BEAUFORTIA

INSTITUTE OF TAXONOMIC ZOOLOGY (ZOOLOGICAL MUSEUM)
UNIVERSITY OF AMSTERDAM

Vol. 41, no. 27 October 22, 1990

DISCONTINUOUS DISTRIBUTION OF THE TROPICAL WEST ATLANTIC HYDROCORAL *MILLEPORA SQUARROSA*

WALLIE H. DE WEERDT

*Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington DC, 20560, U.S.A.**)

ABSTRACT

The hydrocoral *Millepora squarrosa* (Hydrozoa, Coelenterata) exhibits a limited, partly disjunct, distribution in the tropical western Atlantic. In the Caribbean the species is known from the Dominican Republic, Puerto Rico, Vieques, Culebra, the Lesser Antilles arc, and Barbados. It also occurs in Brazil. It is hypothesized that *M. squarrosa* is the descendant of an ancestor shared with the Indo-Pacific species *M. platyphylla* and that vicariance events prior to the Pliocene uplift of the Panamanian Isthmus have induced speciation of this ancestor into these species. The restricted Caribbean distribution of *M. squarrosa* is hypothesized to be the result of extinction of this species in certain parts of the Caribbean and its inability to re-intrude in these areas because of its ecological requirements and life strategy.

INTRODUCTION

Discontinuity in the distribution of Caribbean coral reef organisms seems to be a rarity (e.g., Porter, 1972; Milliman, 1973; Chassaing et al., 1979), and has sofar only been recorded for the hermatypic coral species *Dendrogyra cylindrus* Ehrenberg (cf. Porter, 1972) and the hydroid *Solanderia gracilis* Duchassaing & Michelin (cf. Larson, 1987).

A third example of a discontinuous Caribbean distribution is shown by the hydrocoral *Millepora squarrosa* Lamarck (Milleporidae, Hydrozoa), known only from the Dominican Republic, Puerto Rico, Vieques, Culebra, the Lesser Antilles arc, and Brazil. The present paper intends to present an explanation for this anomaly.

This paper is dedicated to Prof. Dr J. H. Stock on occasion of his retirement.

*) Address for reprint requests: Institute of Taxonomic Zoology (Zoölogisch Museum), University of Amsterdam, P.O. Box 4766, 1009 AT Amsterdam, the Netherlands.

MATERIAL AND METHODS

Collections and observations were made by snorkling and SCUBA diving during two cruises to the Lesser Antilles on board of the R/V Seward Johnson (spring 1989) of the Harbor Branch Oceanographic Institution, Florida, and additional field trips to Belize (Carrie Bow Cay, Twin Cays and Glover's Reef), Venezuela (Los Roques Islands), the Florida Keys, and Puerto Rico (fall 1988, spring 1989, and winter 1990). Earlier field work has been done in Curaçao and Bonaire (1976-1977). The recently collected material has been deposited in the National Museum of Natural History

(NMNH), Washington, catalogued under numbers of the United States National Museum (USNM), and the Zoological Museum, Amsterdam (ZMA). Dr Charles Wahle kindly lent me *Millepora* specimens from several Caribbean localities. Dr Jacques Laborel lent me his material from Brazil.

SITE-DATA OF MATERIAL IN ZMA AND USNM:

PUERTO RICO: ZMA Coel. 8448 (W. of Cayo Turrumote I, on coral heads, 18 m, 21-II-1990, coll. W. H. de Weerdt); USNM 87608 (same data as ZMA Coel. 8448).

