A new and presumably now extinct species of *Millepora* (Hydrozoa) in the eastern Pacific

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A new species of hydrocoral, *Millepora boschmai*, is described from the Gulf of Chiriquí, Pacific Panamá. This species was first found in the early 1970's, but it has disappeared from this area as a result of the severe 1982-83 El Niño-Southern Oscillation (ENSO) event. Because the species has never been encountered outside the Gulf of Chiriquí, it is assumed that it was endemic to this area and that its disappearance marks an extinction event, representing the first documented case of a modern extinction of a tropical marine organism due to natural causes.

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Introduction

The presence of the hydrocoral genus *Millepora* Linnaeus, 1758 (Hydrozoa, Coelenterata) in the eastern Pacific was unknown until the early 1970's when one of us (PWG) found three species in the Gulf of Chiriquí, Pacific Panamá (Glynn, 1972; Glynn et al., 1972; Porter, 1972): *Millepora intricata* Milne Edwards, 1857, *Millepora platyphylla* Hemprich & Ehrenberg, 1834 and a third, still undescribed species. The first two species were previously known from the Indo-West Pacific and Indo-West and Central Pacific respectively (Boschma, 1948), whereas the undescribed species was reported as being endemic to the Gulf of Chiriquí (Glynn, 1972).

It now appears that both *M. platyphylla* and the undescribed species have disappeared from the eastern Pacific as a result of the severe 1982-83 El Niño-Southern Oscillation (ENSO). The prolonged (5-6 months) high temperature anomalies (2-3°C above normal) that accompanied this event caused widespread bleaching and mortality among zooxanthellate corals in the eastern Pacific (Glynn, 1983, 1984, 1988, 1990; Glynn & D'Croz, 1990). The milleporids were among the first photosymbionts to lose their zooxanthellae and subsequently experienced the highest mortalities of all affected coral reef organisms (Glynn, 1983, 1990). Monitoring studies in the Gulf of Chiriquí during and after the ENSO event revealed that all colonies of *M. platyphylla* and the undescribed species had died by April 1983 (Glynn, 1984), and that in December 1990 they were still absent in this area (PWG and WHW, pers. observ.). The only hydrocoral found alive in October 1983 was a 2-cm long branch of *M. intricata* on a coral reef in the Secas Island area (Glynn, 1984). By December 1990, several large, living colonies were found at the Contreras Islands, Secas Islands and Coiba

Island (PWG and WHW, pers. observ.). There is a sense of urgency to study the earlier collections of the undescribed *Millepora* species as no living colonies of the species have been seen since April 1983.

Millepora platyphylla is widely distributed in the Indo-Pacific Ocean (Boschma, 1948), and its local disappearance will not immediately threaten the survival of the species. The new species, however, has never been observed outside the Gulf of Chiriquí, and it is therefore probable that it has become extinct as a result of the 1982-83 El Niño warming event.

The goals of the present paper are to describe the new species and to draw attention to the fact that this is, to our knowledge, the first documented case of the (probable) extinction of a tropical marine organism due to natural causes.

Material and methods

Living colonies of the three *Millepora* species were collected by PWG in March 1970 and August 1974 off Uva Island, Contreras Islands, in the Gulf of Chiriquí, Panamá. The Uva Island study sites have been visited approximately annually, from 1975 to the present (December 1990). All three *Millepora* species were observed alive and in apparently normal condition until January 1983 when they were found in a bleached state. Only live *Millepora intricata* colonies have been observed after 1983. Dead colonies of *M. platyphylla* and the new species were collected by us in December 1990 from Uva and Coiba Island, Gulf of Chiriquí.

Dactylopore and gastropore diameters were measured using a Wild binocular microscope (magnification 25 x); 25 measurements of the pore diameter per specimen were made. Pore densities were calculated by placing a piece of paper with an open square of 0.25 cm^2 on various parts of the coralla, and by counting the pores while using a magnification of 6 x. The pores in twelve areas were counted (cf. De Weerdt, 1984). These areas were not randomly chosen: growing edges and shaded areas, usually with fewer pores than other parts of the coralla, were excluded from the analysis. The species description follows the criteria adopted by De Weerdt (1984) in which both the growth form and pore features are considered as characters with systematic value.

