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TAXONOMIC CHARACTERS IN CARIBBEAN *MILLEPORA* SPECIES (HYDROZOA, COELENTERATA)

by

WALENTINA H. DE WEERDT

Institute of Taxonomic Zoology, University of Amsterdam, P.O. Box 20125, 1000 HC Amsterdam, The Netherlands

SUMMARY

In order to find characters in *Millepora* species with a higher diagnostic value than the growth form (on which species delimitation is hitherto based) a comparison is made of the surface structure, microstructure of the skeleton, structure of the ampullae coverings, size of the gastropores and dactylopores, and pore density in specimens of the four species occurring in the Caribbean region: *Millepora alcicornis*, *M. complanata*, *M. squarrosa*, and *M. striata*. While most characters are of little taxonomic value, pore sizes and densities are surprisingly useful. The species are diagnosed and some biogeographical remarks are given.

RÉSUMÉ

Afin de trouver dans les espèces de *Millepora* des caractères de valeur diagnostique supérieure par rapport aux caractères du habitus (sur lesquels la délimitation des espèces est jusqu'à présent fondée), on a effectué des comparaisons sur: les structures superficielles, les microstructures du squelette, la structure des revêtements des ampullae, la taille des gastéropores et des dactylopores, ainsi que sur la densité des pores, dans des exemplaires des quatre espèces des Caraïbes: *M. alcicornis*, *M. complanata*, *M. squarrosa*, *M. striata*. La plupart de ces caractères s'avèrent être de peu de valeur pour la taxonomie, mais la taille et la densité des pores se montrent remarquablement utiles. Des diagnoses sont fournies et des remarques biogéographiques formulées pour les espèces mentionnées.

INTRODUCTION

Species delimitation in the hydrocoral *Millepora* (Milleporidae, Capitata, Hydrozoa), with about eight Indo-Pacific and six Atlantic species, was hitherto based on the growth form of the corallum and geographical distribution (Boschma, 1948 a & b, 1961, 1962, 1966; Weisbord, 1968; Roos, 1971; Stearn & Riding, 1973; De Weerdt, 1981). Other characters, such as size of the gastropores and dactylopores, pore density and structure of the ampullae, have hardly been studied in the past or were considered useless because of high intraspecific variation (Boschma, 1948 a & b, 1949 a, 1950, 1964; Martínez Estalella, 1982). In some Atlantic species, however, the growth form of the corallum is extremely variable, which often impedes a good identification. This variability may be partly explained by the fact that *Millepora* has a high adaptability to various environmental circumstances, like depth, water movement, current, and turbidity.

In a previous paper (De Weerdt, 1981), in which I reviewed the taxonomic problems in *Millepora*, the need to search for other characters is stressed. However, when it is attempted to distinguish the species of *Millepora* on a more sound base than the growth form, only few characters are available for taxonomic investigation. Another problem is the scarceness of type-specimens and the lack of ecological data in museum collections. Despite these imperfections it seemed nevertheless worth while to present the results obtained from a study of morphological characters of a collection of tropical Western Atlantic *Millepora* species.

This study is restricted to species occurring in the Caribbean region, viz. *Millepora alcicornis* Linnaeus, 1758; *M. complanata* Lamarck, 1816; *M. squarrosa* Lamarck, 1816; and *M. striata* Duchassaing & Michelotti, 1864. The latter species was synonymized by Boschma (1948a) with *M. squarrosa*, but it is here regarded as a valid species, in accordance with an unpublished manuscript of Boschma.

The taxonomic validity of the following

characters is examined: growth form of the corallum, texture of the surface, microstructure of the skeleton, structure of the ampullae coverings, time of reproduction, size of the gastropores and dactylopores, and density of the pores.

The species are diagnosed and some biogeographical remarks are given.

MATERIAL AND METHODS

Most corals were collected by the author in the period from January 1976 till January 1977 during a stay at the Caribbean Marine Biological Institute (Carmabi), Curaçao. Several localities off the coast of Curaçao and Bonaire, representing a wide variety of biotopes, were visited and all growth forms encountered between 0 and 50 m were gathered. About 250 specimens were collected, and deposited at the Instituut voor Taxonomische Zoölogie, Zoölogisch Museum, Amsterdam (ZMA), the Netherlands.

Additional specimens were borrowed from the Rijksmuseum van Natuurlijke Historie, Leiden (RMNH), the Muséum National d'Histoire Naturelle, Paris (MNHN), and the Hessisches Landesmuseum, Darmstadt, Germany. Specimens present in the British Museum (Natural History), London (BMNH), were also studied.

During this work I received great help from some unpublished manuscripts of the late Prof. Dr. H. Boschma, which were put at my disposal by Prof. Dr. W. Vervoort (RMNH).

RESULTS

VARIATION AND TAXONOMIC USEFULNESS OF MORPHOLOGICAL CHARACTERS

Growth form of the corallum

According to Boschma (1948 a & b), who revised the genus *Millepora* after a period of splitting and lumping by different authors (Duchassaing & Michelotti, 1864; Hickson, 1898 a & b; Wood-Jones, 1907), the growth form of the corallum is the only character which is sufficiently distinct in most species to warrant reliable identification. From recent studies on *Millepora* and coral reefs in general it has, however, become apparent that identification of the species occurring in the Atlantic Ocean still remains very difficult, because of the high degree of polymorphy expressed by the species (Goreau, 1959; Weisbord, 1968; Mattraw, 1969; Mergner, 1969; Roos, 1971; Goreau & Goreau, 1973; Stearn & Riding, 1973; Colin, 1978; De Weerdt, 1981; Martínez Estalella, 1982). It will be explained here how this polymorphy can easily lead to wrong identifications, and which growth form may be exhibited by the four Caribbean *Millepora* species.

In Boschma's revision of *Millepora* (Boschma, 1948 a), extensive descriptions of the growth forms of the species are given. Briefly, the growth forms of the Caribbean species are, according to his descriptions:

M. alcicornis: extremely variable, at the growing edge divided into branches which as a rule are laterally compressed but may be more or less finger-like. Some colonies are decidedly delicately branched, others are of a very compact growth form.
M. complanata: upstanding plates, growing out from a common basal part.
M. squarrosa: upstanding thin plates, with numerous lateral expansions, which among each other are united to form a more or less honeycombed complex.
M. striata (Boschma, unpubl. ms.): "pronouncedly branching in all directions".

The growth forms of the other two Atlantic species, known only from the Brazilian region, are described as:

M. braziliensis: "erect cylindrical branches that at their tops divide into smaller branches" (Boschma, 1961: 293).
M. nitida: "low rounded clumps, consisting of short, rapidly forking, rounded or slightly compressed branches, which are obtuse, rounded, or even clavate at the ends" [abbreviated after Verrill, 1868: 362. In Boschma's revision (Boschma, 1948 a) this species was synonymized with *M. alcicornis*. Later (Boschma, 1962) he considered it as a valid species, but he did not redescribe it.]

From these descriptions it is easily, but erroneously, concluded that *M. squarrosa* is the only species showing the growth form which is sometimes called "honeycombed", sometimes "boxwork" (terminology used by Stearn & Riding, 1973; Colin, 1978; and De Weerdt, 1981). It is the growth form in which "upstanding thin plates, with numerous lateral expansions, are among each other united to form a more or less honeycombed complex" (Boschma, 1948 a: 19). However, three of the four Caribbean species may exhibit such a

growth form, viz. *M. complanata*, *M. squarrosa* and *M. striata*. This mistake is among other things demonstrated by Boschma's identification of four specimens in the ZMA collection (ZMA Coel. 8370, 8371, 8372, and 8373) as *M. squarrosa* (Boschma, 1948 a: 102), and one in the RMNH collection (RMNH 16876). Even though Boschma identified them as *M. squarrosa*, he remarked that all specimens have a growth form intermediate between *M. complanata* and *M. squarrosa*. However, on the basis of criteria discussed below, two of the specimens in the ZMA collection belong to *M. complanata* (ZMA Coel. 8372, 8373), whereas the other two specimens belong to *M. striata* (ZMA Coel. 8370, 8371).

Another example of this misleading identification criterion is the following: in a previous paper dealing with *Millepora* (De Weerdt, 1981), I classified the growth forms of *Millepora* encountered on Curaçao and Bonaire in seven categories: boxwork dwarf form, thick bladed boxwork, thin bladed boxwork, bladed, incrusting, coarse branching, and fine branching. Using Boschma's descriptions strictly, the first three categories would represent *M. squarrosa*, the fourth *M. complanata*, the incrusting form would remain unidentifiable, and the latter two would be *M. alcicornis*. Another possibility could not be excluded, viz. a first Caribbean record of *M. braziliensis*. Corals consisting of thick, erect cylindrical branches, distally divided into smaller branches, are regularly found at Playa Abao, Curaçao (ZMA Coel. 8127, 8133, 8166); they seem to agree completely with Boschma's diagnosis of *M. braziliensis*. However, only two species occur on Curaçao and Bonaire, viz. *M. alcicornis* and *M. complanata*, both extremely polymorphous and quite often undistinguishable, which will be discussed later. The corals agreeing with Boschma's description of *M. braziliensis* fall within the variation of *M. complanata* (they were compared with the specimens of *M. braziliensis* in the RMNH collection). Most of the corals collected on Curaçao and Bonaire, no doubt belonging to *M. complanata*, show a boxwork growth form, consisting of plates which are heavily interconnected into strong masses, quite able to resist the high water energy in the surf zone. Corals with an exclusively plate-like growth form on the other hand were rare at Curaçao and Bonaire, and judging from descriptions and photographs (Almy & Carrión Torres, 1963; Colin, 1978), this phenomenon seems not to be restricted to these islands.

