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NEW OBSERVATIONS ON SCLERACTINIAN CORALS FROM INDONESIA: 1. FREE-LIVING SPECIES BELONGING TO THE FAVIINA

by

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Key words: free-living corals; Faviina; soft substrata; Indonesia; Buginesia Project; Snellius-II Expedition.

Five free-living coral species (one new) belonging to four genera (one thus far only known fossil), and their adaptation to soft substrata are discussed.

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INTRODUCTION

Field work on coral reefs in the eastern part of the Indonesian Archipelago in the course of the Buginesia Project (see Wijsman-Best, Moll & De Klerk, 1981) and during the Snellius-II Expedition (Best, Moll & Boekschoten, 1985) revealed a wealth of new observations and material. Now some of the reef coral communities have been analyzed (Moll, 1983; 1986), a start is made to tackle systematical and ecological problems on coral species that came forward while working out the data of both projects. As a result of the Buginesia Project some new coral species have already been described (Moll & Best, 1984).

Both projects yield new information on the coral fauna of Indonesia and offer implications for the development of new ideas in coral systematics and

ecology. Indonesian coral reefs are constructed by approximately 400 coral species (Best e.a., in prep.). They are part of the richest coral reef area on earth, the Central Indo-Pacific. Studies on species diversity and on adaptation in the high variety of habitats can therefore optimally be carried out in this geographic area.

This first paper of a series mainly deals with some free-living species of zooxanthellate shallow-water corals. Only one species treated here belongs to a genus of unattached, deep living non-zooxanthellate corals in the Faviina, *Anthemiphyllia* Pourtalès, 1878. (For the meaning of zooxanthellate and non-zooxanthellate see Schuhmacher & Zibrowius (1985)). The representatives of the other species discussed here usually can be found accumulated at the reef base. At this deepest part of the reef the slope of the bottom gradually becomes less steep, the substratum becomes sandy and coral coverage is low. The coral communities found here are restricted to this zone, as the greater part of the species cannot be found elsewhere on the reef. The corals have to cope with the high mobility of the sediment, which may cause temporary burial. Some free-living corals are able to survive burial by extending their large, fleshy polyps in order to remove sediment that otherwise would cause suffocation. Many scientists studying reef coral communities do not include the reef base in their studies because it is the deepest part of the reef that is least accessible. This part of the reef seems poor in corals, due to the fact that the species living here do not grow as large as many species inhabiting the shallower reef zones. The corals usually remain small; when reaching an optimal coverage, however, their density on the bottom may compensate this. Because of their inconspicuous appearance only little literature deals with such so-called soft-bottom coral communities (e.g. Goreau & Yonge, 1968; Pichon, 1974; Fisk, 1983). Not all species constituting these communities have been discovered and the knowledge about the species already described can still be extended. A family of corals, specialized in having a free-living mature phase is that of the Fungiidae. Studies on the systematics and ecology of these so-called mushroom corals will be published in the near future (Hoeksema, in prep.).

When observing free-living Faviina (Faviidae and Mussidae) we were confronted by the problem how to discern solitary from colonial forms in case intermediate developmental stages are encountered. Some free-living corals are able to divide in a certain stage of their life-history and in doing so become colonial. This has produced much confusion in literature. *Trachyphyllia* Milne Edwards & Haime, 1848, was considered a solitary genus, but its colonial form was described as a separate genus, *Callogyra* Verrill, 1902. *Homophyllia australis* (Milne Edwards & Haime, 1849) was described as solitary, but is regarded to belong to the colonial genus *Scolymia* by Veron & Pichon (1979).

In the Fungiidae the difference between solitary and colonial forms, is usually easy to see. In juvenile stage the colonial species have only one mouth, but later they start to develop other stomata next to or around the first one.

Most recent, free-living corals in the shallow reef habitats belong to the suborder Fungiina. In the suborder Faviina there are only a few recent representatives having an unattached mature stage. The extinct coral group from which the mussids are derived, the montlivaltiids from the Middle Triassic-Eocene have many solitary representatives. Also some fossil genera belonging to the Faviina from the Oligocene and Miocene of Europe and the East Indies had a free-living stage, like *Indosmilia* Gerth, 1933, and *Indophyllia* Gerth, 1921. Well-known recent genera of such corals in the Indo-Pacific are *Trachyphyllia* and *Cynarina* Brüggemann, 1877. A recent representative of *Indophyllia* is reported here for the first time. In the West Indies the fossil genera *Antillia* Duncan, 1863 (= *Antilophyllia* Vaughan, 1932), *Thysanus* Duncan, 1863, and *Teleiphyllia* Duncan, 1864, from the Miocene were free-living. In the Miocene of Europe there existed *Syzygophyllia* Reuss, 1860. Well known recent genera of corals forming part of soft-bottom communities in the Caribbean region are *Scolymia* Haime, 1852, and *Manicina* Ehrenberg, 1834.

Another problem arises in the classification above species level. By comparing free-living coral species in the Atlantic and Indo-Pacific we propose several changes in the classification in these taxa.

The coral species treated here belong to four genera of the Faviina. All material of the species here described is present in the RMNH. Other material mentioned is in the collections of the Rijksmuseum van Geologie en Mineralogie in Leiden (RGM), in the Zoölogisch Museum Amsterdam (ZMA) and in the Muséum national d'Histoire Naturelle in Paris (MNHN).