GUADELOUPE: ZMA Coel. 8438 (Grand Cul-de-Sac Marin, Passe a Caret, NW of Ilet a Caret, 16°21.74'N, 61°38.13'W, 5 m, on dead parts of corals, 23-VI-1989, coll. C. Bouchon); ZMA Coel 8439 (Basse-Terre, central W side, S side of southern Ilets a Goyaves, Pigeon, 16°10.25'N, 61°47.75'W, 4 m, on dead parts of corals, 21-VI-1989, coll. C. Bouchon); ZMA Coel. 8442 (SW Basse-Terre, 16°05.51'N, 61°47.00'W, 15 m, on dead parts of corals, 20-VI-1989, coll. C. Bouchon); USNM 85923 (same data as ZMA Coel. 8439); USNM 85922 (same data as ZMA Coel. 8442); USNM 85926 (Iles de Saintes, Terre D'en Bas, off Gros Cap, 15°50.80'N, 61°39.25'W, 8 m, on rocks, 19-VI-1989, coll. C. Bouchon).

MARTINIQUE: ZMA Coel. 8433 (Cap Enrage, central W side, 14°38.65°N, 61°09.30'W, rock-coral sand slope, on rocks, 12-15 m, 6-VII-1989, coll. W. H. de Weerdt); ZMA Coel. 8436 (Baie du Marin, 14°26.65'N, 60°54.20'W, 12 m, on dead parts of corals, 2-VII-1989, coll. W. H. de Weerdt); USNM 85925 (same data as ZMA Coel. 8433); USNM 85928 (same data as ZMA Coel. 8436).

ST. LUCIA: ZMA Coel 8435 (Vieux Fort Bay, Mathurin Pt., W side, 13°42.96'N, 60°58.10'W, 1.5-2 m, on rocks, 28-VI-1989, coll. W. H. de Weerdt); ZMA Coel. 8437 (N of Southfriere Bay, Grand Caille Pt., 13°52.10'N, 61°05.38'W, 5 m, on dead parts of corals, 27-VI-1989, coll. W. H. de Weerdt); USNM 85927 (same data as ZMA Coel. 8435); USNM 85929 (same data as ZMA Coel. 8437).

ST. VINCENT: ZMA Coel. 8440 (Kingstown Bay, 17°83'N, 61°14.28'W, 3 m, on dead parts of corals, 30-III-1989, coll. W. H. de Weerdt); USNM 85921 (same data as ZMA Coel. 8440).

BARBADOS: ZMA Coel. 8434 (W side, S Hole Town, 13°10.06'N, 59°38.90'W, 3 m, on rocks, 9-IV-1989, coll. W. H. de Weerdt); USNM 85930 (same data as ZMA Coel. 8434).

GRENADA: ZMA Coel. 8441 (Off St. George Harbour, ca. 0.5 mile W of St. John River, 12°03.52'N, 61°45.58'W, 3 m, on rocks, 3-IV-1989, coll. W. H. de Weerdt; USNM 85924 (same data as ZMA Coel. 8441).

BRAZIL: USNM 5340 (labeled: *M. braziliensis*, Pernambuco); USNM 5341 (labeled: *M. braziliensis*, Pernambuco, figured specimen in Boschma, 1962, pl. II & III); USNM 5632 (labeled: *M. braziliensis*, Pernambuco); USNM 6535 (labeled: *M. braziliensis*, Pernambuco); USNM 6537 (labeled: *M. braziliensis*, Pernambuco); USNM 6543 (labeled: *M. braziliensis*, Pernambuco); USNM 6545 (labeled: *M. braziliensis*, Pernambuco): USNM 6548 (labeled: *M. braziliensis*, Pernambuco); USNM 86576 (Maria Farinha, Pernambuco, figured specimen in Boschma, 1962, pl. VI & VII; original label lost).

RESULTS

Millepora squarrosa stands out among other Caribbean *Millepora* species by the possession of an unusually high density of dactylopores (356-816 per cm²), combined with very small-sized dactylopores (0.07-0.15 mm) (for exact data and comparison with other Caribbean *Millepora* species cf. de Weerdt, 1984). The species can also be recognized by its honeycombed growth form, but needs to be compared with *M. complanata* Lamarck, with which it is partly sympatric, and with *M. striata* Duchassaing & Michelotti, with which it has a disjunct distribution. Some taxonomic confusion in *Millepora* is caused by the fact that Boschma, revising the genus *Millepora* (Boschma, 1948), based the species redescriptions entirely on the

