

Reef-building properties of *Tubastraea micranthus* (Scleractinia, Dendrophylliidae), a coral without zooxanthellae

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ABSTRACT: One characteristic of reef-building corals is a skeletal strength sufficient to endure hydrodynamic stress. Porosity, compressive and bending strength, elastic modulus and resistance to abrasion were measured in the reef-inhabiting colonial dendrophylliids *Tubastraea micranthus* and *T. aurea* and in the acroporids *Acropora palmata* and *A. cervicornis*. Dendrophylliids are devoid of zooxanthellae, acroporids possess zooxanthellae and are well recognized reef-builders. The mechanical properties of *T. micranthus* colonies, collected in Philippine reefs, equal or even surpass those of the acroporids, which rank at the high-strength end of the porosity / strength continuum. Skeletal strength and colony form set out *T. micranthus* as a primary framework-builder (*sensu* Goreau, 1963), corroborating field observations on Philippine reefs. Therefore the conventional affiliation of *T. micranthus* to the 'ahermatypic' category (*sensu* Wells, 1933) is not functionally correct. The respective data of *T. aurea*, however, show that this species has little significance as a reef-builder.

INTRODUCTION

Reef-building capacity depends on the ability to endure hydrodynamic stress. From this point of view Chamberlain (1978) and Schuhmacher (1981) discussed the ecological role of mechanical properties of a variety of coral skeletons; their adaptive significance *versus* morphological design was examined by Graus et al. (1977) and Schuhmacher and Plewka (1981a); the relative importance of skeletal strength through geological time was discussed by Schuhmacher and Plewka (1981b) and the obvious change in colony strength through boring sponges was the matter of a paper by Tunnicliffe (1979). The scleractinians studied by these authors are all reef-building and possess zooxanthellae.

A current distinction separates 'hermatypic' corals as reef-building, shallow water forms from 'ahermatypic' corals which are not reef-building and not restricted to shallow depths. This classification goes back to Wells (1933) who not only coined the terms but also equated 'hermatypic' with possessing zooxanthellae and 'ahermatypic' with being devoid of these symbiotic algae.

The present study compares the reef-building capacity of the colonial dendrophylliids *Tubastraea micranthus* (Ehrenberg) and *T. aurea* (Quoy and Gaimard)

with that of the acroporids *Acropora palmata* (Lamarck) and *A. cervicornis* (Lamarck). According to Wells' definition, which emphasizes the importance of zooxanthellae, these dendrophylliids would conventionally be grouped with the ahermatypic corals, since they lack zooxanthellae. The acroporids (with zooxanthellae), on the other hand are affiliated with the hermatypic category. They are major reef-building corals and rank at the high-strength end of the porosity/strength continuum. This study contributes to the bionomy of *T. micranthus* and, by a detailed evaluation of the relevant mechanical properties, intends to throw new light on the conventional separation of 'hermatypes' and 'ahermatypes' as practised in extant literature.

MATERIAL

The systematic position of what is called in this paper *Tubastraea micranthus* (Ehrenberg) and *T. aurea* (Quoy and Gaimard) has long been uncertain (see below) and still requires thorough revision. At least in the case of *T. micranthus* the occasional affiliation with the genus *Dendrophyllia* may have been suggested by the arborescent growth form. The septal arrangement, however, which was used by Vaughan and Wells

(1943) to discern the 2 genera, obviously classifies our material into the genus *Tubastraea* (no Pourtalès plan).