Trachyphyllia – *T. geoffroyi* (Audouin, 1826)
– *T. radiata* (Pichon, 1980)
Indophyllia – *I. macassarensis* spec. nov.
Cynarina – *C. lacrymalis* (Milne Edwards & Haime, 1848)
Anthemiphyllia – *A. dentata* (Alcock, 1902)

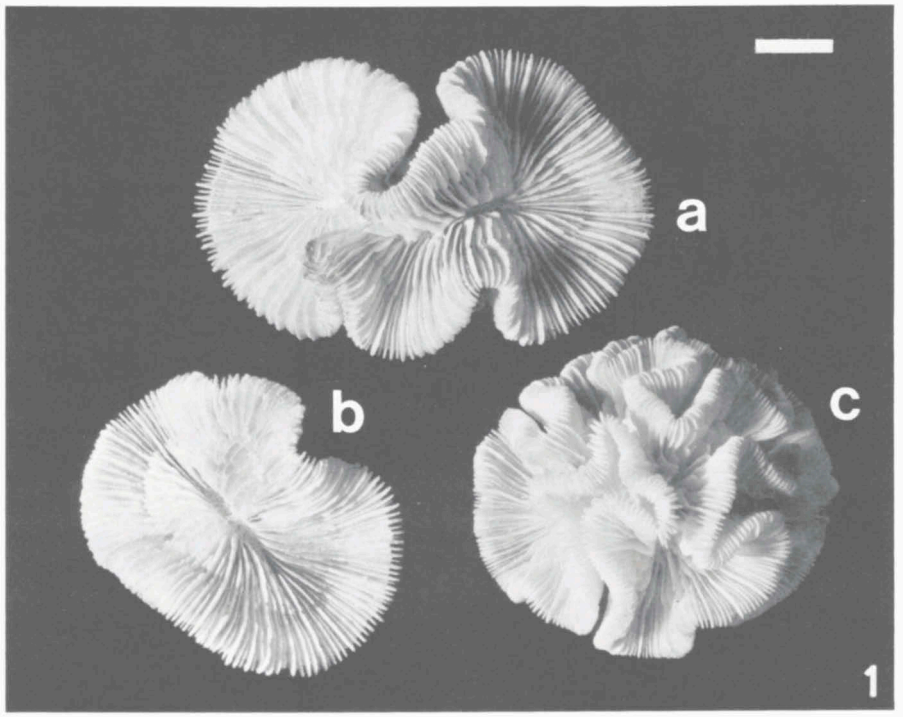


Fig. 1a-c. Variation in growth-form in *Trachyphyllia geoffroyi* (Audouin) from Komodo (RMNH 21396). Scale bar: 2 cm.

DISCUSSION OF THE SPECIES

Trachyphyllia geoffroyi (Audouin, 1826)
(figs. 1-2)

Synonymy according to Veron et al. (1977: 208); in addition new synonyms:
Antillia infundibuliformis Gerth, 1921: 408.
Antillia orientalis Gerth, 1921: 408.
Antillia flabelliformis Yabe & Sugiyama, 1931: 127.
Antillia duncani Yabe & Sugiyama, 1931: 129.

Material. — Ambon: RMNH 22180, 22188. Kei Islands: RMNH 22183, 22184, 22187. Banda: RMNH 22177. Java Sea: RMNH 22186. Sumbawa: RMNH 21344. Komodo: RMNH 21396 (16 ex.). Halmahera: RMNH 22176.

Historical comments. — The species formerly belonging to the genus *Antillia* were incorporated in other coral genera by Vaughan (1932). The fossil mussid European representatives were put in *Syzygophyllia* and the American

Miocene species were placed in the genus *Antillophyllia*. There are several fossil coral species from the Caribbean belonging to the extinct genus *Antillophyllia*. Whether Vaughan's (1932) decision to declare the western Atlantic genus *Antillia* invalid and to establish the genus *Antillophyllia* instead was correct or not, has to be reconsidered in studies concerning Atlantic corals.

All later mentioned fossil or recent species described as *Antillia* from the Indo-Pacific are synonymous with already described species from the area. They appear to fit into the large ranges of varieties which are available for study now. Apart from the species mentioned above in the synonymy list of *Trachyphyllia geoffroyi* also: *Antillia grandiflora* Gerth, 1921, and *A. japonica* Yabe & Sugiyama, 1931, are synonyms of *Cynarina lacrymalis; A. indica* Duncan, 1880, is synonymous with *Scolymia vitiensis,* Brüggemann, 1877.