Using Boschma's descriptions sensu stricto, *M. complanata* would turn out to be a rare species, whereas *M. squarrosa* would be quite common. The reverse, however, is true: *M. complanata* is one of the most common *Millepora* species in the Caribbean region, extremely polymorphous and one of the main constituents of the recent reefs. *M. squarrosa* on the other hand is very rare, probably not polymorphous and it does not contribute to high extent to the building of recent reefs (cf. reliable references of this species, see Systematic descriptions).

Comparing the three species which may have a boxwork growth form, some slight differences are present, constant enough to justify some remarks on them here.

In full-grown colonies of *M. squarrosa* the general aspect of the growth form is more compact than in full-grown colonies of *M. complanata*. The plates remain connected along their whole length, whereas the plates in *M. complanata* show a tendency to divide in their top parts. Corals of the latter species have a looser aspect altogether, suggesting that *M. complanata* grows faster than *M. squarrosa*. Exact data on this aspect are not available, so this remark remains speculative. In plate III fig. 1 the type-specimen of *M. squarrosa* (MNHN, no registration number) is shown. In plate II fig. 1 a large colony of *M. complanata* (ZMA Coel. 8213) is figured. It is rather obvious that the specimen of *M. squarrosa* consists of twisted plates of a very compact aspect. The plates of the specimens of *M. complanata* are much looser. Furthermore, the plates in the type-specimen of *M. squarrosa* are not divided in their top parts; they remain massive along the whole length, whereas the plates in the specimen of *M. complanata* show a

tendency to divide and to form lateral expansions in their top parts.

In younger colonies the differences in growth form are more conspicuous: in *M. squarrosa* young colonies are very stubby with smooth and rounded edges, whereas young colonies of *M. complanata* consist of single small plates or boxwork constructions, with sharp growing edges. (Compare plate III fig. 2 which represents a young colony of *M. squarrosa* with plate II fig. 2, a young colony of *M. complanata.*)

When *M. complanata* and *M. squarrosa* are compared with the third species which may have a honeycombed growth form, *M. striata*, the following, small differences are visible: in *M. striata* the tendency of the plates to divide in their top parts is most strongly developed. The specimen belonging to *M. striata* ZMA Coel. 8370, identified by Boschma as *M. squarrosa* (Boschma, 1948 a: 102, 2nd paragraph) is a very large piece of coral. The greater part has died, but the top part consists of numerous clusters of newly formed plate-like outgrowths in all directions. Plate IV fig. 1 shows a specimen of *M. striata.* The looseness and tendency to divide is here obvious as well.

In brief, the growth forms of the three species may be diagnosed as follows:
Millepora complanata: bladed or honeycombed. General aspect of the corals is rather loose, with a tendency to divide in the top parts of the corallum. Growing edges generally sharp, sometimes truncated.
Millepora squarrosa: honeycombed. General aspect very compact, plates massive, without a tendency to divide in the top parts. Growing edges in young colonies smooth and rounded.
Millepora striata: honeycombed. General aspect very loose, with a pronounced tendency of the plates to branch and to divide in the top parts. Growing edges very sharp.

The growth form of the only remaining species, *M. alcicornis*, is in general branched. The branches vary from extremely delicate (plate I fig. 1) to robust (plate I fig. 2). They may be fused in the basal parts of the corallum to such a high degree that the growth form becomes plate-like. Sometimes it is even difficult to distinguish between the most delicate form of *M. complanata* and the more stouter forms of *M. alcicornis*. The growth form of this species may be diagnosed as follows:
Millepora alcicornis: branching, the branches vary, but they always form upright structures; at their top parts the branches are mostly laterally compressed.

Summarizing, the growth form of the four Caribbean *Millepora* species is highly variable, but within certain limits. However, it can not be used as the sole identification character, since three of the four species may exhibit almost similar growth forms. The slight differences in corals with the honeycombed aspect may be too subtle to warrant reliable identification. In combination with other characters, the growth form may be a support to a good identification.

Texture of the surface

In some species the surface shows constant peculiarities. In *M. squarrosa* the surface is extremely smooth and even, making an almost transparent impression. By the presence of numerous crests and tubercles it is, however, at the same time frilled. These outgrowths are rather strongly developed in the type-specimen of *M. squarrosa* (plate III fig. 1), but also in the other corals investigated; all of them are of a much smaller size than the type, but a marked tendency towards a frilled surface can still be observed.

In *M. striata* the surface is very uneven due to depressions lodging a central gastropore. (In ZMA Coel. 8370 each gastropore and dactylopore is situated in a depression.) Another feature in this species is the presence of longitudinal ridges, which are most pronounced towards the growing edges (see plate IV fig. 1).

Both in *M. alcicornis* and in *M. complanata* the texture of the surface is variable, but generally the surface of *M. alcicornis* is smoother than that of *M. complanata.* In both species gastropores may be situated in depressions but they may also be flush with the surface.

Summarizing, the surface texture may be helpful as a taxonomic character, but it is not absolutely distinctive.

Microstructure of the skeleton

The skeleton of *Millepora* consists of a porous, regular reticulation of solid bars and supports of aragonite. At the surface the skeleton is somewhat lumpy, and consists of spherulitic growths, illustrating the mode of growth and thickening of the bars. Sorauf (1974: 39, pls. I, II, III, figs. 1-3) gives an extensive description of the skeleton of *Millepora*, but the only species involved in his study is *M. alcicornis*. It seemed therefore worth while to present here some scanning electron microscope photographs of the four species treated in this paper (plates V & VI). As a taxonomic character the microstructure of the skeleton is useless, since all species exhibit the same variation.

Structure of the ampullae covering

In *Millepora*, medusae originate in special chambers in the skeleton (called ampullae), which are covered by calcareous trabecular structures as long as the medusae are not yet set free. The taxonomic value of the structure of the ampullae covering was investigated by Boschma (1949 a, 1950, 1964), who finally concluded that this is not diagnostic. Boschma's investigation was limited by the few corals possessing closed ampullae, and only one Caribbean species (*M. alcicornis*) was included in his study. Among the corals collected by the present author (belonging to *M. alcicornis* and *M. complanata*), a high percentage appeared to carry ampullae in closed condition; also one specimen of *M. striata* in the ZMA collection (ZMA Coel. 8371) has a few ampullae which are still partly closed.

In plate V fig. 1, plate VI fig. 3, and plate VII, ampullae coverings of the three species are shown. Different structures of the ampullae covering were found, but they were present even within one coral and are, therefore, not of diagnostic value.

Time of reproduction

Excepting the period March through June, corals were collected throughout the year. No seasonal differences in ampullae formation were found between *M. alcicornis* and *M. complanata*. Both were reproductively active in all months collected.

Size of the pores

According to Boschma (1948 a: 51-54) the size of the pores may be of some help in exceptional cases only, e.g. in *M. intricata* and *M. platyphylla*, two Indo-Pacific species. Martínez Estalella (1982) considered the size of the pores of *M. alcicornis* diagnostically useless because of high intraspecific variation. In the present study this character is examined again, but only those parts of the corals are included which were evidently in the same condition during life. Shaded sides, where the pores are minute or even absent, are left out of consideration, as well as the top parts of the corallum. Twenty pores were measured in each coral.

In table I gastropore and dactylopore diameters of some specimens are shown. In text-fig. 1 the size of the gastropores of *M. alcicornis* and *M. complanata* is plotted against water depth. Different symbols are used to discriminate between purely bladed corals of *M. complanata* and those with a honeycombed growth form. The diameter of the gastropores seems to diminish with increasing depth, but due to the high variation, especially in shallow-water corals, the decrease is not statistically significant (correlation analysis was carried out for each data set). The same applies to the diameter of the dactylopores, of which no figure is given. Among the two species the gastropore and dactylopore sizes differ significantly ($p < 0.05$), but there is an overlap. It is obvious that the honeycombed corals fall within the variation of *M. complanata*. From this fact alone the conclusion that they belong to *M. complanata* is not justifiable, but their identity becomes firmly established when the pore sizes are combined with the pore densities, as will be shown below.

M. complanata has the largest gastropores and dactylopores (table I); the gastropores of *M. squarrosa* are rather large; those of *M. alcicornis* and *M. striata* are about of the same size, and rather small. Conspicuous is the difference in size of the pores in *M. squarrosa*: the dactylopores are much smaller than the gastropores. In *M. striata* both gastropores and dactylopores are rather small.

