle shape. Structural uniformity thus contrasts with variation in colony shape. Typical Azorean *L. eburnea* is repeatedly branching, whereas the clavate form is typically unbranched (as is the slender cylindrical form, with intermediates tending to the clavate one). But there are transitional specimens (occasionally with a clavate tip) that have long sections without bifurcation resulting in consequently smaller colonies. We are not sure that slight size difference, such as larger gastropores, higher and larger dactylopore spines, and wider coenosteal strips are consistent and should be considered as essential arguments for species distinction.

Our comparison may also be biased by the lack of early ontogenetic stages and young colonies of typical *L. eburnea* from the Azores, sorting of dredge contents on "Jean Charcot" cruise BIAÇORES having been less detailed than on "Noroit" cruise SEAMOUNT 1. Obviously more well preserved specimens, including from intermediate areas, must be examined to better understand this group.

REMARKS

Stylasterids from 2 stations of the "Talisman" were referred by CALVET (1906) to the species he had previously described from the Azores and mistaken for a bryozoan. In fact, CALVET's specimens from drag. 128 (Azores) are typical *Lepidopora eburnea*, whereas those from drag. 96 (Mauritania) are here included under *Lepidopora* sp. A (distinction not yet made by ZIBROWIUS, 1982).

DISTRIBUTION AND ECOLOGY

Stylasterids here grouped under *Lepidopora* sp. A are known from Galicia Seamount (675-1125 m), Gorringer Seamount (470-2075 m), Seine Seamount (235 m), off Morocco (1378 m), and off Mauritania (2320-2330 m), i.e. from a wider depth range than typical *L. eburnea* in the Azores. Unbranched specimens, slender cylindrical and clavate, occur down to the greatest depths, whereas specimens more similar to *L. eburnea* were obtained on the seamounts only at shallower depths (235-545 m).

No symbionts are known.

Lepidopora sp. B

Fig. 3 V, 4 F-H

MATERIAL STUDIED

Canary Islands: "Challenger" stn 85, dorsoventrally flattened fragment (BMNH 1890.4.11.24); 3 minor cylindrical fragments from same lot are specifically different and not considered here (accidental mixture in museum collection ? indication of origin reliable ?).

DESCRIPTION

The study material consists of one dorsolaterally flattened, slightly sinuous unbranched upper branch fragment (Fig. 3 V) without the distal end, 10.5 mm high and 1.5 mm wide at the widest point. Coenosteal strips 0.12 mm wide, covered by small granules. Five gastropores arranged along midline of anterior face, each bordered by a very broad crescent shaped proximal lip (Fig. 4 G-H) about 0.7 mm wide and 0.3 mm deep. Elongate gastrostyles present but not available for detailed study. Dactylopore mounds linearly

arranged along each lateral branch edge, their centers about 0.43 mm apart. Dactylopores elliptical (e.g. 78 x 56 μ m in diameter), the greater axis aligned with the branch axis (Fig. 4 G). Dactylopore mounds about 0.15 mm tall and 0.18 mm in diameter. Superficial swellings (? female ampullae) occur proximal to each gastropore on anterior face and in a staggered arrangement on posterior face, each about 0.7 mm in diameter. No efferent pores observed.

COMPARISONS

Lepidopora sp. B is similar to *Lepidopora* sp. A (clavate form), particularly regarding its flattened branches and lateral rows of dactylopore mounds. *Lepidopora* sp. B differs in coenosteal texture (granular, not linear-imbricate), having extremely prominent gastropore lips, lacking dactylopores on branch faces, and having elliptical dactylopores (not circular).

Compared to typical *L. eburnea* from the Azores, *Lepidopora* sp. B has much broader gastropore lips, larger dactylopores, and only two lateral rows of dactylopores. It is similar to the western Atlantic *L. glabra* (Pourtales, 1867) in dactylopore - gastropore coordination, but the coenosteal texture is quite different.

REMARKS

At the BMNH the unique sample of *Lepidopora* sp. B was found labeled "Hydrocorallinae Stylasteridae". MOSELEY (1881) probably had not seen it when he studied the "Challenger" stylasterids.