Characters and variability. — The species is well described in the literature cited above. The figures given in the present study illustrate the extreme variability in our specimens, from pure solitary to meandroid colonies in various sizes (see also Veron et al., 1977). The observed variability in Indonesian waters is even greater than known from other areas. This may be due to

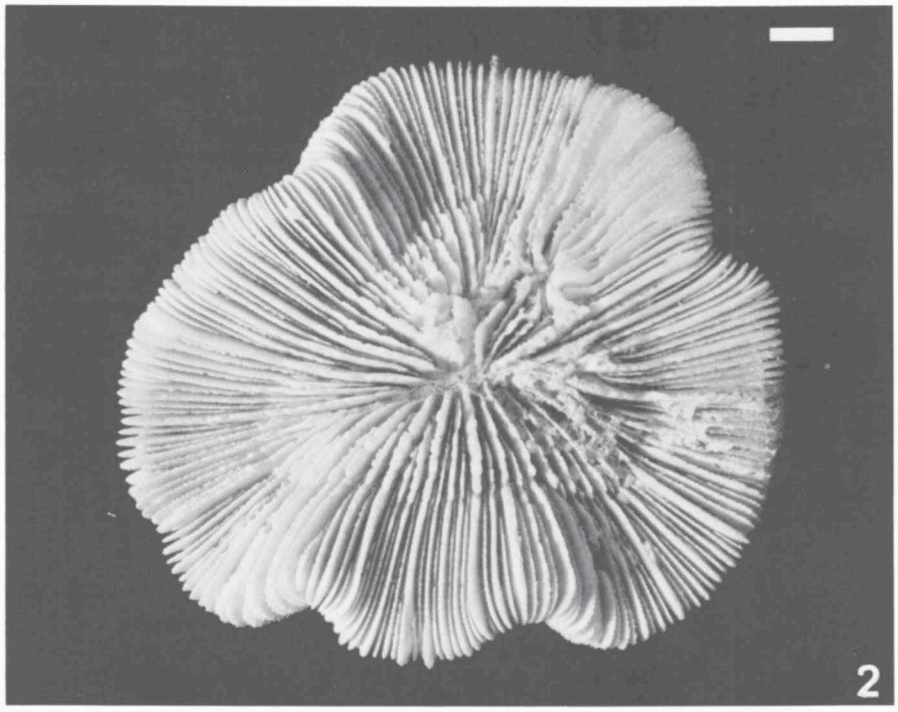


Fig. 2. Extreme growth-form of *Trachyphyllia geoffroyi* (Audouin) from Halmahera (RMNH 22176). Scale bar: 1 cm.

the fact that Indonesian coastal waters have a tremendous variety of habitats.

The animal, solitary or colonial, becomes free-living and is usually found on the sandy bottom at the reef base. The confusion in literature and the many names for this species are a result of the extreme variability in the adaptation to different environmental conditions.

A detailed ecological study may give more insight in the function of the various growth forms. It may indicate for example that extra protecting skeleton material is secreted in the form of an epitheca when the animal is attacked by encrusting and boring organisms. The presence or absence of this epitheca is one of the criteria often used to separate species. The series on which the present study is based seems to illustrate this phenomenon.

Geographical distribution. — The species is widespread in the Indo-Pacific from the Red Sea to New Caledonia.

Trachyphyllia radiata (Pichon, 1980)
(figs. 3-4)

Callogyra formosa sensu Bedot, 1907: 176 (not *C. formosa* Verrill, 1902).
Wellsophyllia radiata Pichon, 1980: 257 (new synonymy).

Material. — Ambon: RMNH 9161. Neira, Kei Islands: RMNH 15219. SW. Sulawesi: RMNH 15672.

Characters and variability. — The species has many characters in common with *T. geoffroyi*. It is only separated from that species because it has the opposite sides in the folds of the corallum wall fused up to the summit (compare figs. 1 and 3). This character separates in most cases the meandroid specimens in the collection on which this paper is based. There are corals in intermediate stages, however, in which we find the opposite sides united laterally and specimens in which this is not so (fig. 4). Therefore we consider it well possible, as suggested by Bedot (1907), that his *Callogyra formosa* specimens (= *Trachyphyllia radiata*) are growth forms of his *Trachyphyllia amarantus* (= *T. geoffroyi*).

Anyway we do not think that the difference is strong enough to keep them separate in two genera. They are best regarded, till more ecological field work is carried out, as two closely allied species of one genus. The size of the corallum and the onset of a meandroid structure are not directly related with age.

Geographical distribution. — The species has only been found in Indonesia, Singapore and NW Australia.

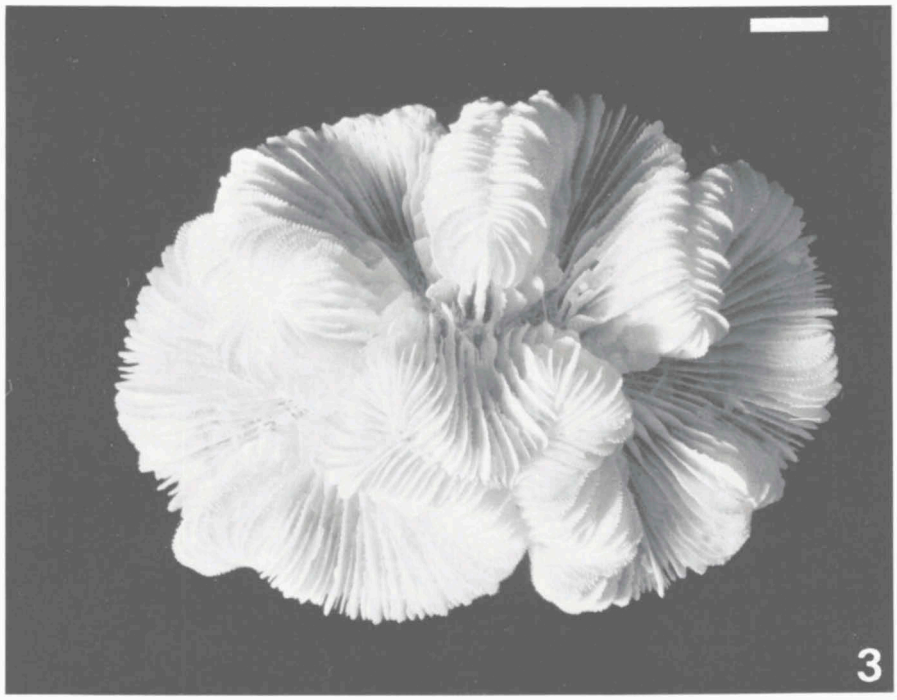


Fig. 3. *Trachyphyllia radiata* (Pichon) from Neira, Kei Islands (RMNH 15219). Scale bar: 1 cm.