The material is deposited in the following institutions: Nationaal Natuurhistorisch Museum (NNM), Leiden, specimens catalogued under numbers of Rijksmuseum of Natuurlijke Historie (RMNH), Leiden; National Museum of Natural History (NMNH), Washington D.C., specimens catalogued under numbers of the United States National Museum (USNM); Zoölogisch Museum Amsterdam (ZMA), Instituut voor Taxonomische Zoölogie, Amsterdam; and Smithsonian Tropical Research Institute (STRI), Republic of Panamá.

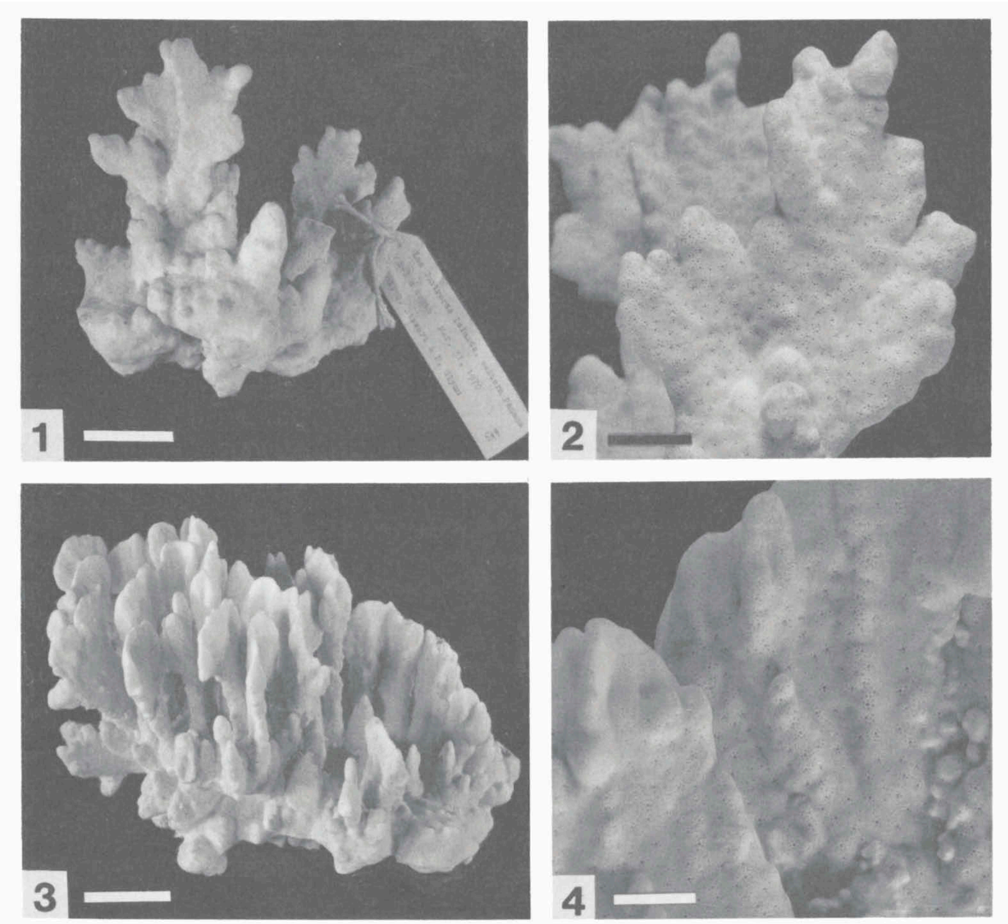
Descriptive part

Class **Hydrozoa**
Order **Capitata** Kühn
Suborder **Zancleida** Peterson

Family **Milleporidae** Fleming, 1828
Millepora boschmai spec. nov.
(figs. 1-4)

Millepora n.sp. 1; Glynn et al., 1972: 488.
Millepora sp. nov.?; Porter, 1972: 116.