A selected list of synonyms of *Tubastraea micranthus* comprises:

<i>Oculina micranthus</i> :	Ehrenberg, 1834: 304
<i>Dendrophyllia nigrescens</i> :	Dana, 1846: 387
<i>Cönopsammia micranthus</i> :	Klunzinger, 1879: 2; 58
<i>Dendrophyllia micranthus</i> :	van der Horst, 1922: 101 (with synonymy)
<i>Dendrophyllia micranthus</i> :	van der Horst, 1926: 1
<i>Dendrophyllia micranthus</i> :	Faustino, 1927: 218
<i>Dendrophyllia micranthus</i> var. <i>grandis</i> :	Crossland, 1952: 173
<i>Dendrophyllia micranthus</i> :	Nemenzo, 1960: 16
<i>Tubastraea micranthus</i> :	Pichon, 1978: 422, 441
<i>Tubastraea micrantha</i> :	Rosen, 1979: 20
<i>Tubastraea micranthus</i> :	Scheer & Pillai, 1983: 175

Tubastraea micranthus occurs from the Red Sea through the Indian Ocean to the Comores and Madagascar, and to the Fiji Islands in the Pacific Ocean; *T. nigrescens* Dana is considered here as the main synonym. The species is conspicuous in the reef by its dark-green to brownish-black soft tissue. Unlike most other members of the family which grow under overhangs and in caves on the reef, specimens of *T. micranthus* in the Philippines were also found from 4 to 50 m depth growing fully light-exposed as other reef corals. Here the colonies grow up to 1 m high and to 15 cm diameter at the stem base. Usually colonies are fan-shaped with 1 to 3 cm thick branches perpendicular to the prevalent current (Fig. 1).

In the Red Sea, however, colonies observed by the author are much smaller. They were found only in the

dim light under ledges of the reef slope down to 12 m. Surveys by a submersible of the deep foreereef in the Gulf of Aqaba between 50 and 200 m depth (Fricke and Schuhmacher, 1983) never encountered *Tubastraea micranthus* colonies. Whereas specimens from shallow depths of the central Red Sea (Port Sudan area) still reached 25 cm length, the many colonies found at similar places in the northern and southern Gulf of Aqaba did not exceed 12 cm. However, one single colony of 42 cm height and 33 cm width was found in 30 m depth near Aqaba during the cooperative French-Jordanian coral reef research program (Dr. Zibrowius, pers. comm.).

In general, a decrease in size can be stated from Philippine to Red Sea forms, when colonies from shallow depths are compared. Correspondingly there is also a decrease in calcification and skeleton-strength. Heavily calcified, low-porous skeletons, common on Philippine reefs, were never recorded by the author in the Red Sea. The Gulf of Aqaba specimens are especially weak. This is also true if equally sized branch tips from both localities are compared. Hence *Tubastraea micranthus* must be regarded as a very variable species. Crossland (1952) who was familiar with Red Sea as well as with West Pacific forms, even hesitated to unify both in one species. The following experimental study and discussion focus on Philippine material only. A systematic revision is also needed for what should be comprised by *T. aurea*. The selection of synonyms hereinafter does not pretend to be such an attempt, it mainly follows Scheer and Pillai (1983):