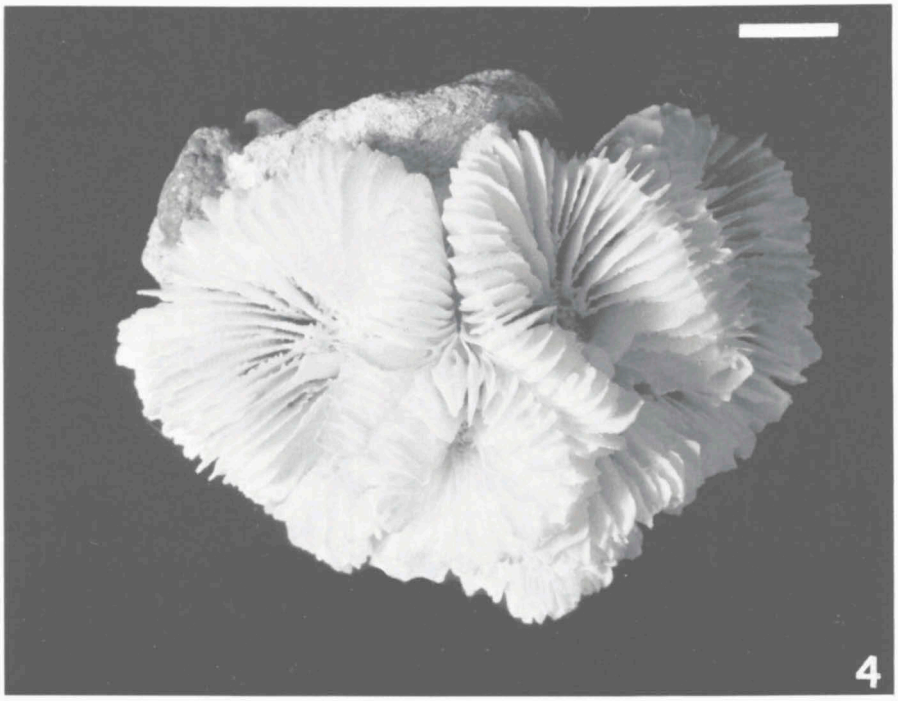


Fig. 4. *Trachyphyllia radiata* (Pichon) from S.W. Sulawesi (RMNH 15672). Scale bar: 1 cm.

Indophyllia macassarensis spec. nov.
(figs. 5-7)

Material. — Spermonde Archipelago, SW Sulawesi: RMNH 22189 (holotype from Samalona), 22190 (5 ex., paratypes from Samalona), 22191 (paratype from Barang Caddi), 22192 (paratype from Bone Tambung).