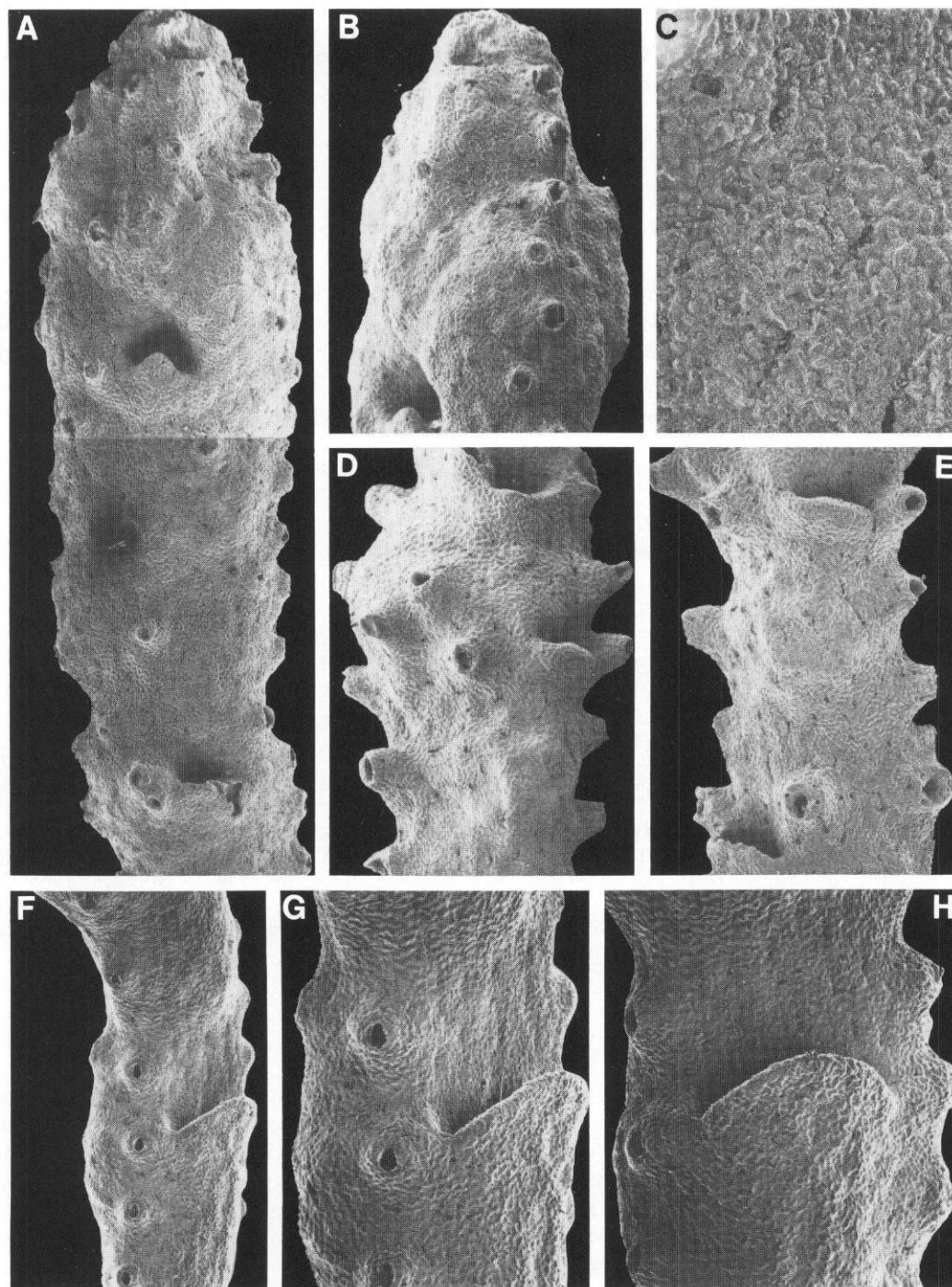


FIG. 4. — *Lepidopora* sp. A (A-E, from "Talisman" drag. 96, MNHN): A, clavate form, distal branch face illustrating gastro- and dactyloporous ($\times 23$); B, clavate form, distal branch edge showing aligned dactyloporous and proximal gastropore lip ($\times 26$); C, slender form, coenosteal texture ($\times 116$); D-E, slender form, branch faces of two female (?) specimens ($\times 28$, $\times 29$, respectively).

Lepidopora sp. B (F-H, from "Challenger" stn 85, BMNH 1890.4.11.24): F-H, lateral, oblique, and top views of branch fragment illustrating dactyloporous and proximal gastropore lip ($\times 23$, $\times 40$, $\times 40$, respectively).

DISTRIBUTION AND ECOLOGY

Lepidopora sp. B is known from only one station in the Canary Islands, at a much greater depth (2100 m) than the typical Azorean *L. eburnea*.

No symbionts are known.

Genus *PLIOBOTHRUS* Pourtalès, 1871

Diagnosis. — Gastro- and dactylopores randomly arranged. Coenosteal texture linear-imbricate; coenosteal pores large. Gastropore tube double-chambered (see CAIRNS, 1983b: 439); no gastrostyles. Dactylopore spines conical or tubular; dactylopore tubes quite long; no dactylostyles. Ampullae usually internal.

Type species: *Pliobothrus symmetricus* Pourtalès, 1868, from the western Atlantic.

Pliobothrus is represented in the study area by 2 species, including the type species.

Pliobothrus symmetricus Pourtalès, 1868

Fig. 5 A-G, 6 A-G

Synonymy:

Pliobothrus symmetricus Pourtalès, 1868: 141.

Hornera gravieri CALVET, 1911: 7, fig. 5.

Chresonymy:

Pliobothrus symmetricus — DUNCAN, 1870: 290, 297; 1873: 336, pl. 49, fig. 7. — POURTALÈS, 1871: 57, pl. 4, fig. 7-8; 1878: 211. — MOSELEY, 1879: 469, 479, 440-442 (Florida), pl. 41, fig. 2 (part, NOT “*Challenger*” stn 23, Sombrero Island); 1881: 47-50, 78, 84, pl. 8, fig. 2 (part, NOT “*Challenger*” stn 23, Sombrero Island). — AGASSIZ, 1888: 138-139, fig. 444. — NUTTING, 1895: 84. — HICKSON, 1912b: 465-466. — BROCH, 1914a: 3-7, pl. 1, fig. 1-3, pl. 3, fig. 19-20, 28-29, pl. 4, fig. 34, 40-42, text-fig. A-B. — DONS, 1939: 196-197, fig. 1. — BOSCHMA, 1956b: F104, fig. 85.1a-b; 1957a: 59-60; 1967: 333-335, pl. 1, fig. 5-6. — SQUIRES, 1965: 24, pl. 2, fig. 7-8. — ZIBROWIUS, 1981: 269; 1982: 982 (part, NOT Hyères Seamount). — ZIBROWIUS & CAIRNS, 1982: 211, 212 (part, NOT Hyères Seamount). — CAIRNS, 1983b: 428, 439-441, fig. 3A-H, 24G, 25G, 27B (part, NOT stn J-S 43); 1986a: 16-17, fig. 6A-H (part, NOT Hyères Seamount).