<i>Lobophyllia aurea</i> :	Quoy & Gaimard, 1833: 195
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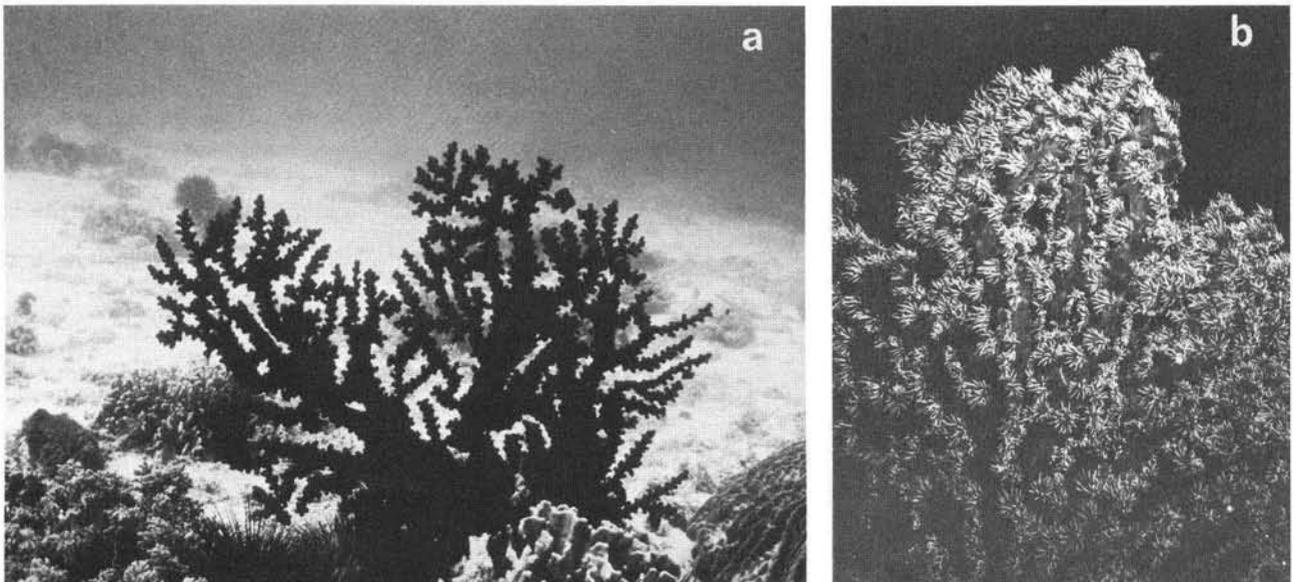


Fig. 1. *Tubastraea micranthus*. Colony at Sumilon Island (Negros, Philippines), 8 m water depth; (a) during day; (b) polyps expanded at night

<i>Tubastraea coccinea</i> :	Lesson, 1834: 515
<i>Coenopsammia ehrenbergiana</i> :	Milne Edwards (& Haime) 1860: 127
<i>Cönopsammia ehrenbergiana</i> :	Klunzinger, 1879: 2; 56
<i>Dendrophyllia aurea</i> :	van der Horst, 1926: 46
<i>Tubastraea aurea</i> :	Boschma, 1953: 112–117
<i>Tubastraea coccinea</i> :	Maragos, 1977: 197
<i>Tubastraea aurea</i> :	Scheer & Pillai, 1983: 173

Tubastraea aurea is a yellow-orange soft tissue coral. In the Red Sea, the species is not as common as in the Indian Ocean and Western Pacific including Hawaii. The plocoid colonies rarely exceed fist-size and usually occur clustered below overhangs and in other shaded parts of the reef. Occasionally they are found fully exposed in the Philippines.

METHODS

Tubastraea micranthus was collected at various sites off Cebu, Philippines; field studies were also undertaken at Sumilon Island (between southern Cebu and Negros) and near Puerto Galera Bay and Verde Island (between Luzon and Mindoro). *T. aurea* material was collected near Puerto Galera Bay. Additional material had kindly been collected by M. Plewka at Hawaii. *Acropora* species which served for comparison were collected at Discovery Bay, Jamaica (see Schuhmacher and Plewka, 1981a).

In order to assess the mechanical resistance of the skeleton, the following parameters were measured: porosity, compressive strength, bending strength, elastic modulus and resistance against abrasion. Since these properties strongly depend on the porosity, this feature was examined in each probe before other measurements were undertaken.

Tests were performed following standards of the German Governmental Material Testing Bureau and using the respective devices. Total porosity, i.e. the share of all voids in the total volume of a probe, was