growth form of the coralla (cf. also Lewis, 1989). *Millepora squarrosa*, for instance, was characterized as being honeycombed, and *M. complanata* as plate-like. *Millepora complanata* is a very variable species, however, much more variable than *M. squarrosa*, and honeycombed ("boxwork" in the terminology of Stearn & Riding, 1973) forms occur frequently in this species (cf. Stearn & Riding, 1973; de Weerdt, 1984). The two species differ in that *M. squarrosa* is really very "squarish", much more squarish than the boxwork forms of *M. complanata*. The tendency to form square areas of interconnected (low) upright structures is very conspicuous in small colonies of *M. squarrosa*, whereas small colonies of *M. complanata* always consist of single plates (pers. observ.; cf. also de Weerdt, 1981, pl. VII figs. 3, 4). The coralla of *M. squarrosa* are extremely sturdy, compact, and broad-based, a phenomenon that may be directly related to its apparent preference for inhabiting places with strong water movement (pers. observ., and Stearn & Riding, 1973). The edges of the plates of *M. squarrosa* are generally smooth, somewhat truncated, whereas they are usually sharp in *M. complanata*. The surface of *M. squarrosa* furthermore is always frilled (cf. Boschma, 1948, and Stearn & Riding, 1973). Finally, *M. complanata* has much larger (0.10-0.30 mm) and much less numerous (45-235 per cm^2) dactylopores.

Because of Boschma's apparent unawareness of the variability of *M. complanata*, boxwork forms of *M. complanata* have regularly, but erroneously been referred to as *M. squarrosa* in papers dealing with coral reef communities (e.g., Boschma, 1948, pl. IX; Roos, 1971, p. I; Zlatarski & Martinez Estalella, 1982, pl. 154 fig. 2, as *M. alcicornis* forma *squarrosa*).

Millepora striata Duchassaing & Michelotti has been synonymized with *M. squarrosa* by Boschma (1948), again on basis of similarities in growth form, but I have shown that the latter is a valid species (de Weerdt, 1984). It differs from *M. squarrosa* by much more loosely connected plates, which have a strong tendency to divide towards the upper part, by the marked sharp edges of the plates, and by somewhat larger (0.08-0.18 mm) and less numerous (278-500 per cm^2) dactylopores.

The other *Millepora* species occurring in the Caribbean is *M. alcicornis* Linnaeus; this species cannot be confused with *M. squarrosa* because of its predominantly branching habit, smooth surface and much less abundant dactylopores (45-200 per cm).

Millepora complanata and *M. alcicornis* occur throughout the Caribbean, whereas *M. striata* seems to be restricted to San Blas and Venezuela (de Weerdt, 1984).

The *Millepora* species usually recorded from Brazil are *M. alcicornis* Linnaeus, *M. braziliensis* Verrill, and *M. nitida* Verrill (Boschma, 1962; Laborel, 1970, 1971; Belem et al., 1986). The single Brazilian record (from Pernambuco) of *M. squarrosa* is from Boschma (1962, p. 307, pl. VI and VII, registered as USNM 86576; the original label is lost). The specimen conforms to *M. squarrosa*. The specimen figured in Boschma, 1962, pl. II and III (USNM 5341), and identified by him as *M. braziliensis*, also from Pernambuco, is in my opinion *M. squarrosa* as well. The same applies to several other specimens in USNM, all from Pernambuco, Brazil (e.g., USNM 5340; 5632; 6534; 6535; 6537; 6545; 6548, see pl. I figs. 1 and 2 of the present paper), and which are labeled *Millepora braziliensis*. All these specimens have extremely abundant and minute dactylopores, a sturdy boxwork growth form with truncated edges, and frilled surface. In addition, I studied Laborel's *Millepora* specimens from Brazil, three of which (two from Recife, the other from Salvador) conform to *M. squarrosa*. The identity of *M. braziliensis* still needs elucidation by study of the type specimen, but it is quite possible that *M. braziliensis* and *M. squarrosa* are conspecific. *Millepora nitida* stands out by its habit of low rounded clumps (cf. Boschma, 1962, p. 308, pl. VIII).