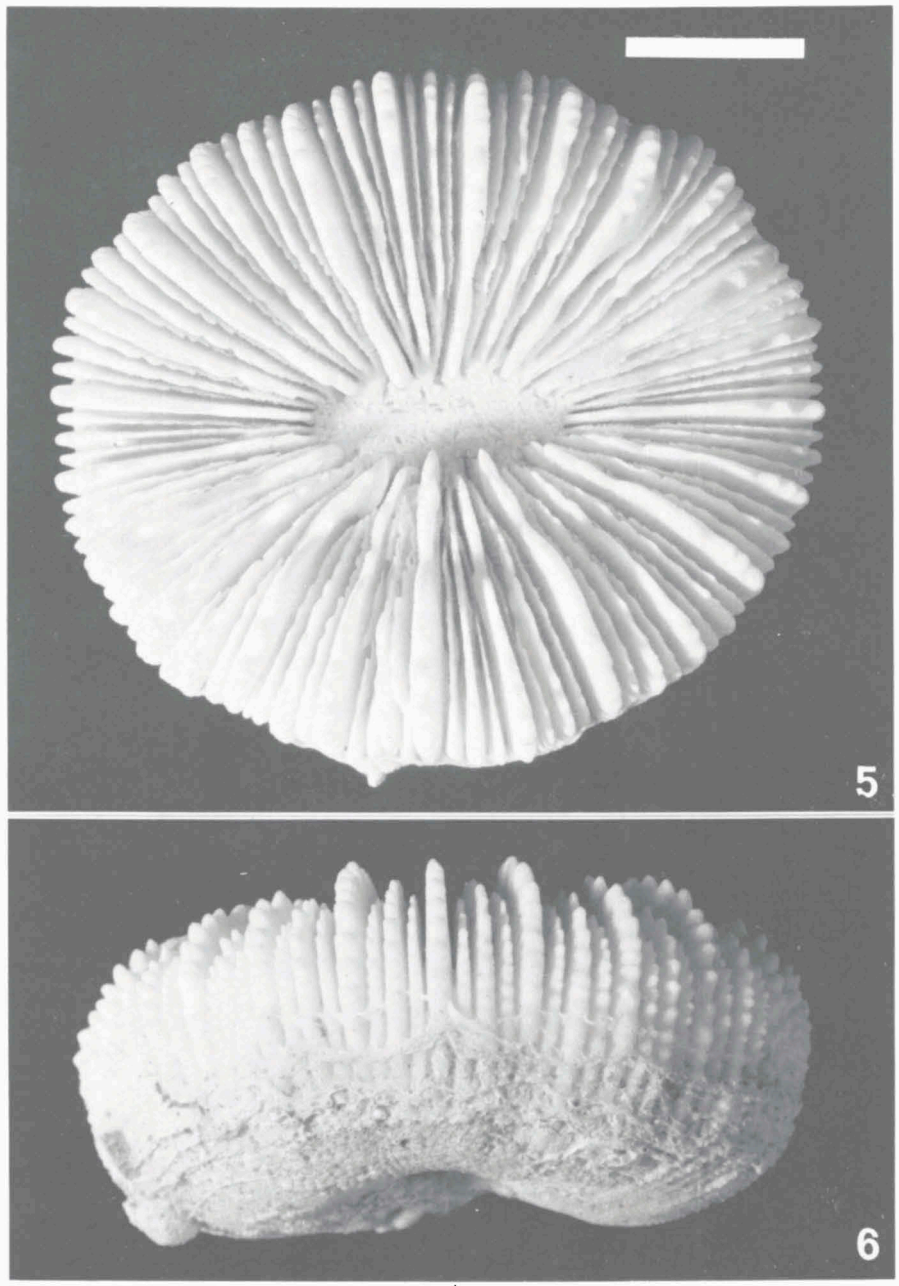
Historical comments. — The fossil genus *Indophyllia* was described by Gerth (1921: 405) as monotypic. The type species *I. cylindrica* (RGM 17700) from Java is figured in Gerth (1921: pl. 56 fig. 3, pl. 57 fig. 40). Later he found other material of the same genus in Borneo and described that as *I. borneensis* (Gerth, 1923: pl. 1 fig. 24, pl. 2 figs. 6-7; RGM 43055). The genus includes solitary, free-living corals much resembling representatives of the genus *Trochocyathus* Milne Edwards & Haime, 1848, (a caryophyllid group), but it differs by having a well developed endotheca. According to Gerth (1921) the young *Indophyllia* is disk-shaped and flat, but in the adult stage the coral is growing cylindrically upward, while forming an epitheca on its wall.

The type species is also figured by Wells (1956: fig. 305-1). Wells characterizes the genus as being "like *Anthophyllia,* but discoid to subcylindrical" and therefore places the genus in the subfamily Trachyphylliinae. Gerth (1921) places *Indophyllia* in the family Lithophyllidae, a group of predecessors of the mussid corals. On the basis of more fossil Tertiary material collected by Gerth in Borneo and our recent material from SW Sulawesi, we conclude that we are dealing with a group of solitary mussid corals, clearly recognizable by their mussid dentations on all the septa. The recent species described here is closely related to the Indo-Pacific genus *Cynarina,* which has also a recent representative, *C. lacrymalis.*

Characters and variability. — The solitary corallum is attached as a juvenile (fig. 7c), but becomes free-living in the mature stage. The diameter of the largest specimen is 45 mm. The calyx is regularly circular to slightly oval. An epitheca is covering the aboral side of all specimens.

The first three cycles of septa (24) are well developed and have all the typical mussid dentations that continue on the costal ridges, what can be seen when the epitheca has not been developed yet. They all reach the columella where they end in a paliform lobe. These septa are evenly exsert and regularly lobed, what gives the corallum a regular appearance. The fourth and fifth cycles are not always complete, depending on the age of the animal. They are less dentated and do not reach the columella.

The paliform lobes are placed as a crown around the regular, well developed columella which consists of tightly packed twisted trabeculae. All septal sides are finely granulated. The granulations are often placed in rows, especially in the upper part of the septa.



Figs. 5-6. Holotype of *Indophyllia macassarensis* spec. nov. from S.W. Sulawesi (RMNH 22189); view of the top (fig. 5) and of the side (fig. 6). Scale bar: 1 cm.