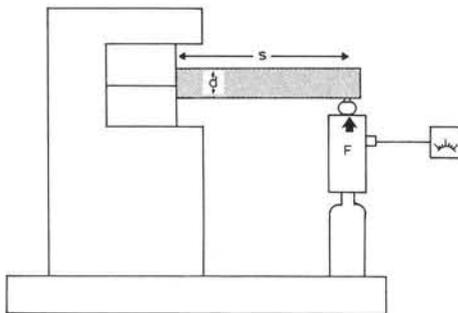


Fig. 2. Device for measuring bending strength. Stippled: coral beam fixed at left end; F = bending force generated by hydraulic press; s = distance between point of exertion of F and point of breakage; d = diameter of coral branch

found by using buoyancy techniques and calculations based on the specific gravity of aragonite. In order to evaluate the compressive strength of the skeleton, cubic prisms (12 × 12 × 24 mm) were exposed to increasing hydraulic compression until collapse in the testing machine, Zwick 1387. The elastic modulus was measured with the E-G-Meter after Kottas, 9,000. These methods are described in Schuhmacher and Plewka (1981a). The bending strength was evaluated by measuring the force acting upon a cantilevered cylindrical branch of 10–12 cm length at rupture (Fig. 2).

The bending force (σ) was calculated from

$$\sigma = \frac{M}{W}$$

with $M = F \cdot s$ and $W = \frac{I}{d}$

For F, s and d see Fig. 2. I, the momentum of inertia, depends on the geometry of the probe, in case of a cylinder

$$I_{\text{geom}} = \frac{\pi \cdot d^4}{64}$$

Since the porosity of the material reduces the real sectional area, the real momentum of inertia is approximated by

$$I_{\text{real}} = I_{\text{geom}} \cdot \frac{(100 - P)}{100}$$

with P = porosity in percent.

Small-scale differences of porosity between central and peripheral parts of the branch cross section were neglected. They are not as pronounced as in the basal parts of a colony.

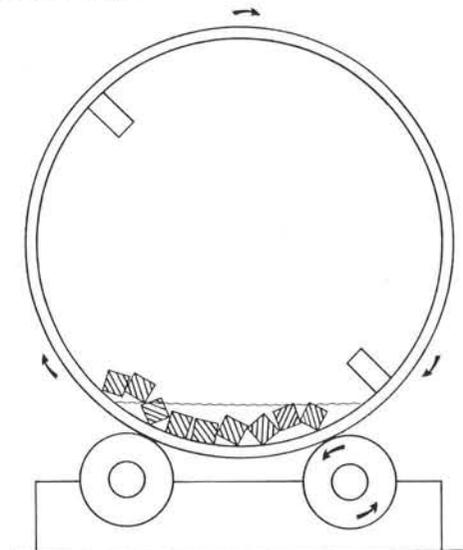


Fig. 3. Rotating cylinder; driving gear is at right (arrows). Hatched: coral cubes in water

Resistance to abrasion was measured in a rotating container (Fig. 3). This device simulates the fate of broken pieces when rolled by currents over the reef. Relative loss by abrasion is another measure of skeleton durability. It depends directly on the porosity of the material. Cubic prisms of 2 cm edge length were cut in *Tubastraea micranthus* and *T. aurea* from basal portions of a colony, in *Acropora palmata* from thick branches. Cylindrical prisms of 2 cm length and diameter were obtained by cutting up appropriate branches of *T. micranthus* and *A. cervicornis*. Fragile prominences of the surface (e.g. side buds and coralites) had been removed before in order not to bias the results. The probes, 10 to 12 specimens per run, were rolled over distances of 5,000 and 10,000 m.

RESULTS

Porosity of *Tubastraea micranthus* skeletons increases considerably from colony base to branch tips. This is due to: (a) greater ratio of corallite-volume/coenosteum at the colony's distal ends, where the coenosteum is not yet thickly developed; (b) subsequent filling of pores due to carbonate deposition by the deeply 'rooted' calicoblastic layer. This solidification becomes particularly evident at the colony base. Here the porosity of the coenosteum decreases from 25 to 35 % at the periphery to no more than 16 % in the core (Fig. 4).

The *Tubastraea aurea* skeleton lacks a coherent coenosteum. Consequently, its porosity was determined by the void of the corallites. Values of porosity range from 60 to 73 %.