The size of the gastropores and dactylopores is not a reliable diagnostic character by itself; in combination with the pore density it is, however, most distinctive as is shown below.

Pore density

For counting the pores, like in measuring the pore sizes, only comparable parts of the corallum were used (shaded sides, growing edges etc. were left out of consideration). In this way, intracolonial variation of the dactylopore density appeared to be rather small: twelve random counts of 0.09 cm^2 (which were later converted to cm^2) appeared sufficient to obtain 95% confidence intervals (Student-Newman-Keul's test).

In text-fig. 2 the diameter of the dactylopores (mm) is plotted against dactylopore density (number of dactylopores per cm^2). The combination dactylopore size / dactylopore density is highly species specific in *M. squarrosa* and *M. striata*; both species are well separated from each other as well as from *M. alcicornis* and *M. complanata*. The latter two species have an overlap, which is, however, much smaller than the overlap in gastropore size.

The high density of the dactylopores in *M. squarrosa* in combination with their relatively small size is very conspicuous, even when a specimen is studied with a simple hand lens. Boschma's unawareness of the validity of this character combination is well demonstrated by his identification of some specimens as *M. squarrosa*, on basis of their growth form: RMNH 16876, ZMA Coel. 8372 and 8373 are without doubt *M. complanata*; ZMA Coel. 8370 and 8371 fall within the variation of *M. striata*. Some of these specimens, as well as the type-specimen of *M. squarrosa*, are indicated in the figure with different symbols.

In table I the gastropore and dactylopore densities of some specimens are given. Gastropore size in combination with gastropore density is not a distinctive character.

Summarizing, the combination of dactylopore size with dactylopore density is a highly species specific character in the four Caribbean *Millepora* species.

CONCLUSIONS

Reliable identification of the four Caribbean *Millepora* species, *M. alcicornis*, *M. complanata*, *M. squarrosa*, and *M. striata* is usually possible when a combination of characters is used. Most distinctive is the combination of dactylopore size with dactylopore density.

M. alcicornis and *M. complanata* have the largest variation and overlap in every character, which makes it often difficult or sometimes even impossible to distinguish them. It is presumed that they are closely related species.

SYSTEMATIC DESCRIPTIONS

Millepora alcicornis Linnaeus, 1758 (Plate I figs. 1-3, plate V figs. 1-2)

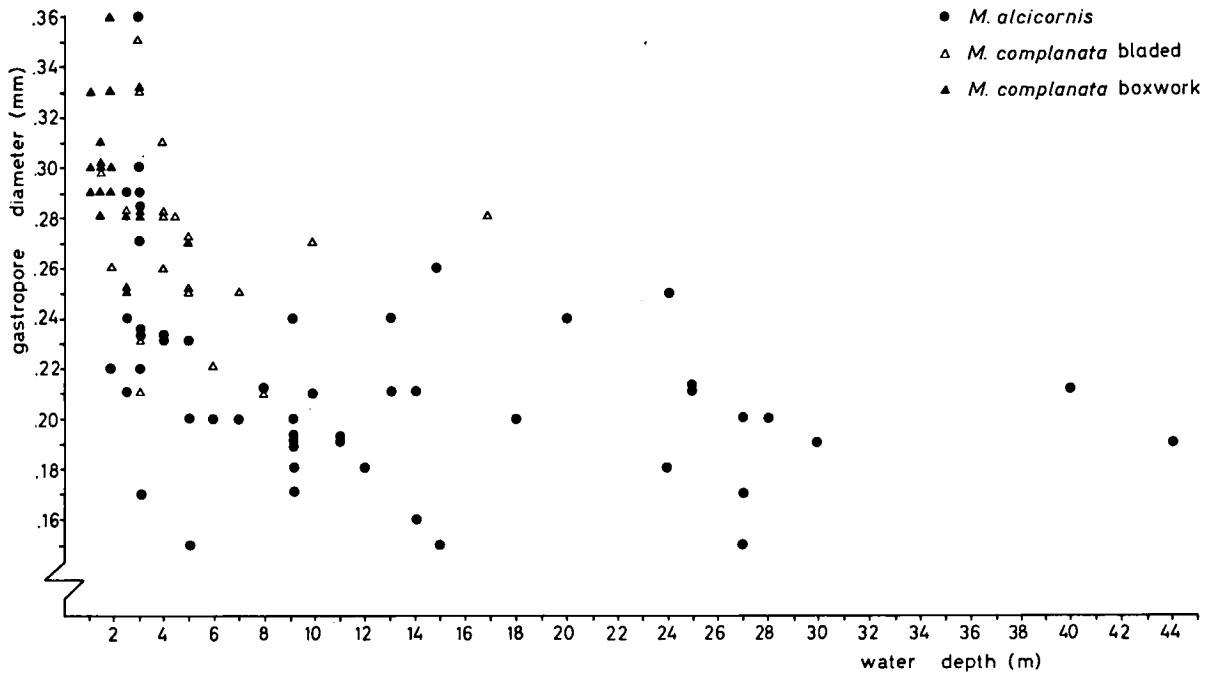
For detailed synonymy cf. Boschma, 1948 a (except *Millepora nitida* Verrill, 1868), Boschma, 1949 b, and Weisbord, 1968.

Millepora alcicornis; Boschma, 1948 a: 23-28, 79-81, 86-88, 100-101, text-fig. 6, pl. XIV fig. 3; Boschma, 1949 b: 661-663; Boschma, 1956: F94, fig. 76A; Goreau, 1959: 83; Stoddart, 1962: 109; Almy & Carrión Torres, 1963: 141, 144, pl. IIa; Weisbord, 1968: 16-21; Laborel, 1969: 222; Mergner, 1969: 279, 281, 286, pl. II; Roos, 1971: 43, 44, pl. II; Goreau & Goreau, 1973: 436; Stearn & Riding, 1973: 197-199, fig. 5c; Colin, 1978: 137, 146, 150; Mattraw, 1979: 29-37, pl. I; De Weerdt, 1981: 1-18, pl. I, pl. V figs. 1 & 2.

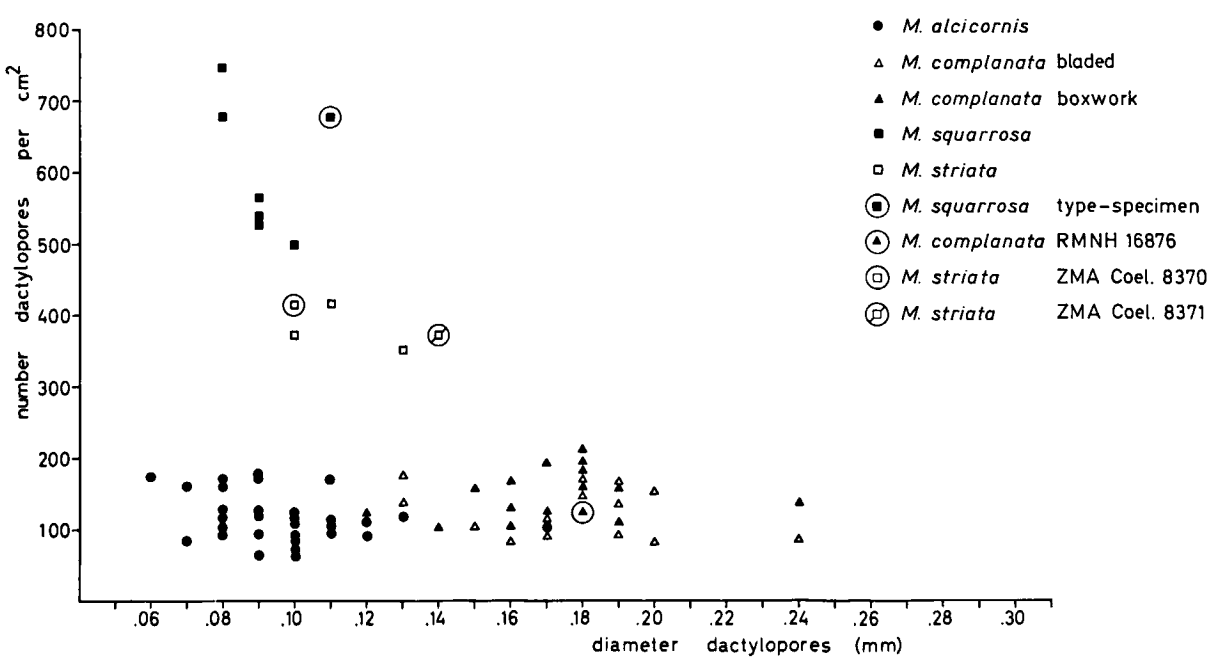
Millepora alcicornis forma *alcicornis*; Scatterday, 1974: 86; Martínez Estalella, 1982: 5-15, 24, figs. 4, 6a.

Millepora alcicornis forma *delicatula* Martínez Estalella, 1982 5-7, 20, 23, 24, fig. 8.

