A unique coral reef formation discovered on the Great Astrolabe Reef, Fiji

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Abstract. A spectacular mound-like reef formation (126 m in circumference, 10 m high) dominated by highly arched and record-size colonies of the unattached mushroom coral *Halomitra pileus*, along with 17 other species of the family Fungiidae, occurs in 31 m of water on the sedimentary lagoon floor of the Great Astrolabe Reef, Fiji. Core samples show radiocarbon dates which indicate that the formation hypothetically began building ~4500 y ago, with a calculated mean accretion rate of $2.2 \text{ mm} \cdot \text{y}^{-1}$. The majority of fossil and living material is contributed by *H. pileus* colonies between 40–70 cm mean diameter, with some individuals up to 1.5 m in diameter. The size, fungiid diversity, and geological history of the bioherm is unprecedented and represents the first example of a coral reef constructed almost entirely by Fungiidae.

Introduction

On soft bottoms, mushroom corals (Fungiidae) may play an occasional role in the initiation of patch reef development by providing the solid-substratum nuclei for settlement of other massive and branching coral species (Sheppard 1981). However, fungiid corals traditionally were thought to be ahermatypic (Chadwick 1988; Hoeksema 1989); i.e., not known to produce enduring reef formations by themselves. Free-living members of Fungiidae frequently occur in large aggregations (Pichon 1978), but the size and geological history of the bioherm described here provides an unprecedented record of coral reef formation by this group.

Materials and methods

On 10 March 1995, we discovered a unique mound dominated by highly arched and unusually large colonies of mushroom corals west

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of Vanuacula Island, Great Astrolabe Reef, Fiji (178° 30.23′ E, 18° 44.15′ S). Sixty-four photographic quadrats (1.0 m by 1.0 m) were taken perpendicular to two 1.0 m-wide belt transects, each delimited by two parallel surveyors' tapes, using Kodachrome 64 film and a Nikonos RS underwater camera with electronic strobe. The first transect (40 m in length) ran north to south and extended from the southernmost margin at 26 m deep over the peak (at 21 m), to the northern margin at 25 m deep. The second transect ran east to west beginning at 24 m deep and ending at 31 m deep (40 m in length). In the laboratory, the transparencies were projected and scored for percent cover by digitizing.

The two 1.0 m-wide transects were also examined to assess fungiid size-frequency distributions. Within the transects, all of the mostly arched coral colonies (Fig. 1A, B) were counted and their average diameter on the convex side was recorded along with taxonomic and status (e.g., live, overturned, asexual origin) information. All measurements of diameter were made through the center of the corallum at right angles to the transect tapes to obtain "average" values. Only those corals with > 50% of their colonies within the transect area were counted.

A general size-frequency survey of large fungiid taxa (mostly *Zoopilus echinatus*), not abundant enough to occur in the belt transects, was made for each quarter of the mound. Taxonomic collections of fungiid taxa were cleaned by bleaching in sodium hypochlorite until only carbonate skeletal material remained. Vouchers were returned to the Smithsonian Institution where they were identified to species (taxonomy followed Hoeksema 1989).

Using hand tools, we were able to excavate and directly examine the substratum beneath the living coral colonies to a depth of 1.4 m on the east side of the mound and to 1.7 m on the west side. Geological samples of fossil coral skeletons also were taken by vertically drilling near the center of the formation with a 2.5 cm-diameter galvanized steel pipe. We removed 20-cm core increments from 6 levels (0.7 m, 1.0 m, 3.0 m, 4.5 m, 5.8 m, and 6.0 m) within the mound. These geological samples were returned to the laboratory in sterile plastic bags and air dried for taxonomic purposes and for radiocarbon dating. Radiocarbon dating was performed by Beta Analytic, Inc. The dates are reported as radiocarbon years before present (RCYBP, "present" = 1950 AD) using the US National Bureau of Standards oxalic acid as the standard and the Libby ^{14}C half life (5568 y). Quoted errors represent one standard deviation based on combined measurements of the modern reference standard, background levels, and the sample being analyzed.