Material.— Holotype (RMNH Coel. 14771), Uva Island, Contreras Islands, Gulf of Chiriquí, Panamá, 2-3 m, 31.iii.1970, coll. R. Stewart and P.W. Glynn. Paratypes (RMNH Coel. 14772), same data as holotype; (USNM 88321), Uva Island, coral reef, Contreras Islands, Gulf of Chiriquí, Panamá, approx. 2 m below mean low spring tide, bottom edge of reef flat, 19.viii.1974, coll. P.W. Glynn; (ZMA Coel. 8449), same data as USNM 88321.
Additional material.— (STRI, no catalogue number), same data as USNM 88321. Coralla of dead specimens; (USNM 88343-47, 88350-52, 88355), N side Uva Island, Contreras Islands, Gulf of Chiriquí, Panamá, 13 m, 14.xii.1990, coll. P.W. Glynn and W.H. de Weerdt; (ZMA Coel. 8450-52), same data as USNM specimens; (RMNH Coel. 17985), same data as USNM specimens; (ZMA Coel. 8453), Rocas Pesado, Coiba Island, Gulf of Chiriquí, Panamá, 20-25 ft., 16.xii.1990, coll. P.W. Glynn.



Figs. 1-4. Coralla and close-ups of *Millepora boschmai* spec. nov. 1, holotype, RMNH Coel. 14771, scale bar: 3.5 cm; 2, close-up of same specimen, scale bar: 1.5 cm; 3, paratype, ZMA Coel. 8449, scale bar: 4 cm; 4, close-up of same specimen, scale bar: 1 cm.

Type locality.— Uva Island reef, Contreras Islands, Gulf of Chiriquí, Panamá.

Description.— Shape and size: irregularly encrusting base from which arise plate-like outgrowths to 12 cm high and 0.5-1 cm thick. The plates are somewhat irregular in outline and usually increase in width distally, where they are irregularly, sometimes rather deeply, indented. Lateral plate-like extensions occasionally develop in between the plates, forming weakly developed box-like frameworks. Coralla of intermediate size, probably not exceeding 30 cm in overall height, 30 cm in length and 17 cm in width.

Surface: generally smooth, sometimes a little warty.

Gastropore diameter (five specimens, n = 125; range, means [in italics] and standard deviation in parentheses): 0.28-*0.37*(0.03)-0.44 mm.

Dactylopore diameter: 0.12-*0.18*(0.03)-0.26 mm.

Pore density: 4-*15*(4.5)-24 gastropores per cm^2; 56-*103.9*(30.2)-180 dactylopores per cm^2.

Cyclosystems: very distinct, far apart, and with only a few dactylopores scattered between the cyclosystems.

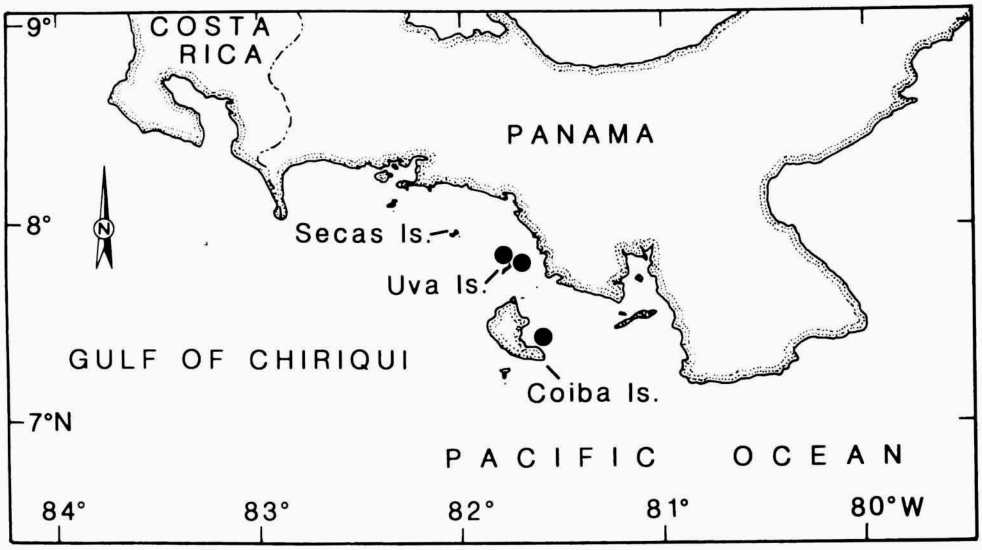


Fig. 5. Distribution of *Millepora boschmai* spec. nov.