?*Millepora alcicornis*; Chevalier, 1966: 1390; Laborel, 1974: 427, 439, 440.



Text-fig. 1. Gastropore diameter of *M. alcicornis* and *M. complanata* plotted against water depth.



Text-fig. 2. Dactylopore density (number of dactylopores per cm²) in relation to dactylopore diameter (mm).

Holotype:
Unknown, probably lost.

Material examined:
Curaçao and Bonaire: numerous specimens in ZMA collection; RMNH 10504 (Curaçao).
Aruba: RMNH 10507.
West Indies: BMNH 42.10.26.43, 51.7.28.26.
Saba: RMNH 8500, 8501, 8502, 8503.
St. Eustatius: RMNH 10588.
Florida: RMNH 4954.

Diagnosis:
Habit: branching; branches may be very delicate or coarse and largely united into plate-like constructions; flattened at the growing edges. Corallum mostly growing upright, but it may also incrust gorgonians, etc.
Surface: rather smooth and even.
Gastropores: 0.15-0.30 mm.
Dactylopores: small, 0.06-0.17 mm.
Pore density: rather low, 5-50 gastropores per cm^2; 45-200 dactylopores per cm^2.

Ecology:
Abundant at the less exposed sites of reefs and in lagoons.

Distribution:
Caribbean (Boschma, 1948a; Goreau, 1959; Stoddart, 1962; Almy & Carrión Torres, 1963; Weisbord, 1968; Mergner, 1969; Roos, 1971; Goreau & Goreau, 1973; Stearn & Riding, 1973; Laborel, 1974; Scatterday, 1974; Colin, 1978; De Weerdt, 1981; Martínez Estalella, 1982); Florida (Verrill, 1868; Boschma, 1948a); Bermuda (Boschma, 1948a; Mattraw, 1969); Brazil (Laborel, 1969); ? West Africa (Chevalier, 1966; Laborel, 1974).

Discussion:
M. alcicornis forma *delicatula* Martínez Estalella, 1982, is a very delicate form of *M. alcicornis*. It is regularly found in Curaçao and Bonaire (ZMA Coel. 8083, 8048, 8057, and several other specimens). There is no reason to regard it as a separate species or variety, since all characters fall within the variation of *M. alcicornis*.

Millepora complanata Lamarck, 1816
(Plate II figs. 1-4, plate V figs. 3-4, plate VII fig. 1)

For detailed synonymy cf. Boschma, 1948a; 1949b.

Millepora complanata; Boschma, 1948a: 34, 35, 83, 84, 94, 95, 103, text-fig. 11, pl. VII fig. 2; Boschma, 1949b: 665; Almy & Carrión Torres, 1963: 141, 144, pl. IIb; Roos, 1971: 43-45, pl. III; Goreau & Goreau, 1973: 419, 436; Stearn & Riding, 1973: 197-199, fig. 5B; Colin, 1978: 140, 143, 150; De Weerdt, 1981: 1-17, pl. II figs. 1-3, pl. V figs. 3-4, pl. VI figs. 1-4.
Millepora alcicornis forma *complanata* Scatterday, 1974: 86, fig. 9; Martínez Estalella, 1982: 5-24, fig. 6 (right).
Millepora alcicornis forma *squarrosa* Scatterday, 1974: 86; Martínez Estalella, 1982: 5-18, fig. 7.
Millepora squarrosa (partim); Boschma, 1948a: 32, 33, 93, 94, 102, pl. IX.
Millepora squarrosa; Roos, 1971: 44, pl. I; Stearn & Riding, 1973: 197-199, fig. 5A.
Millepora "squarrosa"; De Weerdt, 1981: 1-17, pls. III, VII, VIII.

Holotype:
Unknown, probably lost.

Material examined:
Curaçao and Bonaire: numerous specimens in ZMA collection, RMNH 10550 (Curaçao).
West Indies: BMNH, two specimens, no registration number.
Saba: RMNH 8511, 8512.

Diagnosis:
Habit: colonies consisting of simple plates, growing from a common base, or complex masses of interconnected plates forming honeycombed structures. Colonies may remain dwarfish with large incrusting base on sites with strong wave action.
Surface: varying from smooth to rather rough, with sharp rims around the pores. Often it is uneven by depressions with a central gastropore.
Gastropores: large: 0.22-0.36 mm.
Dactylopores: variable, mostly rather large: 0.12-0.24 mm.
Pore density: 10-70 gastropores per cm^2; 45-250 dactylopores per cm^2.

Ecology:
Abundant in the surf zone and at reef flats. Rheophylic, bladed forms growing perpendicular to current direction.

TABLE I

Gastropore and dactylopore diameters (mm) and gastropore and dactylopore densities (number of pores per cm²) of some specimens of *Millepora alcicornis*, *M. complanata*, *M. squarrosa*, and *M. striata*. (Means are printed in bold type, and standard deviations are given between parentheses.)

species	gastropore diameter	dactylopore diameter	*n* gastropores/cm²	*n* dactylopores/cm²
M. alcicornis				
ZMA Coel. 8029, branching, 9 m	0.15-**0.24**(0.02)-0.25	0.08-**0.11**(0.02)-0.15	12-**27.6**(7.8)-39	46-**109.3**(47.3)-189
ZMA Coel. 8004, branching, 13 m	0.15-**0.21**(0.04)-0.28	0.08-**0.09**(0.02)-0.13	8-**22.1**(8.3)-36	88-**122.6**(24.6)-146
ZMA Coel. 8045, almost bladed by fused branches, 9 m	0.15-**0.20**(0.02)-0.20	0.05-**0.11**(0.03)-0.18	23-**33.5**(9.0)-50	78-**118.5**(34.6)-208
ZMA Coel. 8083, very delicately branched, 27 m	0.13-**0.20**(0.03)-0.25	0.05-**0.07**(0.02)-0.10	17-**28.9**(7.8)-46	92-**162.1**(40.0)-203
ZMA Coel. 8048, very delicately branched, 28 m	0.15-**0.20**(0.02)-0.25	0.05-**0.09**(0.03)-0.10	10-**24.3**(8.0)-33	67- **94.5**(22.2)-145
ZMA Coel. 8057, very delicately branched, 2 m	0.18-**0.21**(0.02)-0.25	0.05-**0.09**(0.02)-0.15	23-**27.7**(7.5)-45	110-**172.8**(22.9)-200
M. complanata				
ZMA Coel. 8190, bladed, 17 m	0.25-**0.28**(0.02)-0.30	0.13-**0.16**(0.03)-0.23	12-**18.4**(6.7)-35	50- **89.0**(26.3)-133
ZMA Coel. 8165, bladed, 3 m	0.30-**0.32**(0.02)-0.35	0.15-**0.24**(0.04)-0.30	11-**26.2**(10.3)-46	47- **86.0**(23.2)-124
ZMA Coel. 8143, boxwork, 3 m	0.20-**0.28**(0.03)-0.33	0.13-**0.16**(0.03)-0.23	23-**28.9**(6.3)-33	72-**105.0**(15.6)-123
ZMA Coel. 8216, boxwork, 1.5 m	0.25-**0.28**(0.02)-0.30	0.10-**0.14**(0.02)-0.18	32-**50.5**(12.9)-78	45-**105.0**(28.5)-136
ZMA Coel. 8172, boxwork, 2 m	0.25-**0.28**(0.04)-0.35	0.15-**0.18**(0.03)-0.25	39-**49.5**(7.9)-67	136-**187.9**(32.6)-235
RMNH 16876, boxwork, depth unknown	0.30-**0.34**(0.02)-0.38	0.15-**0.18**(0.02)-0.23	17-**32.3**(11.6)-56	100-**134.2**(23.5)-167
M. squarrosa				
MNHN type-specimen	0.18-**0.24**(0.04)-0.32	0.07-**0.11**(0.02)-0.14	21-**30.3**(6.4)-44	500-**676.8**(95.6)-816
RMNH 8515, 16 m	0.20-**0.25**(0.02)-0.30	0.08-**0.09**(0.02)-0.10	11-**29.8**(12.5)-47	467-**526.0**(38.9)-567
RMNH 8514, 0-15 m	0.25-**0.28**(0.02)-0.30	0.08-**0.10**(0.02)-0.15	35-**43.8**(7.1)-56	378-**484.2**(56.2)-576
ZMA Coel. 8210, 3 m	0.23-**0.26**(0.02)-0.30	0.08-**0.09**(0.01)-0.10	12-**30.8**(11.5)-59	475-**536.1**(54.7)-668
ZMA Coel. 8211, depth unknown	0.20-**0.29**(0.03)-0.33	0.08-**0.09**(0.01)-0.10	14-**28.0**(8.6)-46	356-**564.8**(92.8)-756
M. striata				
ZMA Coel. 8371, depth unknown	0.15-**0.19**(0.02)-0.23	0.10-**0.14**(0.02)-0.18	10-**30.7**(8.6)-45	280-**370.5**(56.5)-488
ZMA Coel. 8370, depth unknown	0.15-**0.19**(0.03)-0.25	0.08-**0.10**(0.02)-0.13	11-**33.9**(9.9)-46	278-**368.6**(58.6)-500
Darmstadt Mus. XI: 66-1a, depth unknown	0.17-**0.20**(0.02)-0.25	0.08-**0.11**(0.02)-0.15	24-**38.2**(8.8)-56	322-**412.9**(51.3)-512
RMNH 14771, depth unknown	0.15-**0.20**(0.03)-0.25	0.08-**0.10**(0.01)-0.13	23-**34.8**(9.2)-44	356-**416.6**(34.4)-467

Distribution:
Caribbean.