Although no other large fungiid accumulations were found during extensive reconnaissance surveys within a 1-km area surrounding the mound, or elsewhere on the Great Astrolabe Reef, we did learn (B. Carlson, M. Pichon, personal communications) of a large aggregation of *Zoopilus echinatus* 70 km away in Suva Bay (on Viti
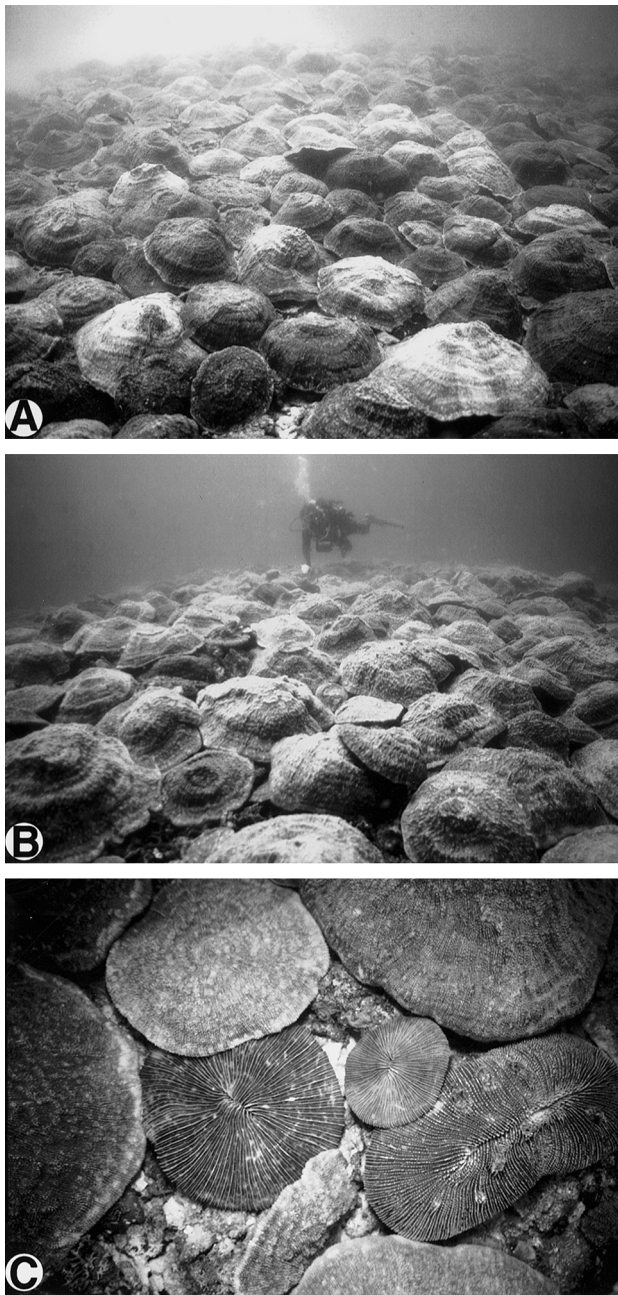
Fig. 1. A Overview perspective of the 10-m high, ∼40-m diameter, mound-like reef (west side). **B** Diver conducting photographic survey 21-m deep near the apex of the Fungiidae bioherm (northward view). **C** Close view showing fungiid diversity in areas between large *Halomitra pileus* colonies

Levu, 178° 23.98′ E, 18° 09.58′ S). For comparative purposes, 48 photographic samples (1.0 m²) were taken on this 15 m-wide by 45 m-long accumulation, again using north to south and east to west transects to quantify fungiid cover.

Results

The bioherm rose 10 m in height from the surrounding soft substratum of the Great Astrolabe Reef lagoon at

a maximum depth of 31 m (Fig. 1A). Nearly half (= 18 out of 40) of the known species of Fungiidae were found on the mound described here (Table 1), which constitutes 70% (= 12 out of 17) of the species previously recorded for Fiji with an additional six species not reported (Hoeksema 1989) for Fiji. Diameters of the coral mound measured from the northernmost to the southernmost perimeters and from the easternmost to the westernmost perimeters were both 40 m in length giving a total surface area for the mound of about 1256 m² and a mean circumference of 126 m.

Colonies (up to 1.0 m in diameter) of *Halomitra pileus* (Linnaeus, 1758) covered 84.6 (±2.6 SE) percent of the quadrats examined ($N = 64$) on the hemispherical bioherm (see Fig. 1A, B). Cover estimates did not include the considerable colony to colony overlap. Sixty-six colonies (11-90 cm diameter) of another dome-shaped fungiid, *Zoopilus echinatus* Dana, 1846, provided 0.6 (±0.2 SE) percent of the projected surface cover (Table 1). Coverages of 17 other species of Fungiidae (Table 1, Fig. 1C) totaled 3.0 (±0.6 SE) percent.

Seventy-six percent of individual *Halomitra pileus* colonies on the hemispherical mound ranged between 1 and 30 cm in diameter, while a further 32% ranged from 31 to 70 cm in diameter (Fig. 2A). The largest colony of *H. pileus* encountered within the transects was 100-cm mean diameter, with some in the 1.2 to 1.5 m range elsewhere on the mound. The majority of the living cover (59%) was contributed by colonies between 41 and 70 cm mean diameter (Fig. 2B), whereas those from 21 to 40 cm covered 20%, and individual colonies greater than 71 cm provided 14% cover.