Resistance to abrasion and compressive strength were measured in all 4 species. Bending strength and elastic modulus are ecologically irrelevant for the plocoid *Tubastraea aurea*. Beyond that it would have been impossible to prepare equal-sized probe-speci-

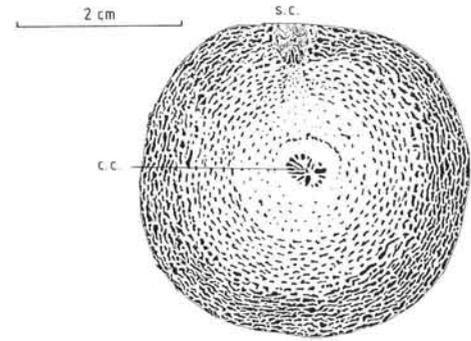


Fig. 4. *Tubastraea micranthus*. Cross section of stem semi-diagrammatic; note the difference in porosity between peripheral and central parts due to secondary calcification. s.c.: side corallite; c.c.: central (primary) corallite

mens as used for the other species. Therefore, *T. aurea* was not considered with regard to bending forces. Resistance to abrasion of the 4 species is shown in Table 1. The material loss by rolling over 5,000 and 10,000 m was comparably low in *T. micranthus* and *Acropora cervicornis*, when cylindrical prisms were tested. Comparison of *T. micranthus* with *T. aurea* and *A. palmata*, based on cubic prisms, showed that *T. micranthus* is most resistant to abrasion, followed by *A. palmata* and – by a wide margin – by *T. aurea*.

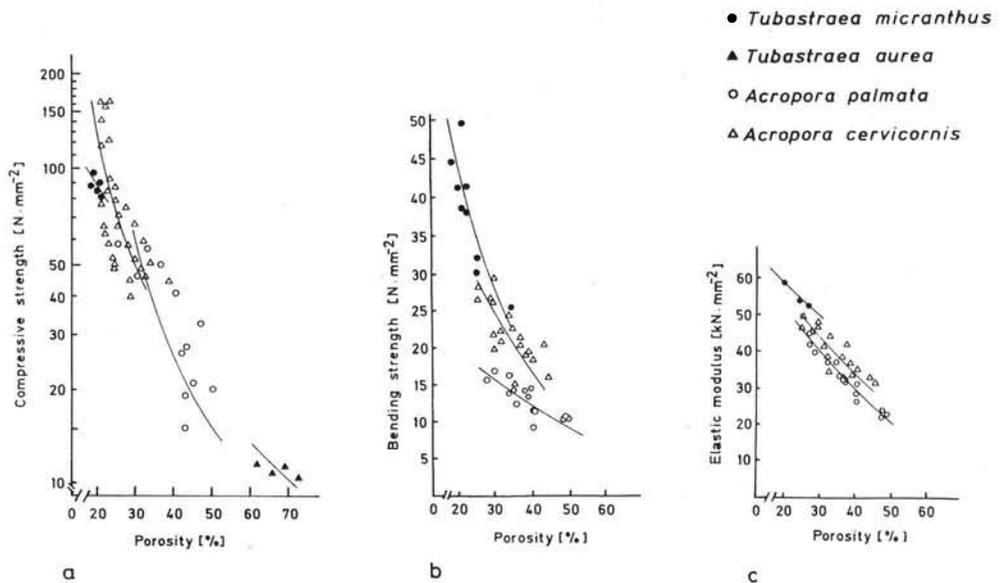
Differences in porosity and abrasive resistance between cubic and cylindrical prisms of *Tubastraea micranthus* exist, because cubic probes were cut from the solidified base, whereas cylindrical probes were cut from middle portions of branches where the coenosteum is still relatively porous. The compressive strength of the 4 species is shown in Fig. 5a. *T. micranthus* turned out to be significantly stronger than *A. cervicornis*; both were stronger than *A. palmata* (*Acropora* data are from Schuhmacher and Plewka, 1981a). Compared to these species, *T. aurea* is very weak. Porosity and compressive strength are inversely correlated.