Discussion:
M. complanata is at the same time one of the commonest and geographically most limited species. It is neither recorded from outside the Caribbean region, nor from Bermuda (Mattraw, 1969). It is well distinguished from *M. squarrosa* by the size and density of the dactylopores, but it has in many respects a rather large overlap with *M. alcicornis*. Some specimens collected show a completely intermediate growth form (ZMA Coel. 8045, 8050), and also in the other characters there is always an overlap. In addition, the two species are partly sympatric with more or less the same ecological preferences. It is presumed that they are two closely related species. It seems worth while to undertake a detailed study on their reproductive patterns and serological properties, of which very little is known.

Millepora squarrosa Lamarck, 1816
(Plate III figs. 1-3, plate VI figs. 1-2)

Restricted synonymy:
?*Millepora folliata* Milne Edwards, 1860 (reference in Boschma, 1948a).
?*Millepora tuberculata* Duchassaing & Michelotti, 1864: 198, pl. XI fig. 4.
Millepora squarrosa (partim); Boschma, 1948a: 32, 33, pl VIII.
Millepora squarrosa; Boschma, 1962: 306, 307, 308, pls. VI, VII; Almy & Carrión Torres, 1963: 144, pl. IIIa; Colin, 1978: 140, 150.

Holotype:
MNHN, no registration number, locality unknown ("Mers de l'Amérique", cf. Lamarck, 1816).

Material examined:
St. Eustatius: ZMA Coel. 8210, RMNH 8514.
Saba: RMNH 8513, 8515 (two specimens).
Puerto Rico: RMNH 16877 (four specimens donated by Dr. T. Goreau to Dr. H. Boschma, cf. Boschma, 1962: 308).
ZMA Coel. 8211, one specimen without data on locality.

Diagnosis:
Habit: colonies consisting of irregularly, heavily interconnected, stubby masses with smooth, rounded edges. In older colonies the growth form becomes more plate-like, and the growing edges sharper, but the plates remain connected along their whole length.
Surface: very smooth, but irregular by the presence of numerous crests and tubercles.
Gastropores: 0.20-0.30 mm.
Dactylopores: very small, 0.07-0.15 mm.
Pore density: gastropores 10-60 per cm^2; dactylopore density very high: 480-750 per cm^2.

Ecology:
Unknown.

Distribution:
Puerto Rico (Almy & Carrión Torres, 1963; Colin, 1978; specimens in RMNH and ZMA collections); St. Eustatius (specimens in RMNH and ZMA collections); Saba (specimens in RMNH collection); Maria Farinha, Pernambuco, Brazil (Boschma, 1962).

Millepora striata Duchassaing & Michelotti, 1864
(Plate IV figs. 1-2, plate VI figs. 3-4, plate VII fig. 2)

Millepora striata Duchassaing & Michelotti, 1864: 198, pl XI fig. 8.
Millepora squarrosa (partim); Boschma, 1948a: 32.

Holotype:
Unknown, probably lost.

Material examined:
San Blas: specimens of the Hessisches Landesmuseum, Darmstadt, labelled XI: 66-1a, c, d and 66-1b, e, f; RMNH 14771.
Venezuela: ZMA Coel. 8370, 8371.

Diagnosis:
Habit: corallum consisting of loosely connected plates, which have a strong tendency to divide in the top parts. Edges very sharp.
Surface: numerous longitudinal folds make the surface very uneven. Gastropores and dactylopores often situated in pronounced depressions.
Gastropores: 0.15-0.25 mm.
Dactylopores: 0.08-0.18 mm.

Pore density: 10-50 gastropores per cm^2; dactylopore density rather high: 270-500 per cm^2.

Ecology:
Unknown.

Distribution:
Guadeloupe (Duchassaing & Michelotti, 1864); San Blas (specimens of the Hessisches Landesmuseum Darmstadt and RMNH collections); Venezuela (specimens in ZMA collection).

Discussion:
In Boschma's unfinished ms. no description of the species is given, but he mentions the peculiar longitudinal folds of the surface. Duchassaing & Michelotti (1864: 198) write in their description: "superficie rugis in series longitudinales approximatis instructa". These folds are very characteristic indeed, making *M. striata* one of the easiest recognizable *Millepora* species of the Caribbean. The distribution is not yet firmly established, since only three reliable records of localities are known. The species was not found in Curaçao and Bonaire.

BIOGEOGRAPHICAL REMARKS

Besides the four *Millepora* species treated in this paper, two other species are described from the tropical Atlantic region, viz. *M. braziliensis* Verrill, 1868 and *M. nitida* Verrill, 1868. They are excluded from this study because of lack of sufficient material, but it is intended to revise all Atlantic representatives of the genus when more material is available. However, on the basis of the few specimens which could be studied for comparison, it is tentatively concluded that *M. braziliensis* and *M. nitida* represent two other valid and distinguishable species. At present their distribution is confined to the Brazilian region (Laborel, 1969). Laborel (l.c.) has doubts about the difference between *M. braziliensis* and *M. squarrosa*. Judging from his figure (pl. VIII fig. 5) I tentatively conclude that his specimens are not conspecific with *M. squarrosa*.

The tropical western side of the Atlantic is biogeographically divided into two provinces: the Caribbean and the Brazilian region (Laborel, 1969). The known distribution of the *Millepora* species is shown in table II. This distribution pattern agrees very well with the distribution patterns of other coral species in the Caribbean and Brazilian region (cf. Laborel, 1969). *M. alcicornis* has the widest geographical range: from 32° N (Bermuda; Mattraw, 1969) to 25° S (coast of Brazil; Boschma, 1948a; Laborel, 1969). The West African record needs verification. Specimens of *Millepora* from the Cape Verde Islands are present in the RMNH. Boschma intended to describe them as a new species (unpublished ms.); the specimens do indeed have some peculiarities which point to the fact that they might be a species distinct from *M. alcicornis*. However, even when West Africa is left out of consideration for the moment, *M. alcicornis* still has a very wide distribution in the western tropical Atlantic, whereas *M. complanata*, with which it is so easily confused, has a more limited distribution, although it is quite common all over the Caribbean. A possible explanation for the differences between *M. alcicornis* and *M. complanata* may be different reproductive strategies, analogous to similar differences observed recently by Van Moorsel (1983) in closely related, sympatric *Agaricia* species. *M. complanata* possibly is an opportunistic species, well adapted to turbulent environments and possessing a short larval stage preventing excessive loss of larvae in extreme circumstances, while *M. alcicornis* could have a longer larval life, intended for greater settlement success in highly competitive, stable environments (cf. also De Weerdt, 1981).

Concerning relationships with Indo-Pacific representatives of the genus, there are four species in the Indo-Pacific which are very similar to Atlantic species. These species are *Millepora dichotoma* Forskål, 1775, and *M. intricata* Milne Edwards, 1857, which resemble *M. alcicornis*; *M. platyphylla* Hemprich & Ehrenberg, 1834, which resembles *M. squarrosa*; and *M. exaesa* Forskål, 1775, which is similar to *M. nitida* Verrill, 1868. Boschma (1962: 310)

TABLE II

Known distribution of *Millepora* species in the tropical Atlantic region.

species	Caribbean region	Brazilian region	Florida	Bermuda	West Africa	Reference
M. alcicornis	×	×	×	×	? ×	see Systematic description
M. complanata	×					see Systematic description
M. braziliensis		×				Verrill, 1868 Boschma, 1961, 1962 Laborel, 1969
M. nitida		×				Verrill, 1868 Boschma, 1962 Laborel, 1969
M. squarrosa	×	×				see Systematic description
M. striata	×					see Systematic description

separates the latter two only on the basis of their geographical distribution, but considers the two species in every respect indistinguishable. This strongly points to a former Tethyan distribution of the genus, and to the existence of twin species in the Atlantic and Indo-Pacific oceans.