Hornera gravieri — CALVET, 1931: 46. — BORG, 1944: 203.

TYPES

Pliobothrus symmetricus: In the original description POURTALÈS (1868) simply reported *P. symmetricus* as being “not rare between 100 and 200 fathoms off the Florida reef”. In a later more detailed and illustrated description (POURTALÈS, 1871) he reported the species from 7 dredging stations in the same area. CAIRNS (1983b: 441) selected one of these as type locality and designated a lectotype (colony illustrated by POURTALÈS, 1871, pl. 4, fig. 7; CAIRNS, 1983b, fig. 3 A; CAIRNS, 1986a, fig. 6 A) and a paralectotype, among material deposited at the MCZ (5529, 5530, respectively). The YPM possesses another paralectotype (CAIRNS, 1986a).

Type locality: Restricted by CAIRNS (1983b) to “*Bibb*” stn 64, 11.5.1868, 24°17'N, 81°43'W, 262 m. Off Sand Key/Key West, Florida.

Hornera gravieri: CALVET (1911) reported *H. gravieri* from 11 stations in the Azores (Prince of Monaco stn 568, 584, 597, 616, 618, 683, 712, 719, 838, 866, 869) and mentioned “several beautiful colonies and many fragments”. CALVET did not designate the type locality and select types. None of the specimens seen by CALVET could be found and all may be lost (see ZIBROWIUS, 1982).



FIG. 5. — *Pliobothrus symmetricus* (A, from "Talisman" drag. 123, MNHN; B, from "Jean Charcot" 1971, unknown station, Azores; C-D, from "Thalassa" z-435, MNHN; E-F, from "Thalassa" z-407, MNHN; G, from "Challenger II" 1977, stn 134, BMNH 1986.11.5.2); A, large colony ($\times 1.3$); B, colony ($\times 1.1$); C, distal branch with *Pedicularia* trace ($\times 3.3$); D, branch illustrating gastro- and dactylopore arrangement ($\times 3.3$); E, distal part of colony ($\times 1.8$); F, detail of E illustrating gastro- and dactylopores ($\times 4.1$); G, dichotomous branch ($\times 2.4$).

Pliobothrus gracilis (H-L, from "Calypso" 1959, drag. 6, MNHN; M-N, from "Calypso" 1959, drag. 4, MNHN): H-I, holotype, opposite faces (both $\times 1.7$); J-K, details from holotype with bulging female ampullae (both $\times 3.0$); L-N, paratypes (all $\times 1.3$).

MATERIAL STUDIED

W Atlantic: Lectotype and paralectotype of *P. symmetricus* and additional specimens identified by POURTALÈS (MCZ; BMNH 1869.1.25.16, 1891.2.4.42, 1891.12.18.1).

Faroës: "*Michael Sars*" 25.2.1904, colony + fragments (VSM).

Faroës — Hebrides area: "*Porcupine*" 1869, station data uncertain, colony + branch (BMNH 1883.12.10.131, 1898.5.7.17).

W Ireland: "*Challenger II*" 1977, stn 134, 4 branches (BMNH 1986.11.5.2). "*Challenger II*" 1981, stn 30, colony (BMNH 1989.6.16.1).

Celtic Sea: "*Thalassa*" stn z-407, branch (MNHN); stn z-415, distal branch fragment (MNHN); stn z-435, 31 colonies + 60 branches/fragments (most MNHN; USNM 77121).

S Bay of Biscay: "*Travailleur*" drag. 70, branch (MNHN).

Galicia and Josephine Seamounts: "*Noroit*" 1987, cruise SEAMOUNT 1, stn DW-56, 6 fragments (MNHN); stn DW-58, 3 fragments (MNHN); stn DW-111, 2 poorly preserved fragments, probably of *P. symmetricus* (MNHN).

Madeira Archipelago: "*Jean Charcot*" 1966, stn 49, 4 poorly preserved fragments probably of *P. symmetricus* (MNHN).

Azores: "*Talisman*" drag. 123, colony (MNHN). — "*Jean Charcot*" 1971, cruise BIAÇORES, stn 34, branch (MNHN); stn 161, colony + 2 branches (MNHN); stn 197, colony (MNHN); stn 213, colony (MNHN); stn 218, 4 colonies + fragments (most MNHN; USNM 75601); stn 229, 5 colonies + 2 branches (MNHN); stn 231, 12 colonies + 9 branches (most MNHN; USNM 77120); stn 232, 4 colonies + 2 branches (MNHN); stn 240, 15 small colonies on pebbles, provisionally included here, identity uncertain — see comparisons (most MNHN; USNM 77119); unknown station, 2 colonies + fragments (MNHN).

Imprecise locality southwest of the Azores: said to come from seamount 260 miles (?) [475 km] southwest of Faial, ca. 500 m, fishing boat "*Tomiguel*", coll. J.G. PEREIRA, Sept. 1976, 2 colonies + 8 branches/fragments (MNHN).

DESCRIPTION

Eastern Atlantic specimens: colonies uniplanar, up to 60 mm high and 68 mm wide (Fig. 5 A-B). Branches robust, cylindrical to slightly flattened along branching plane, 2.5-3.0 mm in diameter. Branches gradually taper to blunt tips; branch axils U-shaped. Coenosteal strips 80-95 μ m wide, separated by large, round to elongate pores up to 65 μ m wide. Platelets variable in ornamentation, ranging from broad flat platelets (Fig. 6 F), to corrugated narrow platelets (Fig. 6 D-E), to an irregular arrangement of imbricating spines (Fig. 6 G). Sometimes two different textures occur on the same colony.