By calculating the 1256-m² total area of the mound and the numbers of all fungiids sampled in the 80-m² transect area, we arrived at a conservative estimate (the multitude of tiny colonies in crevices or beneath larger colonies were not quantified, see Fig. 1C) of 14 400 separate living *Halomitra pileus* colonies occupying about 85% of the surface of the mound; 66 *Zoopilus echinatus* (0.6% cover), 5400 other fungiid colonies (17 species, 3.0% cover), and dead fungiid rubble (>10%) comprised the rest. Of the *H. pileus*, only 1.2% were of sexual origin and 1.5% were overturned (concave side upward). All 66 *Z. echinatus* colonies had asexual origins and were upright, ranging in size from 11 to 90 cm in diameter.

Conversely, the Suva Bay *Zoopilus echinatus* accumulation represented only a scattered population (asexual in origin) lying atop dead *Acropora* spp. rubble and anthropogenic debris. This surficial population is concentrated in a shallow depression 20 m-deep on the coral reef 75 m southeast of the marker buoy at Fishpatch Reef, where it continues to propagate by frequent fragmentation. The 675-m² isolated aggregation contained only 19.5 (±2.5 SE) percent cover of small *Z. echinatus* (no colonies exceeded 40 cm diameter and thousands occurred that were less than 5 cm diameter); few colonies of other fungiids were present and no *Halomitra pileus* were observed. This system is not comparable to the mound reef (Fig. 2), since no enduring skeletal fungiid deposits were present.

In contrast, the underlying uniform bioherm on the Great Astrolabe Reef consisted of well-preserved, densely

Table 1. Taxa and coverages of 18 Fungiidae recorded in 80-m² belt transects sampled on the hemispherical bioherm.

Taxa	Mean percent cover ($\pm$SE, $N = 64$)
Halomitra pileus (Linnaeus, 1758)	84.6 $\pm$ 2.6
Zoopilus echinatus Dana, 1846	0.6 $\pm$ 0.2
Other Fungiidae	3.0 $\pm$ 0.6
Ctenactis albitentaculata Hoeksema	
Ctenactis crassa Dana, 1846	
Ctenactis echinata Pallis, 1766	
Fungia (*Cycloseris*) *costulata* Ortmann, 1889	
Fungia (*Cycloseris*) *cyclolites* Lamarck, 1816	
Fungia (*Cycloseris*) *distorta* Michelin, 1842	
Fungia (*Danafungia*) *horrida* Dana, 1846	
Fungia (*Danafungia*) *scruposa* Klunzinger, 1879	
Fungia (*Fungia*) *fungites* Linnaeus, 1758	
Fungia (*Lobactis*) *scutaria* Lamarck, 1801	
Fungia (*Pleuractis*) *gravis* Nemenzo, 1955	
Fungia (*Pleuractis*) *paumotensis* Stutchbury, 1833	
Fungia (*Verrillofungia*) *concinna* Verrill, 1864	
Fungia (*Verrillofungia*) *repanda* Dana, 1846	
Fungia (*Wellsofungia*) *granulosa* Klunzinger, 1879	
Herpolitha limax Esper, 1797	
Total cover of Fungiidae	88.2

packed, fragmented skeletons of *Halomitra pileus* completely infilled with white silty clay. Hypothetically, the entire depositional formation is about 4500 y old, based on the depth of our cores and the mean radiocarbon ages of the fossil *H. pileus* at 0.7 m (430 $\pm$ 70 RCYBP), 1.0 m (580 $\pm$ 60), 3.0 m (660 $\pm$ 80), 4.5 m (1460 $\pm$ 80), 5.8 m (2520 $\pm$ 70), and 6.0 m (2800 $\pm$ 90). The calculated mean upward accretion rate was 2.2 mm per year.

Discussion

This study documents an important new discovery of unusual reef formation by mushroom corals. It shows for the first time that free-living mushroom corals by themselves are capable of building a substantial enduring reef structure. Interestingly, this 4500 y-old mound reef was surrounded by sedimentary environs and occurred rather deep (31 m). These conditions suggest that the free-living mushroom corals colonized and built the reef directly on soft substratum. This ability of fungiids to move and survive on soft substrata (Chadwick-Furman and Loya 1992) is unique among corals, most of which require hard surfaces as a reef base.