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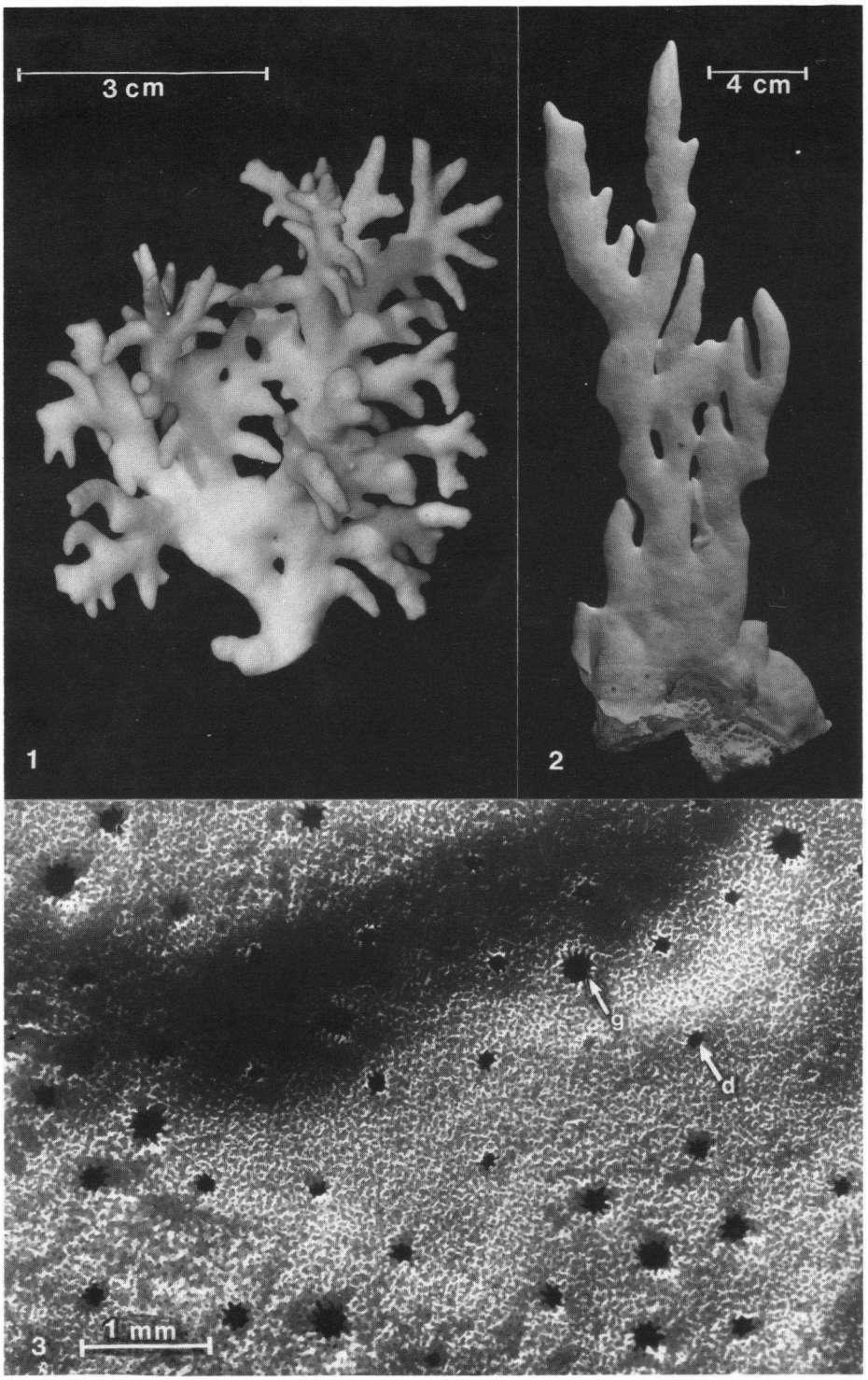

PLATE I

1, *Millepora alcicornis*, very delicately branched (ZMA Coel. 8053).
2, *Millepora alcicornis*, branches stouter and fused in the basal parts (ZMA Coel. 8074).
3, *Millepora alcicornis*, detail of surface (ZMA Coel. 8074) (g = gastropore, d = dactylopore).

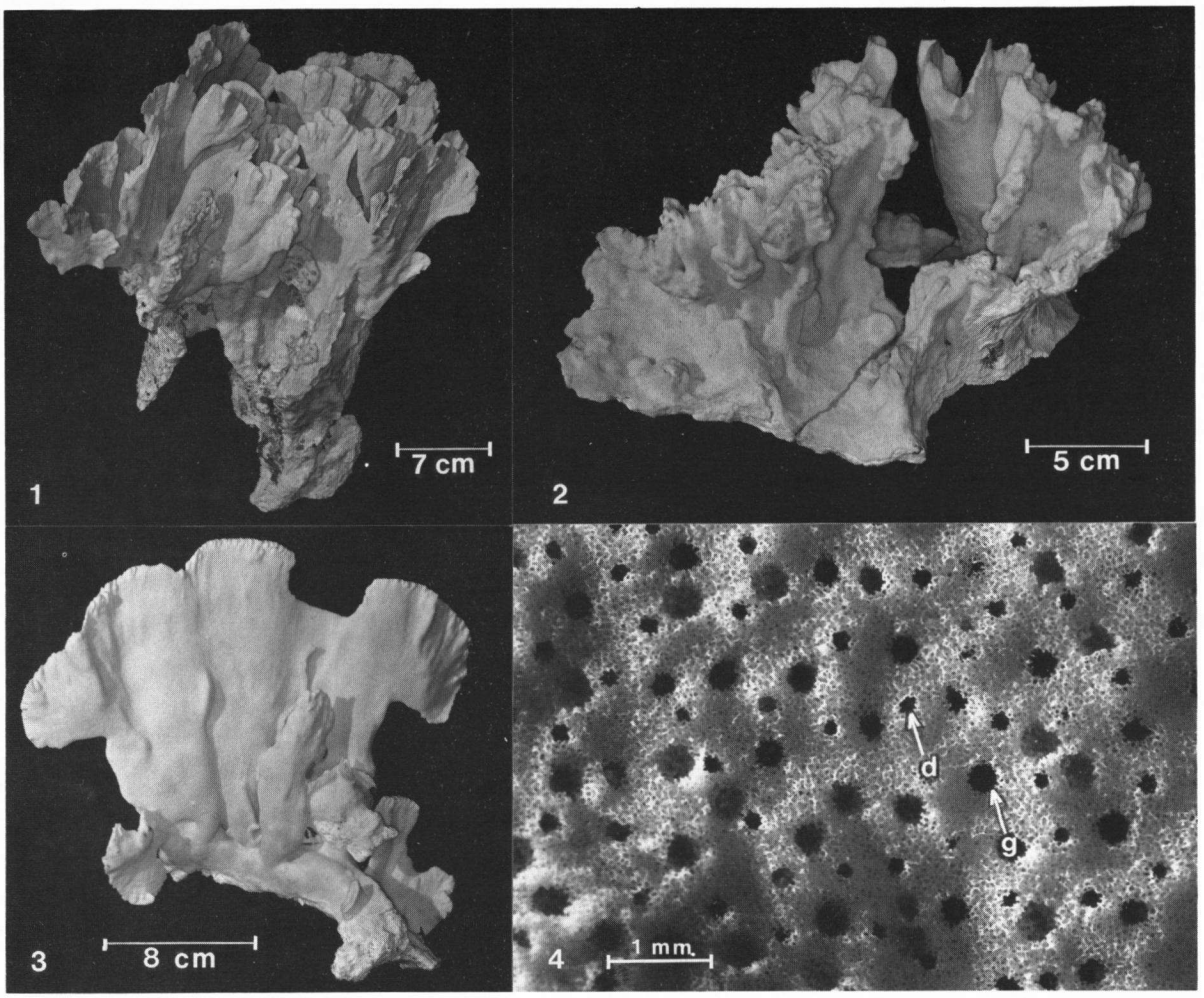

PLATE II

1, *Millepora complanata*, boxwork growth form (ZMA Coel. 8213).
2, *Millepora complanata*, young colony, dwarfish boxwork growth form (ZMA Coel. 8216).
3, *Millepora complanata*, bladed growth form (ZMA Coel. 8006).
4, *Millepora complanata*, detail of surface (ZMA Coel. 8006) (g = gastropore, d = dactylopore).