Gastro- and dactylopores occur on all branch surfaces but are more common on anterior branch face (Fig. 5 D-G). Gastropores round to slightly elliptical and 0.30-0.45 mm in

diameter, although most colonies have some smaller diameter gastropores (e.g. 0.20 mm), which may reflect developing gastropores or a different size class. Dactylopore spines tubular, up to 0.20 mm tall and 0.15 mm in diameter, with a wall thickness of about 38 μ m.

Female ampullae internal and 0.8-0.9 mm in diameter, communicating to branch surface by a tube that terminates in a spongy area on coenosteum 0.15-0.25 mm in diameter. Male ampullae also internal and round to elliptical, with greater axis perpendicular to branch surface. Male ampullae 0.3-0.4 mm long, terminating in a slit like efferent pore 0.05-0.11 mm long aligned with a coenosteal slit. Ampullae from western Atlantic material figured by CAIRNS (1986a) were female.

COMPARISONS

Of the 3 other species in the genus (all occurring in the Atlantic), *P. symmetricus* is distinguished from *P. tubulatus* (Pourtalès, 1867), by its shorter dactylopore spines and more robust

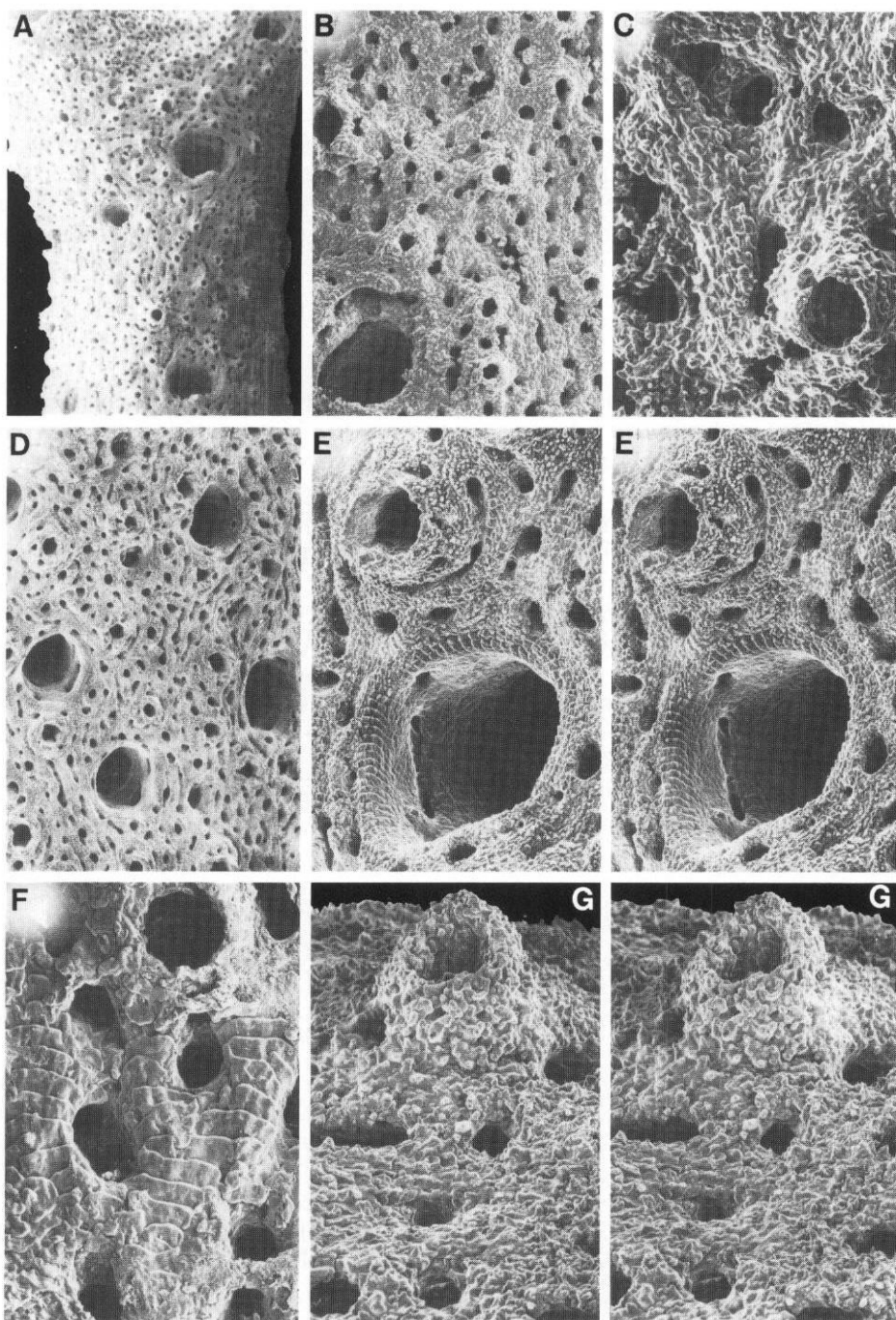


FIG. 6. — *Pliobothrus symmetricus* (A-C, from "Jean Charcot" 1971, stn 218, male, USNM 75601; D-E, from "Thalassa" z-435, male, USNM 77121; F, from imprecise "Tomiguel" locality, male, MNHN; G, from "Talisman" drag. 123, MNHN): A, branch face illustrating gastro- and dactylopores ($\times 11$); B, gastropore and several dactylopores ($\times 33$); C, dactylopore and coenosteal texture ($\times 96$); D, branch face illustrating large gastropores, smaller dactylopores, and even smaller irregularly shaped coenosteal pores ($\times 19$); E, detail of large gastropore and one dactylopore, coenosteal texture of narrow imbricate platelets ($\times 55$, stereo pair); F, coenosteal texture of broad flat platelets ($\times 121$); G, dactylopore and rough coenosteal texture of imbricate spines ($\times 119$).

branches; from *P. echinatus* Cairns, 1986, by its nonspinose coenosteum and smaller gastropore diameter; and from *P. gracilis* n. sp., by its internal female ampullae and larger gastropores.