Little is known about the demography of mushroom corals (e.g., Highsmith 1982; Fadlallah 1983; Harrison 1985; Richmond 1987; Hoeksema 1989). The size-frequency and size-cover patterns of extraordinarily large colonies (14% >71 cm diameter) on the bioherm were unprecedented as was the fungiid diversity. Of the 40 species of Fungiidae, most are unattached (Hoeksema 1989) as were all 18 of the species reported here. Free-living species are able to migrate as much as 10 m in 6 months, some by tissue swelling and pushing along the soft sedimentary bottoms they inhabit (Catala 1964; Goreau and Yonge 1968; Hubbard 1972; Pichon 1974; Fisk 1983; Chadwick-Furman and Loya 1992). In the Fungiidae, asexual reproduction by auto-fragmentation is

particularly important as a dispersal strategy for forms living on sedimentary substrata that are remote from areas suitable for larval settlement (Hoeksema 1989; Nishihira and Poung-In 1989). Therefore, it is enigmatic that all of the fungiid colonies, whether living or dead, occurred on the mound with none dispersed nearby. However, in fungiid corals, locomotion rate decreases exponentially with coral size (Chadwick-Furman and Loya 1992) and the mound is dominated by exceptionally large colonies (Fig. 2B).

Species such as *Halomitra pileus* and *Zoopilus echinatus*, which formed most of the biomass on the mound, are the two largest members of the Fungiidae, with published colony diameters of up to 63 cm and 93 cm, respectively (Hoeksema 1989). We recorded colonies of *H. pileus* of over twice the record diameter, and *Z. echinatus* colonies up to record diameter on the mound. Such colonies may move and disperse at a slower rate than do fungiids with smaller coralla (see also Hoeksema 1988 for comparison of locomotion rates between species). Both of these large species have thin coralla and utilize reproduction by auto-fragmentation more than most other fungiids (Hoeksema 1989). Fragmentation was common on the mound, although the presence of central calices (mouths) on 1.2% of the *H. pileus* colonies (Fig. 1A, B) indicated limited successful sexual reproduction occurs as well.

Fungiidae commonly co-occur in close proximity to one another and some small species that reproduce asexually can exceed densities of 1000 per m² as juveniles (Goreau and Yonge 1968). However, mushroom corals often behave aggressively towards other families of corals when they come into contact (Sheppard 1979; Chadwick 1988; Chadwick-Furman and Loya 1992), but are not known to directly affect other fungiid taxa through aggression (Sheppard 1979; Hoeksema 1989). Interference interactions may explain the co-existence of the remarkably diverse 18 species assemblage and the low abundance of other families of Scleractinia on the mound. Large
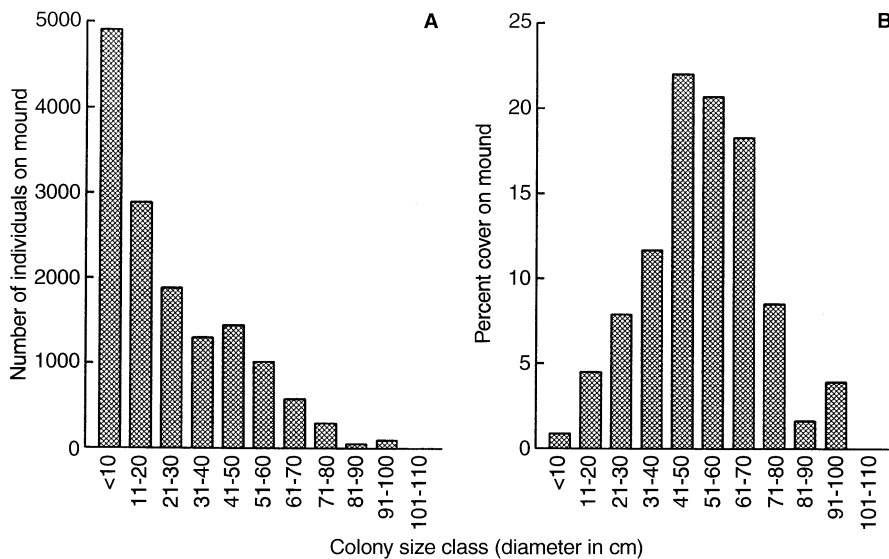
Fig. 2. A Numbers of *Halomitra pileus* colonies by size class on the 1256-m^2 bioherm (based on two belt transects, 80 m^2). **B** Percent cover of *Halomitra pileus* colonies by size class on the bioherm (based on two belt transects, 80 m^2).

Zoopilus echinatus colonies, which covered about 0.6% of the mound and 20% of the Suva Bay aggregation, also showed positive association with six other mushroom corals in the Spermonde Archipelago, Indonesia (Hoeksema 1989). It is also conceivable that chemical attractants may play a role in such diverse multispecies fungiid associations. Different fungiid species often lie on top of one another with no direct harm, except that the lower animals have less access to light and food. Some species are able to free themselves in these situations and form optimal side by side arrays, such as the pattern we observed (Fig. 1A) for the larger colonies of *Halomitra* and *Zoopilus*.

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