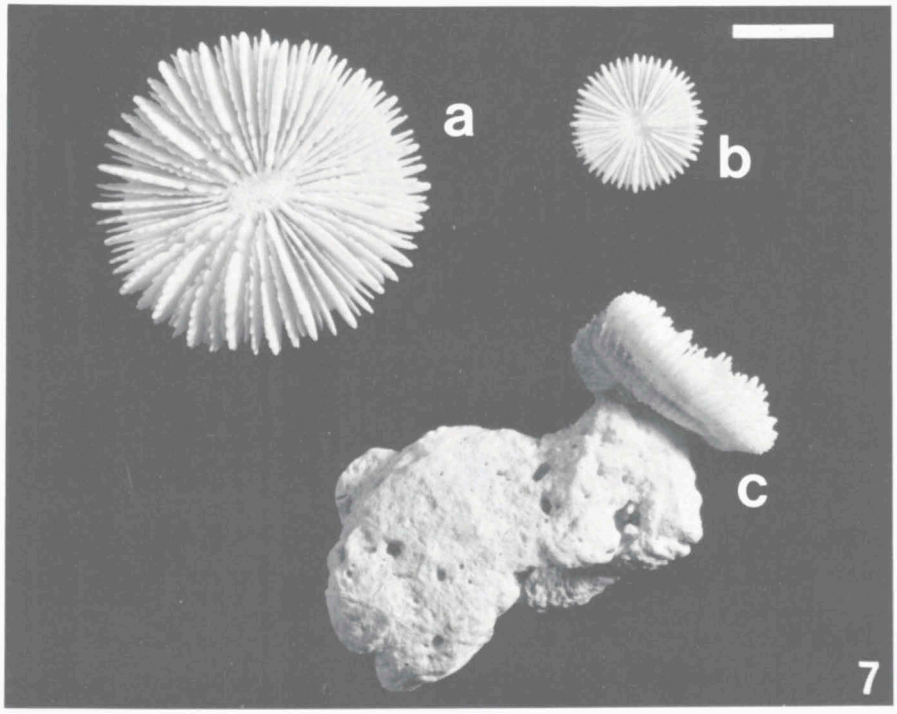


Fig. 7a-c. Paratypes of *Indophyllia macassarensis* spec. nov. from S.W. Sulawesi; two unattached specimens, fig. 7a (RMNH 22190) and 7b (RMNH 22192), and one attached fig. 7c (RMNH 22190). Scale bar: 1 cm.

The polyp is fleshy and transparent-brown what makes it possible to see its white skeleton.

Habitat. — All specimens have been found on the sandy bottom under reef slopes in a depth-range from 21 to 36 m, usually at the leeward sides of the islands which are sheltered from wave action. Here the reefs have a low coral coverage and are relatively rich in free-living corals consisting of the soft-bottom coral community.

Affinities. — This is the first reference of a living species in the genus. The corallum does not grow high up as described for *I. cylindrica.* The recent specimens resemble in this respect more *I. borneensis,* but in the latter the septa are less lobed and their margins are finely serrated. Small specimens resemble those of *Anthemiphyllia* species, but corals of that genus lack the epitheca which is very distinct in *Indophyllia.*

Etymology. — The species is named after the Makassar Strait in which the Spermonde Archipelago is situated. The name Makassar is also still used for the port of Ujung Pandang, the city in which vicinity the species was found.

Cynarina lacrymalis (Milne Edwards & Haime, 1848) (fig. 8)

Synonymy according to Veron & Pichon (1979: 238); in addition new synonyms:
Caryophyllia deshaysiana Michelin, 1850: 238.
Antillia grandiflora Gerth, 1921: 409.
Antillia japonica Yabe & Sugiyama, 1931: 128.
Antillia nomaensis Yabe & Sugiyama, 1931: 128.
Acanthophyllia deshaysiana - Wells, 1937: 242.

Material. — Kei Islands: RMNH 22196, 22200. Halmahera: RMNH 22197, 22198, 22199. SW Sulawesi: RMNH 20901, 22193, 22194, 22195 (9 ex.). Komodo: RMNH 21395.

Historical comments. — The holotype of this species is in the MNHN-collection at Paris, with the Philippines as type locality. Because the species is known up from the Miocene of Europe and the Pacific, and is very variable in form, the fossil as well as the recent specimens of this animal have been described under many different names (see historical comments under *Trachyphyllia geoffroyi*).

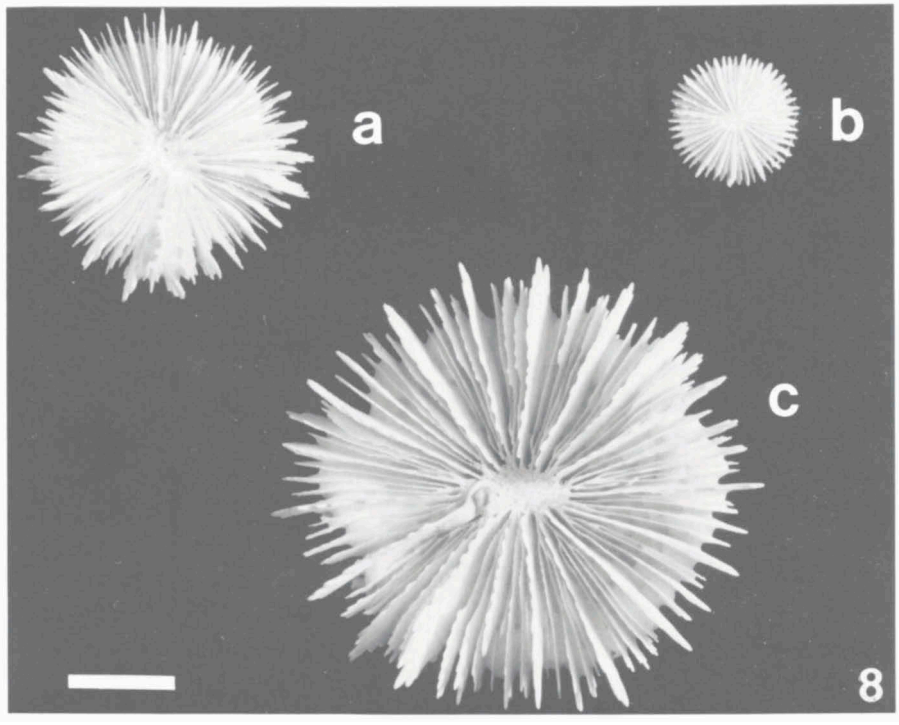


Fig. 8a-c. *Cynarina lacrymalis* (Milne Edwards & Haime) from Komodo (RMNH 21394). Scale bar: 2 cm.