In table I the data concerning the distribution of *M. squarrosa* are presented. Both presence and absence are scored, and based on my own observations and literature references, the latter confined to those which give maximal information, e.g., provided with photographs of good

quality. Doubtful records (e.g., Porter, 1972) are left out of consideration.

In fig. 1 the distribution of *M. squarrosa* is presented. Plate I figures three specimens, with close-ups of the corralla.

The distribution pattern of *Millepora squarrosa* easily leads to the conclusion that the species has a discontinuous distribution in the Caribbean, stretching from the Dominican Republic, Puerto Rico, the Lesser Antilles arc to Grenada as its southern limit, with a disjunct distribution in Brazil. This can be tested by conducting field work in the missing localities.

DISCUSSION

The restricted distribution of *Millepora squarrosa* in the Caribbean seems to be unique, since it does not match with the two other coral reef organisms with a restricted distribution in this area, namely the coral species *Dendrogyra cylindrus* Ehrenberg (cf. Porter, 1972) and the hydroid *Solanderia gracilis* Duchassaing & Michelin (cf. Larson, 1987). *Dendrogyra cylindrus* seems to be absent only from Panama and Colombia (Porter, 1972), and is thus more widespread than *M. squarrosa*. *Solanderia gracilis* has a disjunct distribution throughout the entire Caribbean, and occurs intermittently from North Carolina to Brazil (Larson, 1987).

Like *Solanderia gracilis*, *Millepora squarrosa* seems to favor turbulent places (Larson, 1987), but unlike *S. gracilis*, it needs no shelter. The species is usually found on dead corals parts and boulders, and is most abundant in the uppermost parts of back reef areas. When applying the question of *K* and *r* selection (MacArthur & Wilson, 1967; Loya, 1976; Rosen, 1981) or the *C-S-R* triangle of Grime (1979: cf. also Rosen, 1981) to *Millepora*, *Millepora squarrosa*, as far as the Caribbean populations are concerned, could be considered a *S*-strategist sensu Grime (stress tolerant), which is equivalent to a *K*-strategist (Rosen, 1981). Caribbean specimens of *M. squarrosa* are generally small, probably slow growing, very sturdy, and possibly with a short reproductive period (ampullae have not been observed in the specimens studied by me, whereas they were frequently found in *M. complanata* and *M. alcicornis*, cf. de Weerdt, 1984). *Millepora complanata* could be interpreted as a