One lot of 15 specimens of *Pliobothrus* from the Azores ("Jean Charcot" 1971, cruise BIAÇORES stn 240) is specially discussed here (Fig. 7 A-I). These specimens are unlike any of the other known species of *Pliobothrus* in a number of characters. Their gastropores are circular and only 0.16-0.18 mm in diameter. Coenosteal pores are very narrow (e.g. 9 µm) producing a very dense coenosteal texture, not porous as in the other species. The dactylopore spines are conical mounds instead of thin walled tubes and all of the colonies are short and sparsely branched (or unbranched) with a firmly attached base. Several colonies bear low superficial female ampullae about 1 mm in diameter, invariably with an efferent pore on the upper (distal) edge of the ampulla.

REMARKS

P. symmetricus has occasionally been confused with each of the other species of *Pliobothrus* occurring in the western and eastern Atlantic (rectification in CAIRNS, 1986a, and herein). MOSELEY (1879, 1881) erroneously attributed to *P. symmetricus* a specimen of *P. tubulatus* (Pourtalès, 1867) from "Challenger" stn 23 (Sombrero Island, West Indies). Nevertheless, he based his detailed study of the skeleton and of the soft parts on authentic *P. symmetricus* (specimens from Florida, sent to him by POURTALÈS, cf. MOSELEY, 1879: 440; 1881: 47). CAIRNS (1983b) mistakenly included under *P. symmetricus* a record which he subsequently (1986a) transferred to a new species, *P. echinatus* Cairns, 1986. In the eastern Atlantic *Pliobothrus gracilis* n. sp. from Hyères Seamount, described in this paper, had also erroneously been included under *P. symmetricus* (ZIBROWIUS, 1982; ZIBROWIUS & CAIRNS, 1982; CAIRNS, 1986a).

In the eastern Atlantic, *P. symmetricus* has been mistaken for a bryozoan, described as *Hornera gravieri* Calvet, 1911. Only much later CALVET (1931: 45-46) became aware that his *H. gravieri* was a stylasterid hydrocoral. This rectification was mentioned again by BORG (1944: 203) and COOK (1968: 238). The "transphyletic" synonymy of CALVET's (1911) bryozoan with POURTALÈS' (1868) stylasterid was noted by ZIBROWIUS (1982).

DISTRIBUTION AND ECOLOGY

In the western Atlantic, which includes the type locality of *P. symmetricus*, distribution and depth range have been studied by CAIRNS (1986a). The species occurs mostly between 150 m and 400 m from the Blake Plateau off South Carolina through the Lesser Antilles, including the Pourtalès Terrace off Florida.

In the eastern Atlantic *P. symmetricus* is known from many stations between 63°35'N and 31°26'N: southeast of Iceland, east of the Faroes, between the Faroes and the Hebrides, Norway (62°31'N and 62°15'N), west of Ireland, Celtic Sea, Bay of Biscay, Galicia and Josephine Seamounts, Madeira Archipelago (to be confirmed, presently available material in poor condition), Azores, and an unidentified seamount southwest of the Azores. We have seen material from most of these areas except from southeast of Iceland and from Norway; however, the specimens reported from these two areas have been adequately described and figured (BROCH, 1914a; DONS, 1939) and are included here without hesitation.

Its depth range in the eastern Atlantic is from 80 m and 250-300 m for the shallowest stations off Norway (DONS, 1939) to 1550 m and 1600 m for the deepest stations in the Azores (CALVET, 1911, as *Hornera gravieri*). It is unknown whether live material had been obtained at these deepest stations; in the Azores, with locally very irregular and steep slopes, dead specimens are occasionally collected at uncommonly great depths. The deepest confirmed record of live material is 1050 m in the Celtic Sea ("Thalassa" stn Z-435).