Ecology.— Occurring from the upper, forereef slope (2 m) to deep, sand and rubble slopes (18 m). *Millepora boschmai* spec. nov. was the least abundant of the three hydrocoral species on the reef proper. It was most abundant at the reef base (5-6 m) and deeper outer slope (to 12-15 m).

Distribution.— Gulf of Chiriquí, Panamá (fig. 5).

Etymology.— Named after the late Prof. Dr H. Boschma to honor his important contributions to the taxonomy of *Millepora*. He actually recognized and intended to describe the present new species on the basis of the specimens sent to him by P.W. Glynn in the early 1970's (RMNH 14471 and 14472) (Boschma, in litt.).

Discussion

Apart from the new species, ten extant *Millepora* species are recognized in the Indo-Pacific: *M. dichotoma* Forskål, 1775; *M. exaesa* Forskål, 1775; *M. intricata* Milne Edwards, 1857; *M. latifolia* Boschma, 1948; *M. murrayi* Quelch, 1884; *M. platyphylla* Hemprich & Ehrenberg in Ehrenberg, 1834; *M. tenera* Boschma, 1949; *M. foveolata* Crossland, 1952; *M. tuberosa* Boschma, 1966; and *M. xishaensis* Zou, 1978.

The following six Atlantic species are currently recognized (Boschma, 1948; De Weerdt, 1984): *Millepora alcicornis* Linnaeus, 1758; *M. braziliensis* Verrill, 1868; *M. complanata* Lamarck, 1816; *M. nitida* Verrill, 1868; *M. squarrosa* Lamarck, 1816; and *M. striata* Duchassaing & Michelotti, 1864.

Of these 16 extant species, *Millepora boschmai* is most similar to the western Pacific *M. latifolia*, (see Serene & Nguyen, 1959; Ditlev, 1980; Randall & Myers, 1984; Randall & Cheng, 1984). In *M. latifolia* the cyclosystems are (also) quite isolated, but less so than in *M. boschmai*. Moreover, the dactylopores, and especially the gastropores, have a higher density in *M. latifolia* (dactylopores: 96-*148*(31.7)-196 per cm², gastropores: 12-*23.3*(6.1)-32 per cm²; RMNH Coel. 13748, the figured specimen of Boschma, 1948 pl. III, has been examined; the specimen is attached to a colony of *M. intricata* and partly overgrowing it). Other differences are smaller gastropores (0.26-*0.32*(0.02)-0.36 mm), smaller dactylopores (0.12-*0.14*(0.03)-0.20 mm), and a greater tendency towards a dendritic colony form in *M. latifolia*. Unfortunately, the material of both species is scanty, which impedes a more thorough comparison.

Another species with distinct cyclosystems is the fossil *Millepora tornquisti* Boschma, 1951, which has been described from a single specimen from the Eocene of Madagascar (cf. also Boschma, 1956). *M. tornquisti* has thick branches (Boschma, 1951: 9, fig. 2e), which distinguishes it from both *M. boschmai* and *M. latifolia*.