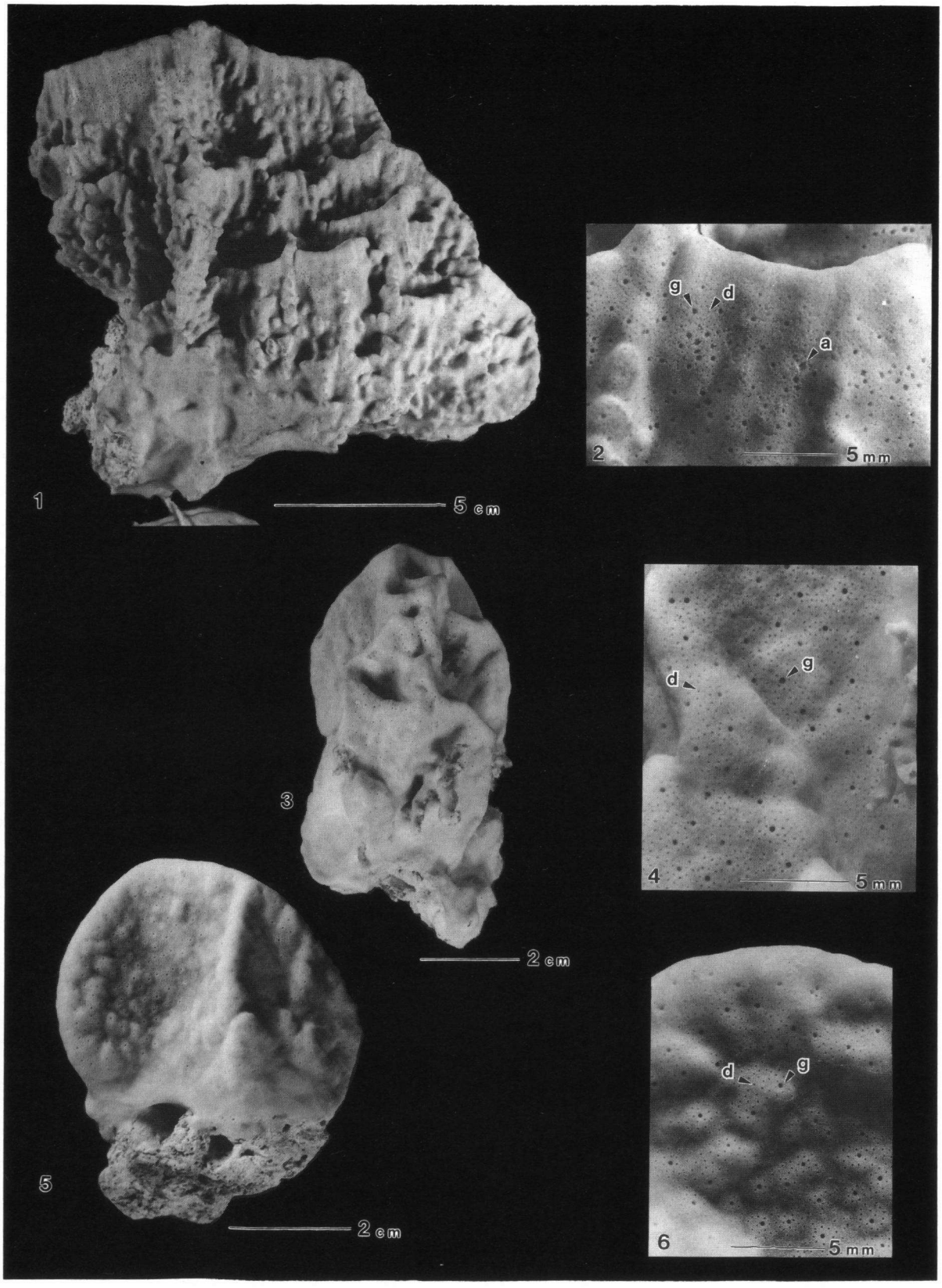
TABLE I. Data on the distribution of *Millepora squarrosa*.

Locality	present (+)/ absent (-)	reference/material
Caribbean:		
Dominican Republic	+	specimen in the collection of C. Wahle
Puerto Rico	+	Almy & Carrión Torres (1963, as *M. squarrosa*); Colin (1978, as *M. squarrosa*); de Weerdt (1984, as *M. squarrosa*); present paper
Vieques	+	specimens in the collection of C. Wahle
Culebra	+	specimens in the collection of C. Wahle
Saba	+	de Weerdt (1984)
St. Eustatius	+	de Weerdt (1984)
Guadeloupe	+	Chassaing et al. (1979, as *M. squarrosa*); present paper
Martinique	+	present paper
St. Lucia	+	present paper
St. Vincent	+	present paper
Barbados	+	Stearn & Riding (1973, as *M. squarrosa*); present paper
Grenada	+	present paper
Florida	-	Wheaton & Jaap (1988); present paper
Bahamas	-	Squires (1958)
Cuba	-	Duarte Bello (1961); Zlatarski & Martinez Estalella (1982, record of *M. alcicornis* forma *squarrosa*, but which is *M. complanata*)
Jamaica	-	Goreau (1959); Aranson (pers. comm.)
Bonaire	-	pers. observ.; de Weerdt (1981, 1984)
Curaçao	-	pers. observ.; de Weerdt (1981, 1984)
Venezuela	-	Olivares & Leonard (1971); present paper
Belize	-	Cairns (1982); present paper
Brazil:		
Recife	+	Laborel (1971, as *M.* cf. *braziliensis*); specimens in the collection of J. Laborel
Salvador	+	idem
Pernambuco	+	Boschma (1962, as *M. squarrosa* and *M. braziliensis*); present paper

Fig. 1. Distribution of *Millepora squarrosa.*

"competitor", thus as a *C*-strategist sensu Grime, being fast-growing and large. *Millepora alcicornis* may take the place of the *R*-strategist, being "small" (at least smaller than *M. complanata*) and fast-growing.