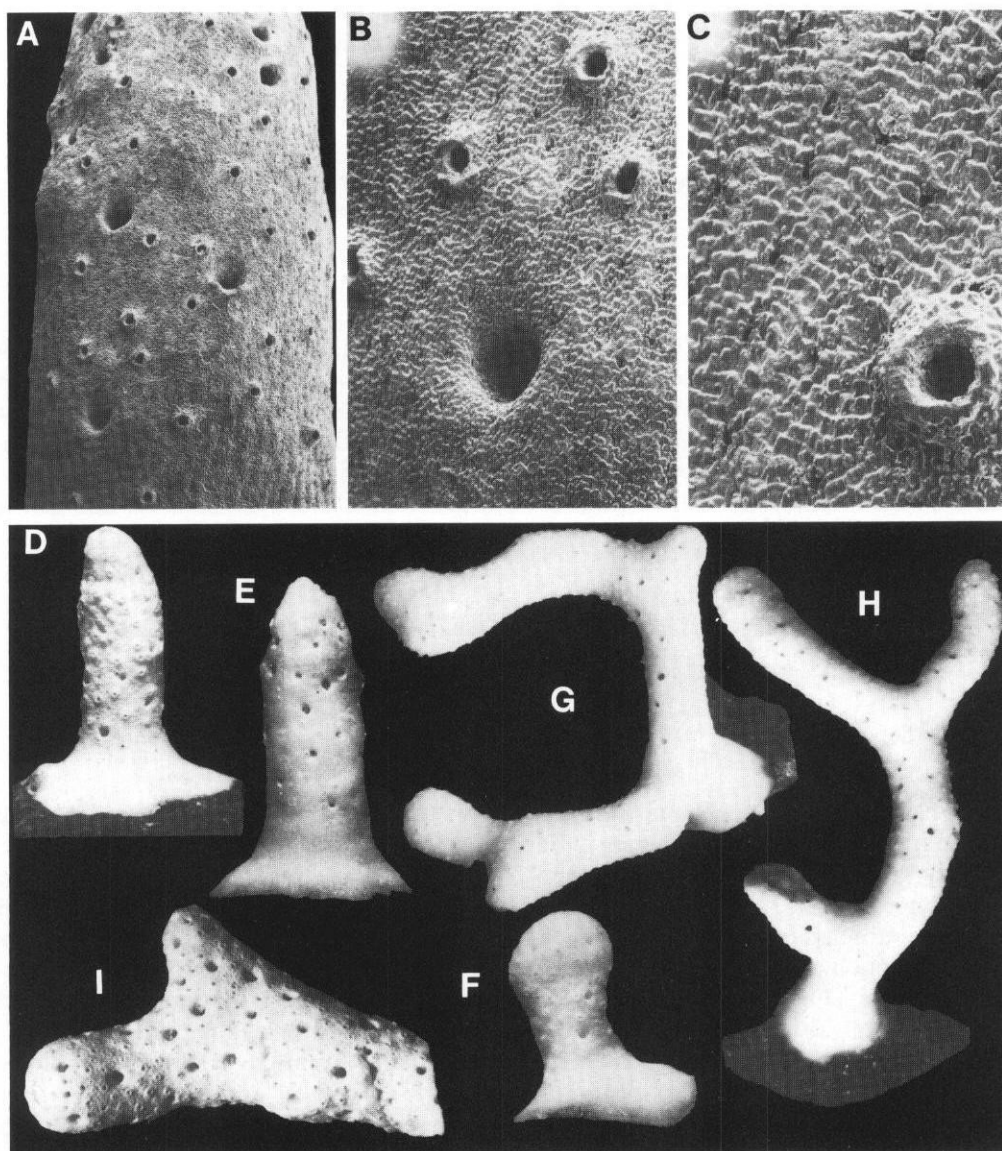


FIG. 7. — *Pliobothrus* sp. (A-I, from "Jean Charcot" 1971, stn 240, MNHN): A, tip of small unbranched colony illustrating several gastropores and more numerous smaller dactylopores ($\times 17$); B, coenosteum bearing one gastropore and four dactylopores ($\times 49$); C, detail of branch showing a dactylopore and coenosteal texture ($\times 76$); D-F, small unbranched colonies ($\times 4.1$, $\times 4.1$, $\times 3.9$, respectively); G-H, larger branched colonies ($\times 2.7$, $\times 2.6$, respectively); I, distal branch tip illustrating gastro- and dactylopore arrangement ($\times 3.9$).

SYMBIONTS

In the northeastern Atlantic, *P. symmetricus* is the host of *Pedicularia*, but, curiously, among the abundant material studied here, only 3 branches from 2 stations in the Celtic Sea have been found with the characteristic traces of the gastropod ("Thalassa" stn z-415, z-435; Fig. 5 C).

MOSELEY (1879: 469; 1881: 78) reported parasitic organisms thought to be pycnogonid larvae from the gastric cavities of gastrozooids of *P. symmetricus* dredged off Florida by POURTALÈS. No similar association is yet known from the northeastern Atlantic.

Pliobothrus gracilis new species

Fig. 5 H-N, 8 A-G

Chresonymy:

Pliobothrus symmetricus — ZIBROWIUS, 1982: 982 (part: Hyères Seamount). — ZIBROWIUS & CAIRNS, 1982: 212 (part: Hyères Seamount). — CAIRNS, 1986: 17 (part: Hyères Seamount).

TYPES

Holotype and paratypes of *Pliobothrus gracilis* from 2 stations on slope of Hyères Seamount, "Calypso" 1959, drag. 4 and drag. 6. Holotype a female colony collected alive from drag. 6, without base (Fig. 5 H-I). Paratypes 3 colonies (2 with base) from drag. 4 and 3 colonies or branches (all without base) and 2 minor fragments from drag. 6; paratypes up to 30 mm high and 35 mm wide. Holotype and most paratypes at MNHN, 1 paratype from drag. 6 at USNM (77118).

Type locality: "Calypso" 1959, drag. 6, 13.8.1959, 31°27.7'N, 28°55.6'W, 620-700 m, Hyères Seamount.

MATERIAL STUDIED

Hyères Seamount: holotype and paratypes.

DESCRIPTION

Colonies uniplanar: holotype 38 mm high and 36 mm wide, paratypes smaller. Branches cylindrical, gradually tapering through regular dichotomous branching to blunt, rounded branch tips. Branches slender, subterminal branches 1.25-1.75 mm in diameter; branch axils U-shaped. Coenosteum linear-imbricate (Fig. 8 E), the strips 65-80 µm wide and of variable length, producing a very porous coenosteum. Platelets flat and irregularly shaped, about 25 µm wide, occurring three or four across a strip. Granular coenosteum sometimes also present on same specimen bearing linear-imbricate texture, the granules about 18 µm in diameter (Fig. 8 F).

Gastropores occur in low density on all branch surfaces but are most common on anterior face.

Gastropores small and usually circular (e.g. 0.18-0.25 mm in diameter) but may also be elliptical, the greater axis parallel to branch axis (e.g. 0.29 x 0.19 mm). Dactylopore spines also scarce but most common on anterior branch face. Dactylopore spines tubular, up to 0.10 mm tall and 0.15 mm in diameter, with thin walls about 38 µm thick (Fig. 8 B).