Bending strength is the mechanical property which

Table 1. Mean material loss due to abrasion

Species	Number of test pieces	Probe geometry	Porosity %	Abrasion after 5,000 m %	Total abrasion after 10,000 m %
<i>Tubastraea micranthus</i>	12	Cylindrical prisms, 2 cm \emptyset	28.9	4.5	7.2
<i>Acropora cervicornis</i>	20	Cylindrical prisms, 2 cm \emptyset	24.4	4.5	7.0
<i>Acropora palmata</i>	100	Cubic prisms 2 cm edge length	35.5	4.6	7.6
<i>Tubastraea micranthus</i>	12	Cubic prisms 2 cm edge length	16.5	3.2	5.4
<i>Tubastraea aurea</i>	12	Cubic prisms 2 cm edge length	63.5	35.0	45.5

Fig. 5. Mechanical properties of *Tubastraea* and *Acropora* test specimens. (a) Compressive strength; (b) bending strength; (c) elastic modulus. *Acropora*-data are from Schuhmacher and Plewka (1981a)



is most important in branching colonies. Unlike bushy corals of the *Stylophora*- or *Pocillopora*-type, *Tubastraea micranthus*, *Acropora cervicornis* and *A. palmata* colonies extend far into the water current. As shown in Fig. 5b, the bending strength of *T. micranthus* is significantly higher than that of the *Acropora* species examined. This is especially noteworthy, because the relatively large and irregularly dispersed corallites may be thought to favour premature fractures. Measurements of elastic modulus underline the relative strength of *T. micranthus* (Fig. 5c): its skeleton can absorb more strain energy per unit volume than that of *A. cervicornis* and *A. palmata*.

Porosity-dependent differences in mechanical properties of *Tubastraea micranthus*, *Acropora cervicornis* and *A. palmata* are accounted for when pieces of identical porosity are compared (Table 2). In spite of the small number of replicates, the data suggest that the specific microarchitecture of *T. micranthus* results in a better skeletal bond than that of the *Acropora* specimens.

DISCUSSION

Comparative studies of reef-building corals possessing zooxanthellae (hermatypic *sensu* Wells) (Schuhmacher, in prep.) show that *Acropora* species

rank at the high-strength end of the porosity/strength continuum. Therefore, in the present comparison of 'ahermatypic' and 'hermatypic' corals the 2 *Acropora* species can be regarded as having high mechanical properties, necessary to erect a durable framework. *Tubastraea micranthus* equals or even surpasses the skeletal strength of *A. cervicornis*. In contrast, *T. aurea* is characterized by much lower strength values than the *Acropora* species.

The skeletal weakness of *Tubastraea aurea* is generally expected from an 'ahermatypic' coral. It should be mentioned here that some 'hermatypic' species, such as *Colpophyllia natans* (Müller), *Pectinia lactuca* (Pallas) and *Euphyllia glabrescens* (Chamisso and Eysenhardt), rank similar or even lower than *T. aurea* (Schuhmacher, in prep.). A detailed discussion of this phenomenon is beyond the scope of this paper. On the other hand, the superior material properties of *T. micranthus* are noteworthy. They are due to low porosity and, most likely, to a specific microarchitecture, not yet analysed.

The colony's mechanical strength is supplemented by a shape advantageous to counter high bending forces: the stem is broadened at its base, where the bending momentum is highest. Schuhmacher and Plewka (1981a) documented the significance of this morphological adaptation. Infestation by boring

Table 2. Comparison of skeletal strength at the same porosity (25%)

Species	Compressive strength [N mm ⁻²]	Bending strength [N mm ⁻²]	E - modul [kN mm ⁻²]
<i>Tubastraea micranthus</i>	80	32	55
<i>Acropora cervicornis</i>	80	32	52
<i>Acropora palmata</i>	55	18	48

sponges, which often weaken the colony base, is extremely low in *Tubastraea micranthus*. Hence this species is designed well to withstand hydrodynamic attacks and to colonize a current-exposed habitat. In fact, only *T. micranthus* colonies, 60 to 90 cm high, remained erect in dynamite-blasted reef parts at Sumilon Island. Near Verde Island (Puerta Galera Bay), *T. micranthus* colonies were found in 5 to 8 m water depth on the tops of uprising rocks, where currents of 1 m s^{-1} were recorded. In this position, a solid foothold as well as a durable stand in the current are necessary. *T. micranthus* is completely dependent on food carried by the water.