Characters and variability. — The species and its variability are well described in Veron & Pichon (1979). The series from Indonesia on which the present paper is based, shows so much variation, that it even extends the range as discussed by Veron & Pichon from eastern Australia. Some specimens found in Indonesia are e.g. almost identical with the *Caryophyllia deshaysiana* Michelin, 1850, described by Wells (1937) as *Acanthophyllia deshaysiana.* These specimens, however, fit within the range of variability of *C. lacrymalis.* This large, free-living Indo-Pacific solitary coral is easily recognized. The corallite can reach a diameter of 10 cm and a height of 8 cm. The septa bear the mussid dentations that can reach a height of up to 15 mm. How well the epitheca is developed depends on the environment where it grows, like in *Trachyphyllia geoffroyi.* The corallum as a whole is strongly dentated. In the juvenile stage (fig. 8b) it resembles that of *Indophyllia macassarensis.* It is remarkable that this coral, despite its large size, never shows any indication of budding.

The polyp is large and fleshy; it shows a variety of colorful patterns.

Geographical distribution. — The species is widely distributed, from the Red Sea to New Caledonia.

Habitat. — The species is generally found in protected lagoon or bay waters where light and water movement is tempered.

Affinities. — The species shows affinities with the solitary forms of the genus *Scolymia* and as already stated above with *Indophyllia macassarensis. Scolymia* species become colonial (see under discussion) and *Indophyllia* has a smaller disk-shaped corallum.

Anthemiphyllia dentata (Alcock, 1902)
(fig. 9)

Synonymy according to Cairns (1984: 10).

Material. — Binongko, Tukang Besi Islands: RMNH 18013 (3 ex.).

Historical comments. — The genus *Anthemiphyllia* has puzzled many coral taxonomists. As an ahermatypic it looks like a trochocyatoid coral, but its strongly serrated septal margins place it rather in the faviids than in the caryophyllids. Pourtalès (1878) mentioned its resemblance with *Leptophyllia* Reuss, 1854, a fossil fungiid and with the Monlivaultinae, an extinct Mesozoic predecessor group of the Mussidae (faviids). To avoid all further confusion, Vaughan (1907) therefore placed the species in a new family, Anthemiphyllidae, closely allied to the Mussidae.

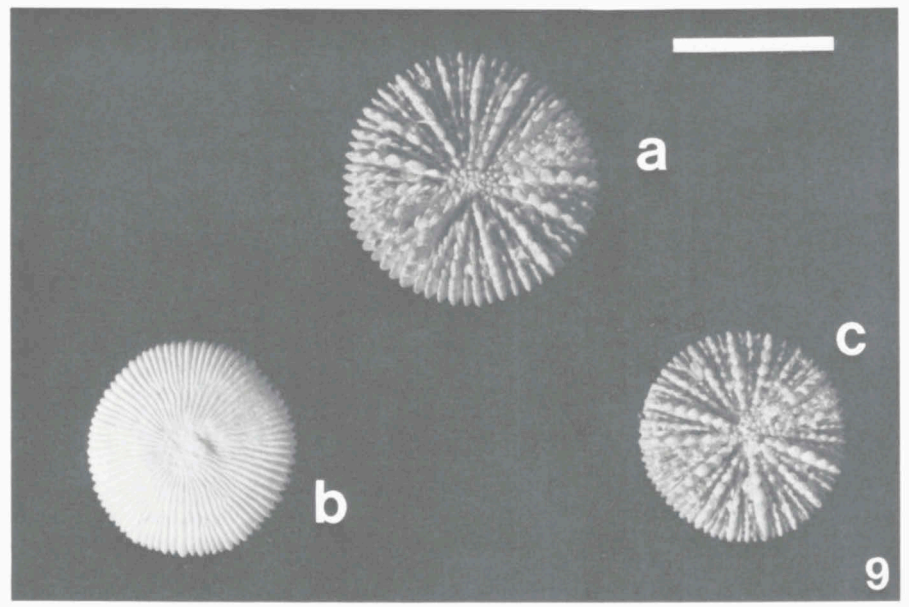


Fig. 9a-c. *Anthemiphyllia dentata* (Alcock) from Binongko, Tukang Besi Islands (RMNH 18013). Scale bar: 1 cm.

Characters and variability. — The species is well described and figured by Alcock (1902) (syntypes: ZMA 716-718, 7 ex.; type locality Celebes Sea). The diameter of the specimens treated here is 14-17 mm.The number of septa varies from 52 to 66. The long septal serrations are very apparent, strong and rounded. The septal sides are granulated. There is no clear variation in the characters.

Geographical distribution. — The species is known from the western Indian Ocean, Japan, Philippines, Indonesia, Tasmania and the Hawaiian Islands.