It is quite possible that localities with moderately high-energy conditions, like the islands of the Lesser Antilles arc (Adey, 1978) provide the three niches, high wave energy, moderate wave energy and low wave energy for


1
5 cm
2
g
d
a
5 mm
3
2 cm
4
d
g
5 mm
5
2 cm
6
d
g
5 mm

Millepora squarrosa, *M. complanata* and *M. alcicornis* respectively, thus enabling their coexistence. Places with moderately low-energy favor a more luxurious growth of *M. complanata*, which may result in lack of space for *M. squarrosa*, and hence its absence in these places. Remarkable in this respect is the fact that *M. squarrosa* apparently reaches larger sizes in Brazil than in the Caribbean (the Brazilian specimens in the USNM are much larger than the Caribbean specimens seen by me). *Millepora complanata* does not occur in Brazil, and it is quite possible that *M. squarrosa* shifts to a *C*-strategist here, taking over the niche of *M. complanata*.

Competition with *Millepora complanata* (and maybe also with other rapidly growing species, like *Acropora palmata*) may thus very well contribute to the restricted distribution of *M. squarrosa* in the Caribbean, although it does not, in my opinion, explain the complete absence of the species in a large, continuous part in this area.

A phylogenetic analysis of the genus *Millepora* is still pending, but it is tentatively hypothesized that *M. squarrosa* and the Indo-Pacific and eastern Pacific *M. platyphylla* Hemprich & Ehrenberg (cf. Boschma, 1948; Glynn, 1972; Glynn et al., 1972) are each others closest relatives, sharing a common ancestor with a former Tethys distribution. The high dactylopore density, although less high in *M. platyphylla*, viz. 120-366 per cm², small dactylopore size (0.12-0.15 mm; data of Red Sea specimens obtained from Walstijn & Spil, unpublished graduate report, Institute of Taxonomic Zoology, University of Amsterdam), frilled surface, and sturdy growth form with truncated growing edges are interpreted as synapomorphous (shared derived) characters.

The Pliocene uplift of the Panamanian Isthmus is generally recognized as the vicariance event leading to sister-group relations at both sides of the Isthmus (e.g., Ekman, 1953; Rosen, 1976). The conspecifity of the Brazilian and eastern Caribbean populations of *M. squarrosa* does not fit very well with this timing, since the age of the Amazone-Orinoco barrier has been hypothesized by Laborel (1970) to be of Miocene age, thus older than the Isthmus. Glynn (1972, 1982) has presented the hypothesis that a restriction of flow across Central America occurred already before the rise of the Isthmus. This, together with the theory of Miocene mass extinctions in these areas (e.g., Fagerstrom, 1987), may explain the distribution of *M. squarrosa*. It is suggested that speciation of the ancestor of *M. squarrosa* and *M. platyphylla* into these species has taken place before the rise of the Isthmus, that *M. squarrosa* became extinct in the eastern and southern parts of the Caribbean, and that it has not been able to re-intrude in these areas because of its life strategy and inability to compete with *M. complanata*. The eastern Caribbean and Brazilian areas are considered refugia for *M. squarrosa*.