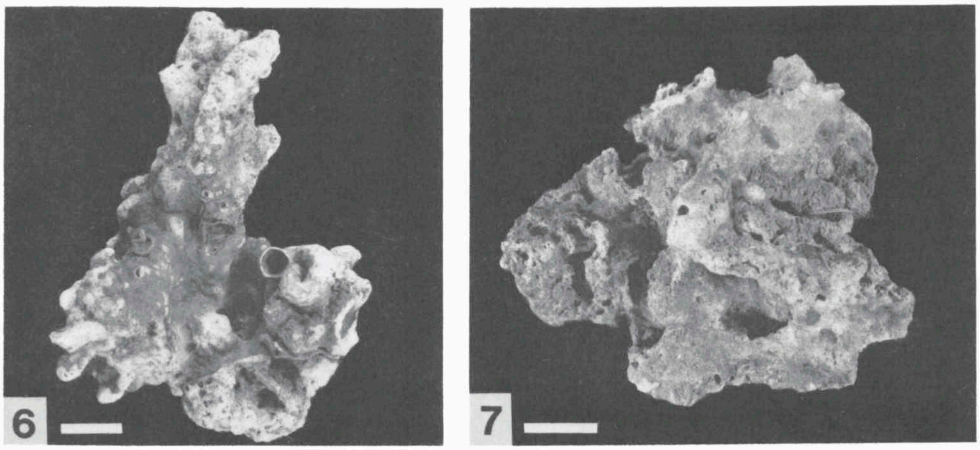
Assuming that the pore characters (i.e., density and size of the dactylopores and degree of isolation of the cyclosystems) are phylogenetic features in nature (cf. De Weerdt, 1990), we hypothesize that *M. boschmai* is more closely related to *M. latifolia* and *M. tornquisti* than to any of the other *Millepora* species. The assumed synapomorphous (shared derived) character state uniting these species is the presence of very distinct cyclosystems.

In the eastern Pacific, *Millepora boschmai* as well as *M. intricata* and *M. platyphylla*, are restricted to the Gulf of Chiriquí, as concluded from intensive coral reef studies in the Panamic Pacific Province (Mexico, El Salvador, Costa Rica, Colombia, mainland Ecuador, Galápagos Islands) (e.g., Durham & Barnard, 1952; Squires, 1959; Durham, 1966; Glynn, 1972; Glynn et al., 1972; Porter, 1972; Bakus, 1975; Birkeland et al., 1975; Gierloff-Embden, 1976; Glynn & Wellington, 1983; Cortes & Murillo, 1985; Von Prahl & Alberico, 1986; Guzman & Cortes, 1989). *M. intricata* occurs also in the West Pacific, and *M. platyphylla* is widely distributed in the Indo-West and Central Pacific (Boschma, 1948). Thus, *M. boschmai* is the only species of *Millepora* endemic to the eastern Pacific (Glynn, 1972).

The only other zooxanthellate coral species endemic to the eastern Pacific is the scleractinian *Pocillopora capitata* Verrill, 1864, which is assumed to have diverged from an Indo-West Pacific species (cf. Wells in Glynn & Wellington, 1983; Vermeij, 1989). All the other 25 species are conspecific with Indo-Pacific species (see Wells in Glynn & Wellington, 1983; Hoeksema, 1989, for Fungiidae). Except for *Millepora* *platyphylla*, which forms a twin-species pair with the western Atlantic *M. squarrosa* (cf. De Weerdt, 1990), none of the eastern Pacific zooxanthellate coral species seems to have its closest relative at the Caribbean side of the Panama Isthmus. This pattern is in strong contrast with other invertebrates, including azooxanthellate corals, which clearly comprise an eastern Pacific-Caribbean track. The relatively recent (late Pliocene) uplift of the Panama Isthmus is generally recognized as the prime vicariance event responsible for these East Pacific-West Atlantic sistergroup relationships (see Ekman, 1953; Olsson, 1972; Rosen, 1975; Vermeij, 1978; Budd, 1989; Lessios & Cunningham, 1990; Cairns, 1991). The strong Indo-Pacific affinity of the modern eastern Pacific hermatypic coral fauna is generally linked to the massive Eocene and Pleistocene extinctions in the eastern Pacific (e.g., Fagerstrom, 1987; Colgan, 1989) followed by re-introduction of Indo-West Pacific species by long-distance dispersal (e.g., Newell, 1971; Dana, 1975; Hoeksema, 1989). However, an opposite view was adopted by McCoy & Heck (1976) and Heck & McCoy (1978), which advocates survival of some coral populations in eastern Pacific refugia, providing the source for recolonisation of places close enough to these refugia (see Rosen, 1988, for a review of the different theories).