Female ampullae superficial mounds (Fig. 5 J-K, 8 G) 1.0-1.2 mm in diameter occurring on both anterior and posterior branch faces. Efferent pores 0.17-0.19 mm in diameter and usually slightly off center from apex of bulge. Male ampullae not discerned in limited material available.

COMPARISONS

P. gracilis is distinguished from the other 3 species of *Pliobothrus* by its superficial female ampullae and very small gastropores. It is further distinguished from *P. symmetricus* by its very slender branches and low density of gastro- and dactylopores. *P. gracilis* is similar to the Azorean *Pliobothrus* from "Jean Charcot" 1971, cruise BIAÇORES stn 240 (see *P. symmetricus*, Comparisons) in having superficial female ampullae and small circular gastropores, but differs in other characters, such as: placement of efferent pore, coenosteal texture, colony size, and polyp density.

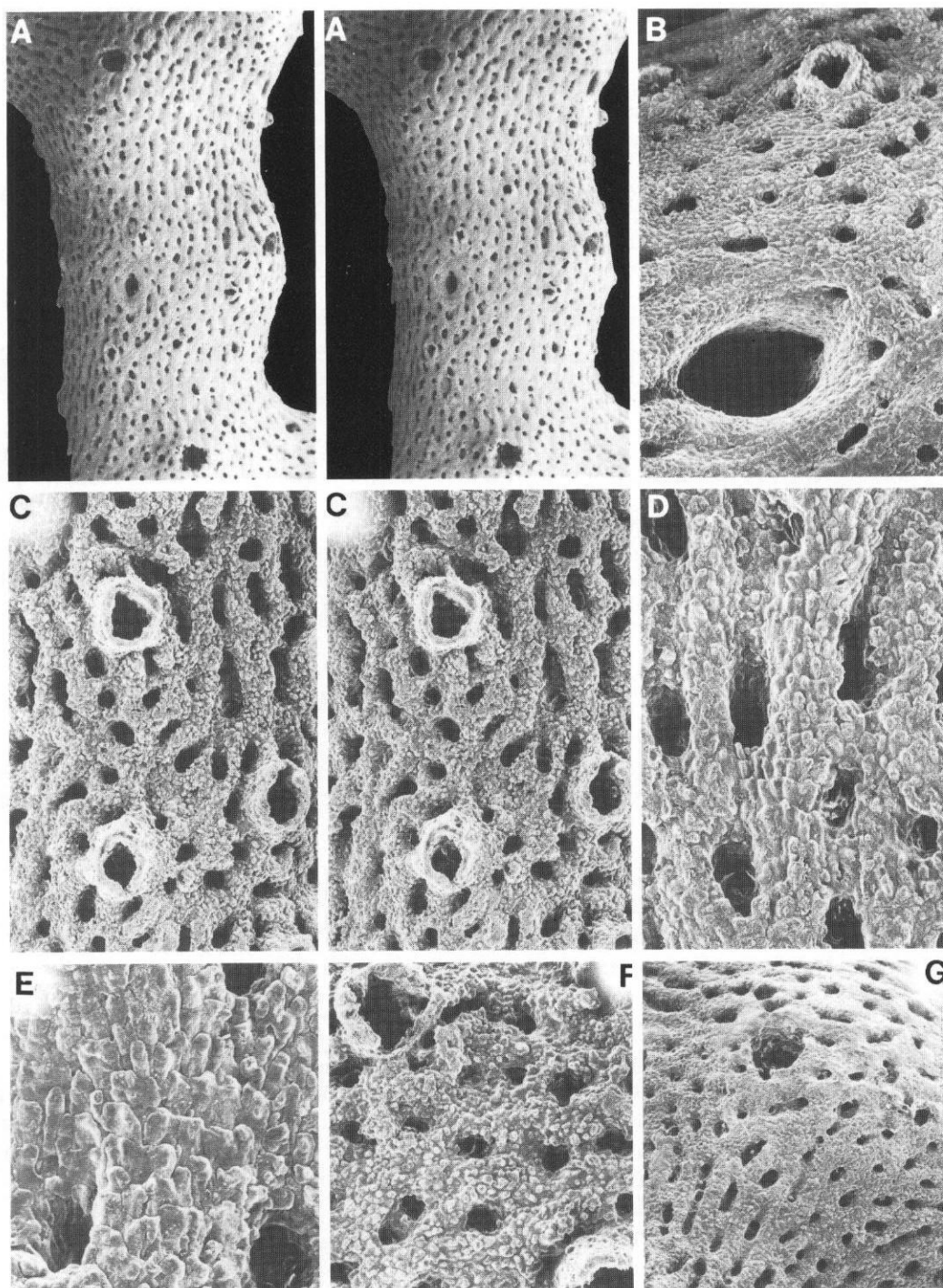


FIG. 8. — *Pliobothrus gracilis* (A-G, from "Calypso" 1959, drag. 6, female paratype, USNM 77118): A, branch face showing efferent pores of three female ampullae, no gastropores evident ($\times 18$, stereo pair); B, oblique view of coenosteum illustrating elliptical gastropore and conical dactylopores ($\times 66$); C, top view of coenosteum illustrating three dactylopores and coenosteal texture ($\times 61$, stereo pair); D-E, coenosteal texture ($\times 143$, $\times 235$, respectively); F, granular coenosteum and two dactylopores ($\times 87$); G, female ampulla with large apical efferent pore ($\times 40$).