ACKNOWLEDGEMENTS

I am most grateful to Dr. Shirley Pomponi (Harbor Branch Oceanographic Institution, Florida) for inviting me to participate in two cruises to the Lesser Antilles with the R/V Seward Johnson, and for providing logistical support during my visit to the Florida Keys. Field work in Belize and Venezuela was funded by a grant from the Caribbean Coral Reef Ecosystems Program (CCRE), National Museum of Natural History, partly supported by the EXXON Corporation (Contribution no. 285). These field trips were primarily aimed at sponges, but enabled me to make observations on *Millepora* as well. Drs Charles Wahle and Jac-

Plate 1. 1, *Millepora squarrosa*, corallum, USNM 6548 (Pernambuco, Brazil). 2, *Millepora squarrosa*, USNM 6548, detail of surface. a = ampulla, d = dactylopore, g = gastropore. 3, *Millepora squarrosa*, corallum, USNM 85925 (Martinique). 4, *Millepora squarrosa*, USNM 85925, detail of surface. d = dactylopore, g = gastropore. 5, *Millepora squarrosa*, corallum, ZMA Coel. 8437 (St. Lucia). 6, *Millepora squarrosa*, ZMA Coel. 8437, detail of surface. d = dactylopore, g = gastropore.

ques Laborel kindly lent me their *Millepora* specimens. I thank Mike Carpenter for making photographs of the corals. Drs Klaus Rützler, Suzanne Fredericq, and Stephen Cairns critically reviewed the manuscript.

Because this volume is dedicated to Prof. Dr J. H. Stock on occasion of his retirement, I would like to thank him for all those years that he supervised me, first as a graduate student working on *Millepora*, and later as a post-graduate student working on sponge systematics. I appreciate his interest in my work, his flexibility, and the freedom he always gave me.

REFERENCES

ADAMS, R. D., 1968. The leeward reefs of St. Vincent, West Indies. Jour. Geol., **76**: 587-595.

ADEY, W. H., 1978. Coral reef morphogenesis: a multidimensional model. Science, **202**: 831-837.

ALMY, C. C. & C. C. CARRIÓN TORRES, 1963. Shallow water stony corals of Puerto Rico. Caribb. J. Sci., **3** (2-3): 1-162.

BELEM, M. J. C., C. ROHLFS, D. O. PIRES, C. B. CASTRO & P. S. YOUNG, 1986. S.O.S. Corais. Ciencia Hoje, **4** (26): 35-42.

BOSCHMA, H., 1948. The species problem in Millepora. Zool. Verh. Leiden, **1**: 1-115, pls. I-XV.

——, 1962. On Milleporine corals from Brazil. Proc. kon. ned. Akad. Wetensch., (C) **65** (4): 303-312, pls. I-VIII.

CAIRNS, S. D., 1982. Stony corals (Cnidaria: Hydrozoa, Scleractinia) of Carrie Bow Cay, Belize: 271-302. In: Rützler, K. & I. G. Macintyre (eds): The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize, I. Structure and Communities (Smithsonian Institution Press, City of Washington).

CHASSAING, J. P., A. DELPLANQUE & J. LABOREL, 1979. Coraux des Antilles françaises. Rev. fr. Aquariol., **5** (3): 56-84.

COLIN, P. I., 1978. Caribbean reef invertebrates and plants. A field guide to the invertebrates and plants occurring on coral reefs of the Caribbean, the Bahamas and Florida: 1-512 (T.F.H. Publications, Hong Kong).

DUARTE BELLO, P. P., 1961. Corales de los Arrecifes Cubanos. Acuario Nacional, **2**: 1-85.

EKMAN, S., 1953. Zoogeography of the sea: I-XIV, 1-417 (Sidgwick & Jackson, London).

FAGERSTROM, J., 1987. The evolution of reef communities: i-xv, 1-600, pls. 1-51 (Wiley Interscience, New York).

GLYNN, P. W., 1972. Observations on the ecology of the Caribbean and Pacific coasts of Panama. Bull. Biol. Soc. Wash., **2**: 13-30.

——, 1982. Coral communities and their modifications relative to past and prospective Central American Seaways. Adv. Mar. Biol., **19**: 91-132.