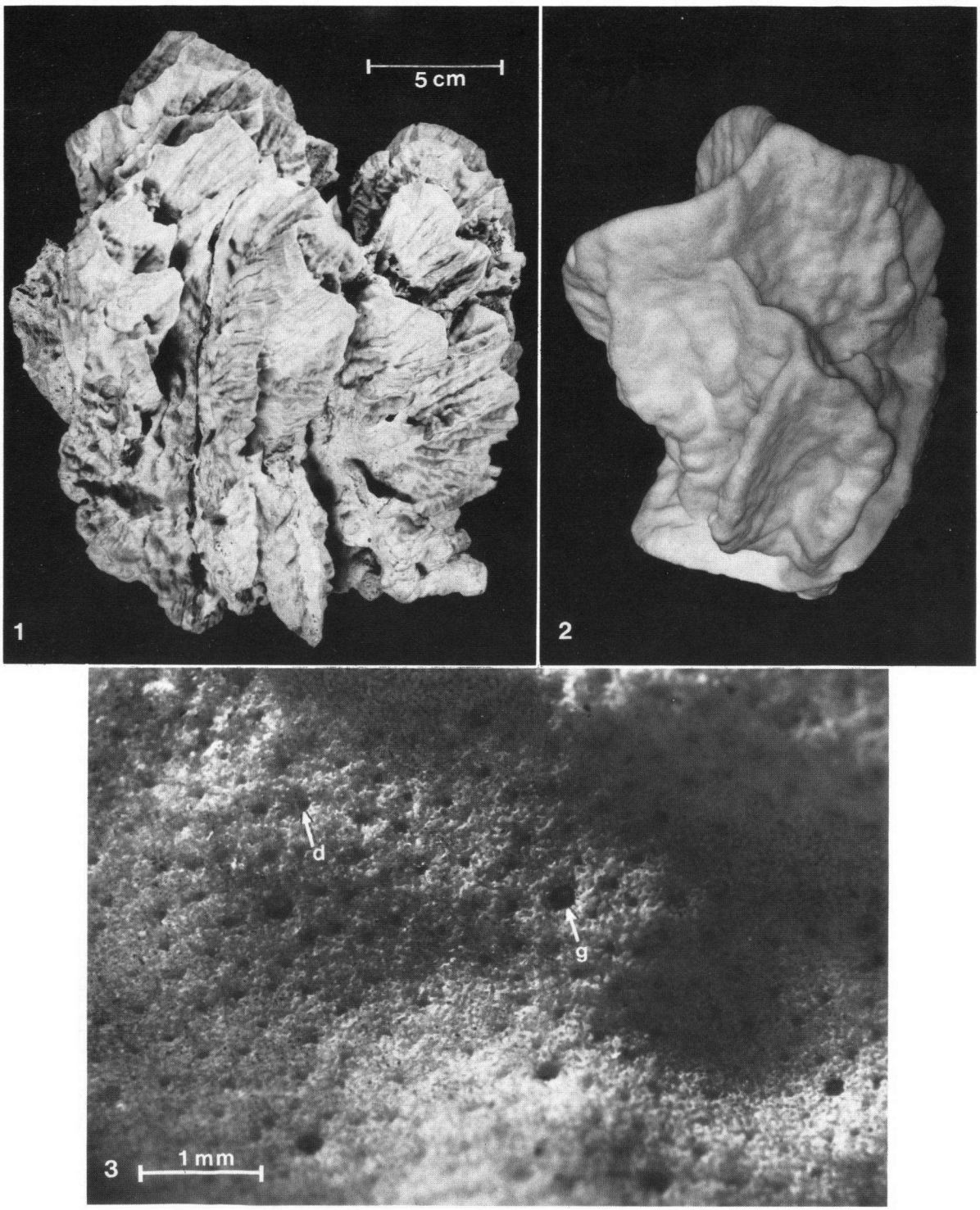

PLATE III

1, *Millepora squarrosa*, type-specimen.
2, *Millepora squarrosa*, young colony with smooth edges, actual size (RMNH 8514).
3, *Millepora squarrosa*, detail of surface (type-specimen) (g = gastropore, d = dactylopore).

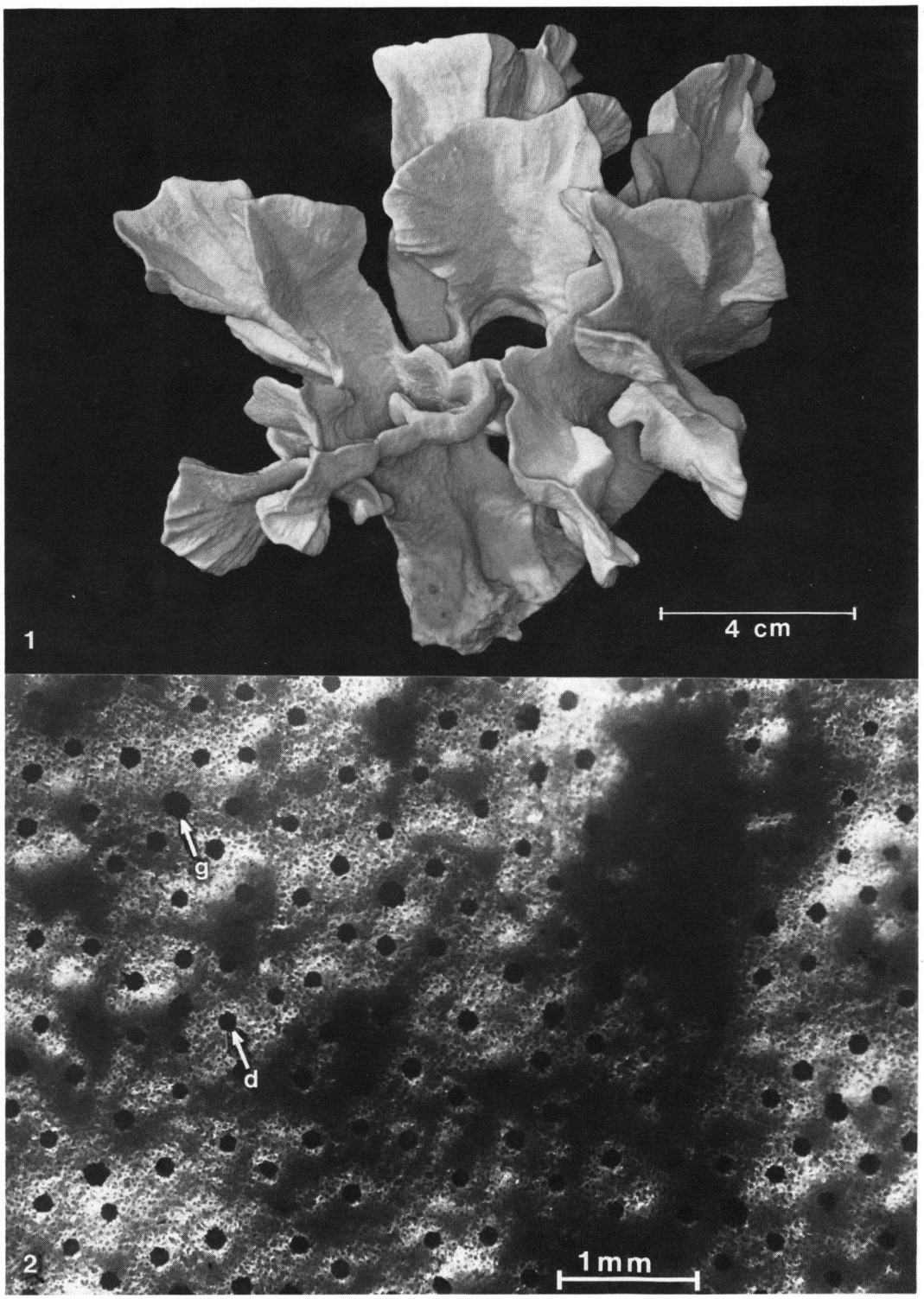

PLATE IV

1, *Millepora striata* (Landesmuseum Darmstadt XI: 66-1b).
2, *Millepora striata*, detail of surface (g = gastropore, d = dactylopore).