The polyps expand at night, spanning up to 3 cm. They were observed to catch large planktonic organisms such as salps and polychaetes (up to several cm long). *Tubastraea micranthus* grows longitudinally at a rate of 4 cm yr^{-1} (Drs Wellington and Trench, pers. comm.); this is remarkable for a coral without symbiotic algae, but nevertheless relatively slow compared to the rate of up to 12 cm yr^{-1} in branching acroporids (Gladfelter et al., 1978).

Tubastraea micranthus does not conform with the conventional conception of an 'ahermatypic' coral except for being devoid of zooxanthellae. The large and robust colonies rather represent what Goreau (1963) and Goreau and Goreau (1973) distinguished as primary framework-builders. These authors described another category of corals as secondary hermatypes, which are more fragile and tend to fill the interstices between the present frame. Hence *T. micranthus*, a morphological frame-builder, should be affiliated with the 'hermatypic' rather than the 'ahermatypic' corals, in the literal sense (presence or absence of zooxanthellae not taken into account).

Wells (1933) also used the bathymetric range as another criterium to distinguish 'hermatypic' and 'ahermatypic' corals. Again, *Tubastraea micranthus* fits into the 'hermatypic' type. It was never observed or dredged from really deep water – the 'classic' realm of the 'ahermatypic'. For example, an extensive survey of the upper 200 m of the coastal slope by a submersible in the Gulf of Aqaba showed that *T. micranthus* and *T. aurea* occurred closer to the surface than *Leptoseris* spp. and ecologically similar coral species possessing zooxanthellae (Fricke and Schuhmacher, 1983). In addition, SCUBA investigations down to 70 m off Port Sudan did not record the 2 *Tubastraea* species between 20 and 70 m (Kühlmann, 1983).

Tubastraea micranthus, as well as *T. aurea*, lack zooxanthellae which are considered a prerequisite of a reef-builder: 'Reef-building (hermatypic) corals are inevitably associated with the endosymbiotic dinoflagellate *Gymnodinium microadriaticum*' (Chalker, 1976). Acquisition of zooxanthellae, with the side

effect of enhanced calcification, was most probably the major factor for the evolutionary success and geomorphological importance of scleractinians (e.g. Goreau, 1959; Schuhmacher, 1976; Muscatine and Porter, 1977; Stanley, 1981). In fact, zooxanthellae-driven calcification enables rapid compensation of losses caused by hydrodynamic destruction. But the integration of a symbiotic pacemaker for enhanced calcification is not the only strategy for attaining reef-building capacities. The present study shows that there is still the option of uncompromised augmentation of skeletal strength. Long-lasting, high resistance to hydrodynamic stress is derived from a maximal solidified skeleton – most likely at the expense of growth. Presumably, this strategy was common among ancient reef-builders (Schuhmacher and Plewka, 1981b).

Tubastraea micranthus can be regarded as one of the few recent pursuers of this evolutionary route. Its constructional role on the reefs of the Philippines and adjacent waters qualifies this species as reef-building. Therefore, *T. micranthus* is 'hermatypic' in the strict sense of the word without requiring the support of zooxanthellae. There is growing disagreement with the conventional definition of 'hermatypic' and 'ahermatypic' (Rosen, 1981; Fricke and Schuhmacher, 1983). This paper emphasizes the necessity to reconceptualize this problem.

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