	<i>E. aspera</i>	<i>E. dabneyi</i>	<i>E. atlantica</i>
colony shape	uniplanar to slightly bushy	uniplanar	bushy, sparsely branched
branches: taper; distal branch diameter	gradual taper; 0.7 mm	abrupt taper; 0.6 mm	gradual taper; 0.9 mm
coenosteal texture	reticulate-granular but imbricate dactylopore spines	reticulate-granular	reticulate-granular
gastropore lip	absent	present	absent
gastrostyle shape	ridged H:W = 1.5-3.3	ridged H:W = 3.5	ridged H:W = 2.3-3.3
dactylopore spines: individuality; height, width	some clustering; up to 0.65 mm, 0.27 mm	individual; 0.13-0.15 mm, 0.15 mm	individual; 0.14-0.16 mm, 0.25-0.27 mm
male ampullae: position; efferent pore location	internal; one irregularly shaped efferent pore 30-40 µm in diameter	superficial; 1-3 apical efferent pores	primarily internal; one round efferent pore 50-60 µm in diameter
other diagnostic characters	many small dactylopores without associated spine	coenosteal papillae sometimes present, branch anastomosis occasionally	larger colonies with eunicid polychaete

REMARKS

The specific name given to the new species refers to the slender form of the branches.

Previously, this form from Hyères Seamount had not been distinguished from the presumed widespread *P. symmetricus*.

DISTRIBUTION AND ECOLOGY

P. gracilis is known only from 2 stations on the slope of Hyères Seamount, depth 600-700 m. No symbionts are known.

Genus *ERRINA* Gray, 1835

Diagnosis. — Gastro- and dactylopores usually randomly arranged. Coenosteal texture reticulate-granular or linear-imbricate. Proximal gastropore lips common; gastrostyles present, having a moderate H:W ratio. Dactylopore spines U-shaped, with groove directed proximally; walls of dactylopore spines thick; no dactylostyles. Ampullae superficial.

Type species: *Millepora aspera* Linnaeus, 1767, from the Mediterranean.

Errina is represented in the study area by 3 species, including the type species.

Errina aspera (Linnaeus, 1767)

Fig. 9 A-I, 10 A-H

Synonymy:

Millepora aspera Linnaeus, 1767: 1283.

Errina aspera mascarina Boschma, 1965a: 3-6, text-fig. 1, pl. 1, fig. 1-4.

<i>E. cochleata</i>	<i>E. altispina</i>
uniplanar	uniplanar
abrupt taper; 0.3-0.7 mm	gradual taper; 0.4 mm
linear-imbricate, multiloculate platelets	linear-imbricate, broad platelets
present, prominent not ridged H:W = 3.6	present, prominent not ridged H:W = 4.9
individual; 0.10 mm, 0.10-0.13 mm	individual, two types of spines 1) 0.10 mm, 0.11 mm 2) 0.50 mm, 0.12 mm
* superficial; several apical efferent pores giving ampullae spiny aspect	* similar to that of <i>E.</i> <i>cochleata</i>
gastropores restricted to center of anterior face and branching axils	coenosteal papillae sometimes present

TABLE 1. — Distinguishing characters of the five North Atlantic species of *Errina* (with new information on two species from the West Indies *)

Chresonymy:

- Millepora aspera* — ESPER, 1790: pl. 18, fig. 1-4; 1795: 106. — LAMARCK, 1816: 202. — RISSO, 1826: 347-348. — DARWIN, 1854: 477, pl. 19, fig. 5a. — ARADAS & BENOIT, 1876: 301.
- Errina aspera* — GRAY, 1835: 85. — DANA, 1848: 570-571. — SAVILLE KENT, 1871: 282-283. — MOSELEY, 1879: 479; 1881: 84. — CARUS, 1885: addendum. — FOL, 1885: 668-669. — BOSCHMA, 1953a: 32-33; 1953b: 301, etc.; 1954: 143, etc., pl. 1-3; 1956a: 283, 284, 286, 288; 1956b: F100; 1957a: 50-51; 1963a: 337, etc.; 1964f: 284; 1964g: 288; 1965b: 19; 1967: 329, 330, 331, 333. — ARNAUD & ZIBROWIUS, 1979: 123-124. — FREDJ & GIERMANN, 1982: 284-285, photo 1-8. — CAIRNS, 1983b: 428, 459-462, fig. 11A-G. — DI NATALE & MANGANO, 1985: 344.
- GIACOBBE & LEONARDI, 1985. — DI GERONIMO & FREDJ, 1988: 243, pl. 1, fig. 1-4.
- Errina aspera aspera* — BOSCHMA, 1965a: 1-3, text-fig. 2, pl. 1, fig. 5-7.
- Errina (Labiopora) aspera* — HICKSON, 1912a: 888-889, pl. 95, fig. 6; 1912b: 462.
- Errina aspera mascarina* — VERVOORT & ZIBROWIUS, 1981: 29.
- Hydrocoralliaire — PÉRÈS, 1964: 21.
- NOT *Errina aspera* — VERRILL, 1864: 46 (Azores). — POURTALÈS, 1867: 116 (Azores).
- NOT *Erina aspera* — BOSCHMA & LOWE, 1969: 15, pl. 5, map 2.
- NOT *Errina (Eu-Errina) aspera* — BROCH, 1942: 40, fig. 10.

TYPES

Millepora aspera: In the original description, LINNAEUS (1767) characterized a structure which we now recognize as typical dactylopore spines (prominent outgrowths with slit-like pore on the lower side). This is a detail that he could not have found in the previous literature (MARSILI, 1725; GUALTERI, 1742) and proves that he had before him at least one authentic specimen. The type could not be found and is probably lost. HICKSON (1912a: 888) said that he examined "the type-specimen of this species [*aspera*] in the British Museum" on which GRAY (1835) founded the genus *Errina*. This simply means that he has seen the specimen previously studied by GRAY who made LINNAEUS' species the type of the genus *Errina*.