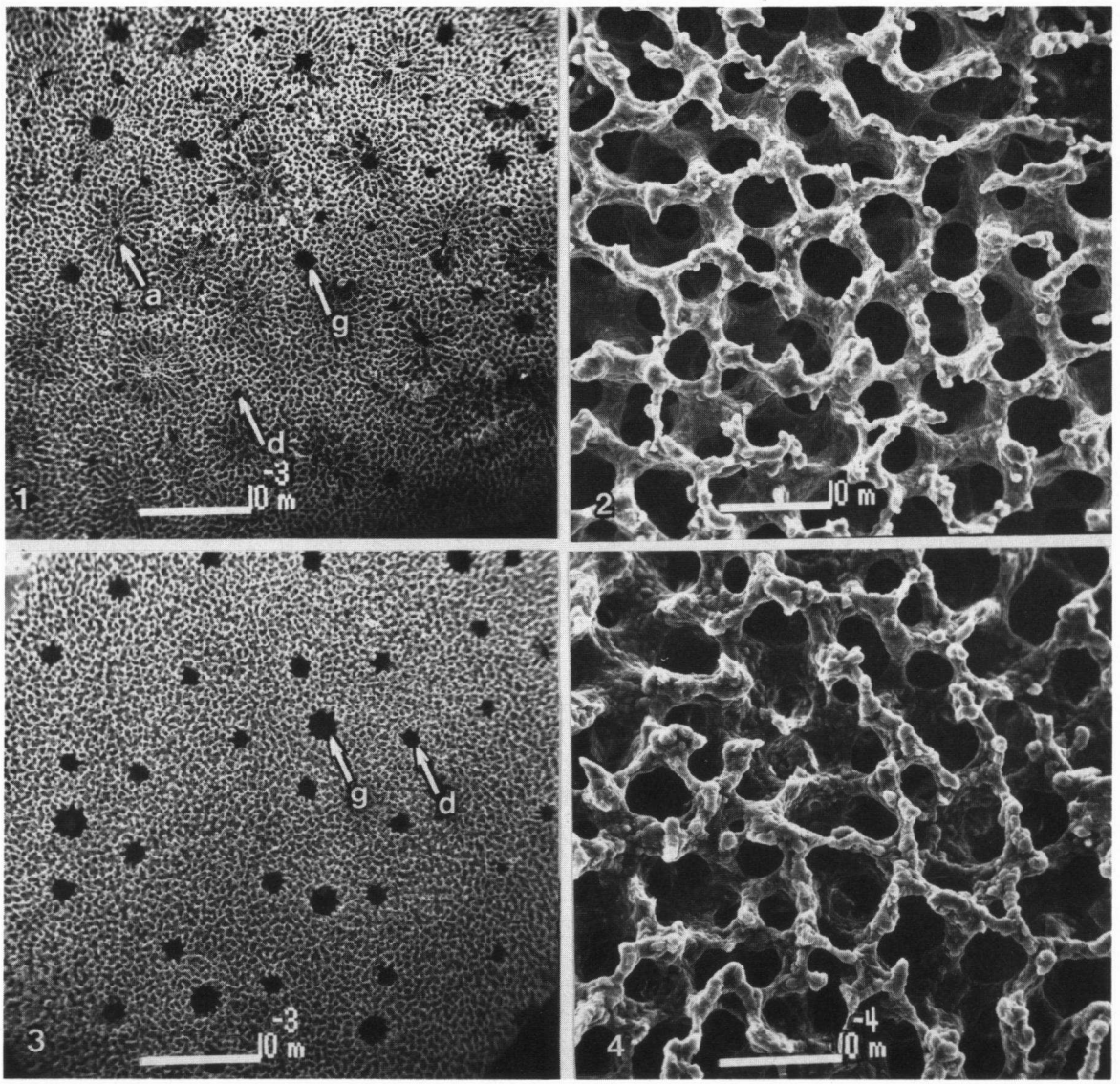

PLATE V

Scanning electron microscope photographs (g = gastropore, d = dactylopore, a = ampulla):
1, *Millepora alcicornis*, surface with numerous ampullae in closed condition (ZMA Coel. 8374).
2, *Millepora alcicornis*, microstructure of skeleton (ZMA Coel. 8374).
3, *Millepora complanata*, surface (ZMA Coel. 8006).
4, *Millepora complanata*, microstructure of skeleton (ZMA Coel. 8006).

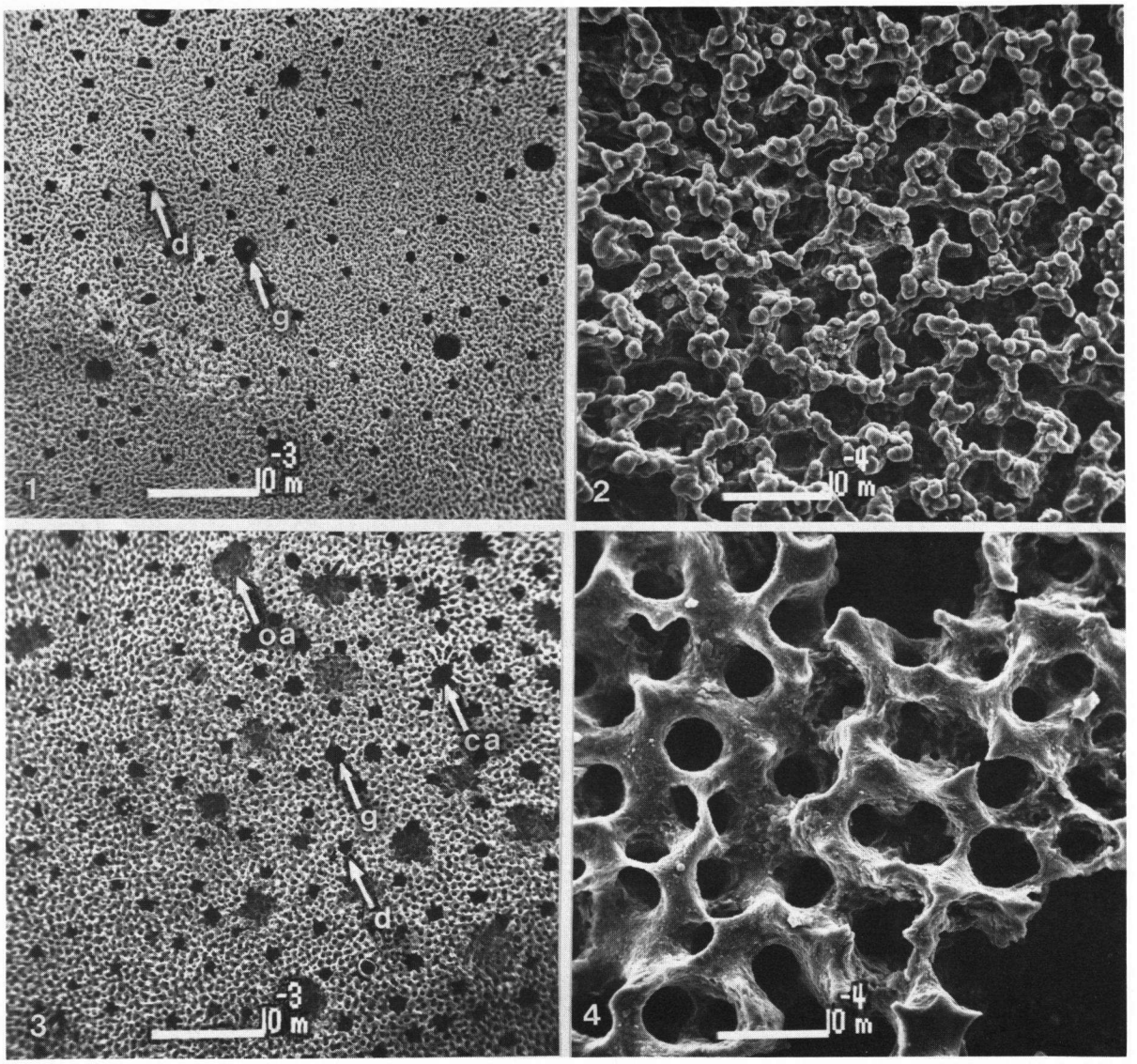

PLATE VI

Scanning electron microscope photographs (g = gastropore, d = dactylopore, ca = closed ampulla, oa = open ampulla):

1, *Millepora squarrosa*, surface (ZMA Coel. 8211).

2, *Millepora squarrosa*, microstructure of skeleton (ZMA Coel. 8211).

3, *Millepora striata*, surface with closed and open ampullae (ZMA Coel. 8371).

4, *Millepora striata*, microstructure of skeleton (ZMA Coel. 8371).

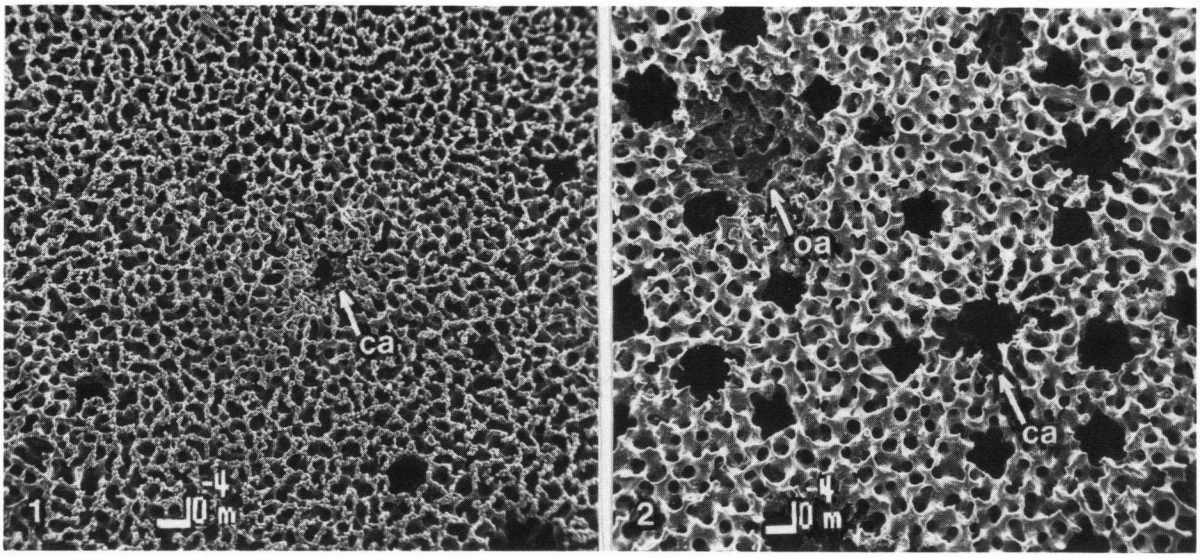

PLATE VII

Scanning electron microscope photographs (ca = closed ampulla; oa = open ampulla):
1, Closed ampulla of a specimen of *Millepora complanata* (ZMA Coel. 8005).
2, Detail of ampullae of the specimen of *Millepora striata* of pl. VI fig. 3.