GLYNN, P. W., R. H. STEWARD & J. E. MCCOSKER, 1972. Pacific corals reefs of Panama: structure, distribution and predators. Geol. Rundschau, **61**: 438-519.

GOREAU, T. F., 1959. The ecology of Jamaican coral reefs, I. Species composition and zonation. Ecology, **40**: 67-90.

GRIME, J. P., 1979. Plant strategies and vegetation processes: 1-222 (John Wiley & Son, New York).

LABOREL, J., 1970 [1969]. Les Peuplements de Madréporaires des côtes tropicales du Brazil. Ann. Univ. Abidjan, Ser. E, **2** (3): 1-260.

——, 1971 [1969-1970]. Madréporaires et Hydrocoralliaires recifaux des cotes brésiliennes. Systématique, écologie, répartition verticale et géographique. Rés. scient. Camp. Calypso, **9** (= Annls. Inst. océanogr. Monaco, (N.S.) 47): 171-229, pls. I-VII.

LARSON, R. J., 1987. The ecology of the western Atlantic athecate Hydroid, Solanderia gracilis. Bull. mar. Sci., **40** (3): 512-515.

LEEWIS, J. B., 1989. The ecology of *Millepora*. A review Coral Reefs, **8** (3): 99-107.

LOYA, Y., 1976. The Red Sea coral Stylophora pistillata is an *r* strategist. Nature, **259**: 478-480.

MACARTHUR, R. H. & E. O. WILSON, 1967. The theory of island biogeography: 1-203 (Princeton University Press, Princeton).

MILLIMAN, J. D., 1973. Caribbean Coral Reefs: 1-50. In: Jones, O. A. & R. Endean (eds): Biology and geology of coral reefs, vol. I: Geology 1.

OLIVARES, M. A. & A. B. LEONARD, 1971. Algunos corales petreos de la Bahia de Mochino, Venezuela. Bol. Inst. Oceanogr. Univ. Oriente, **10** (1): 49-70.

PORTER, J. W., 1972. Ecology and species diversity of coral reefs on opposite sides of the Isthmus of Panama. Bull. Biol. Soc. Wash., **2**: 89-116.

ROOS, P. J., 1971. The shallow-water stony corals of the Netherlands Antilles. Stud. Fauna Curaçao Caribb. Islands, **37**: 1-108, pls. I-LIII.

ROSEN, B. R., 1981. The tropical high diversity enigma - the corals'-eye view: 103-129. In: Forey, P.L. (ed.). The evolving biosphere (British Museum (Natural History), London & Cambridge University Press, Cambridge).

ROSEN, D. E., 1976. A vicariance model of Caribbean biogeography. Syst. Zool., **24** (4): 431-464.

SQUIRES, D. F., 1958. Stony corals from the vicinity of Bimini, Bahamas. Amer. Mus. nat. hist. Bull., **115**: 215-262.

STEARN, C. W. & R. RIDING, 1973. Forms of the hydrozoan Millepora on a recent coral reef. Lethaia, **6**: 187-200.

WEERDT, W. H. DE, 1981. Transplantation experiments with Caribbean Millepora species (Hydrozoa, Coelenterata), including some ecological observations on growth forms. Bijdr. Dierk., **51** (1): 1-19.

——, 1984. Taxonomic characters in Caribbean Millepora species (Hydrozoa, Coelenterata). Bijdr. Dierk., **54** (2): 243-262.

WHEATON, J. L. & W. C. JAAP, 1988. Corals and other prominent benthic Cnidaria of Looe Key National Marine Sanctuary, Florida. Florida Mar. Res. Publ., **43**: 1-25.

ZLATARSKI, V. N. & N. MARTINEZ ESTALELLA, 1982. Les Scleractiniaires de Cuba avec des données sur les organismes associés: 1-472, pls. 1-161. (Editions de l'Académie bulgare des Sciences, Sofia).

Received: August 3, 1990

Institute of Taxonomic Zoology (Zoölogisch Museum), University of Amsterdam,
P.O. Box 4766, 1009 AT Amsterdam, the Netherlands