Long-distance dispersal by planktonic larvae occurs in many invertebrates (Scheltema, 1986, 1988), but although some coral larvae may live over 100 days (Harrigan, 1972; Richmond, 1989), long-distance dispersal of clonal benthic forms is most likely to take place by rafting (Jokiel, 1984, 1989; Jackson, 1986; Scheltema, 1986). Jokiel (1989) reported one case of a *Millepora* specimen found on pumice. Modern studies on the reproduction of *Millepora* are virtually lacking (Lewis, 1989), but according to Hickson (e.g., 1888, 1900) *Millepora* medusae and larvae are probably short-lived. Assuming that rafting is the most probable means for long-distance dispersal of *Millepora*, the rarity of this dispersal mode might explain the isolation and divergence of *M. boschmai* from a Recent or extinct Indo-Pacific species. This scenario, however, conflicts with the conspecificity of the eastern Pacific populations of *M. platyphylla* and *M. intricata* with the Indo-West and Central Pacific populations of these species. Therefore, the refugia theory seems more plausible, but this would imply widespread disappearance of *M. boschmai* from other localities (perhaps including the Caribbean), now probably followed by final and total extinction of its remnant population in the eastern Pacific, as a result of the severe 1982-83 El Niño warming event. Together with *M. platyphylla* and *M. intricata*, colonies of *M. boschmai* were, as already mentioned in the introduction, among the first that bleached and died in 1983 in the Gulf of Chiriquí (Glynn, 1984), and by December 1990 live colonies of *M. boschmai* and *M. platyphylla* were still not found over their former ranges. Dead colonies of the two species were found in growth position and easily recognizable by their growth form (see figs. 6-7). Colonies of *M. boschmai* were up to 20.2 cm high and 13.3 cm wide; colonies of *M. platyphylla* were found up to 50.8 cm high and 84 cm wide. Also during the December 1990 survey, living colonies of *M. intricata* up to 80 cm in diameter were found off Uva Island, in the Secas Islands and off Coiba Island, indicating that this species has experienced extensive recovery. Although future recovery of *M. boschmai* and *M. platyphylla* may still be possible by recruitment from presently unknown refuge populations, we assume that the two species now no longer exist in the eastern Pacific region.

The single other known recent extinction of a marine invertebrate is a temperate



Figs. 6-7. Coralla of dead specimens of *Millepora boschmai* spec. nov. and *Millepora platyphylla*, collected in December 1990 in the Gulf of Chiriquí, Panamá. 6, *Millepora boschmai* spec. nov., USNM 88344, scale bar: 3 cm; 7, *Millepora platyphylla*, ZMA Coel. 8454, scale bar: 4 cm.

limpet living on the blades of the eelgrass *Zostera marina* Linnaeus, 1753 in the eastern and western North Atlantic Ocean (Carlton et al., 1991). Carlton et al. (l.c.) suggest that a drastic range reduction of *Zostera* in the early 1930's, probably induced by a "wasting disease" caused by the slime mold *Labyrinthula*, has led to the extinction of this stenotopic limpet. Thus, the fate of the new species *M. boschmai* would seem to represent the second known recent extinction of a marine invertebrate, and the first documented case of extinction of a tropical marine organism due to natural causes.

Elements of the eastern Pacific reef coral fauna, consisting of several small, geographically isolated populations in a highly varying environment, would seem to be especially vulnerable to extinction (MacArthur & Wilson, 1967; MacArthur, 1972; Simberloff, 1976; Vermeij, 1978; Leigh, 1981; Diamond, 1984; Morain, 1984; Carlton et al., 1991). ENSO events, which started about 2.8 million years ago after the rise of the Panama Isthmus (Colgan, 1989), and have since then occurred continuously but unpredictably (Colgan, 1990; Glynn, 1990), probably contribute to the poor development of eastern Pacific coral reefs (Glynn, 1990). Range reductions, which affected the hydrocoral *M. platyphylla* and possibly three scleractinian species (Colgan, 1990; Glynn, 1990), may therefore have occurred regularly in the eastern Pacific since the onset of said events. If *M. boschmai* was endemic to the Gulf of Chiriquí prior to its disappearance, recovery of the species seems highly unlikely, but this can only be ascertained in due time.

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