Habitat. — The species is known to occur in deep water, from 65 to 700 m (Cairns, 1984). Our material comes from a depth of 280 m.

Affinities. — The affinities of the species with its closest relative, *A. pacifica* Vaughan, 1907, from the Hawaiian Islands have already been discussed by Cairns (1984). Both species are interesting relicts of an old coral genus. We have treated the species not only because it is a free-living faviid, but also because it resembles small specimens of *Indophyllia macassarensis*. *Anthemiphyllia* lacks the epitheca which is typical for *Indophyllia* (compare figs. 6 and 9b).

DISCUSSION

Many species of free-living corals, either solitary or colonial, inhabit reef sites with soft substrata. They form an interesting group especially adapted to reject sediments (Fisk, 1983). In such soft bottom coral assemblages we may also encounter extreme growth forms of normally sessile corals, that try to survive in this habitat by adapting their morphological structure (Wijsman-Best, 1972). The free-living reef corals, however, of which the Fungiidae form the greater part, constitute the majority of individuals.

The Faviina are derived from the predominantly solitary procyclolitids, a Triassic group from which the suborder Fungiina also descended (Wells, 1956). Later development led to the montivaltids in the late Jurassic, that owed their success to the broadening of the edge zone, reduction of the epitheca and an exploitation of various modes of colony formation. All are good characters for an attached colonial mode of living. Most recent faviid genera therefore consist of species which form compact reef colonies and thus are important builders of the reefstructure. Only a few of them live unattached, without assisting in the construction of the hard bottom parts of the reefs. The genera treated in this paper are therefore exceptional in the Faviina. In the western Atlantic only the genera *Manicina* and *Scolymia* are free-living recent representatives.

Of the Fungiina, derived from the procyclolitids, one line developed highly perforated septa and smaller corallites, leading to the successful group of the Poritidae, important reef builders. The other line developed species having compound trabeculae, solid low order septa and large flat-based coralla. They form the Fungiidae, which now not only inhabit soft bottoms, but also can live on the more solid substrata found on the reef flat and reef slope. The separate species of this family do not all live in the whole depth range of the reef but are restricted to certain zones. Consequently not all of the species form necessarily part of the sandy bottom assemblages at the reef base. Species which do live there usually are even specialized to live in a limited zone of that part of the reef (Hoeksema, in prep.). Some of the species which live on a soft substratum have developed special structures and mechanisms to overcome burial, like a certain degree of mobility (Abe, 1939; Hubbard, 1972) or sediment removal (Schuhmacher, 1977; 1979).

The free-living fungiids just lie flat and loose on the bottom. Therefore they do not need an epitheca. Apart from *Anthemiphyllia* the unattached faviids live partially buried in the sand. Once they have settled in the sand or mud, they are not able to displace themselves anymore. There are also species in the Fungiidae which remain small and have developed the ability to reproduce

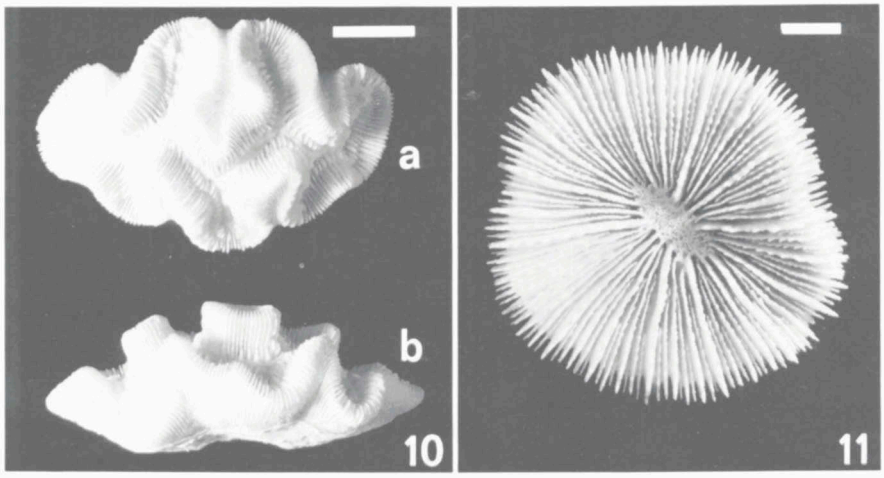


Fig. 10a-b. *Manicina areolata* (Linnaeus) from St. Martin, Caribbean Sea (RMNH 8647). Scale bar: 2 cm. Fig. 11. *Scolymia lacera* (Pallas) from Saba Bank, Caribbean (RMNH 8542). Scale bar: 1 cm.

asexually by fragmentation. In that way they become less dependant on the vicinity of a hard substratum. Another unattached coral species, *Goniopora stokesi* Milne Edwards & Haime, 1851, often living in the soft-bottom community together with free-living faviids and fungiids, uses budding as a means to reproduce asexually (Rosen & Taylor, 1969). In the faviids these mechanisms, fragmentation and budding, are not used for reproduction. In the Fungiidae colonial forms have developed independantly from each other into seven genera, two remaining fixed and five having an unattached stage. Of the faviids the majority of the colony-forming genera and species remain attached.

When we compare the free-living faviids treated here, *Trachyphyllia geoffroyi* and *Cynarina lacrymalis,* we see a striking resemblance with the West Atlantic representatives. *Trachyphyllia geoffroyi* (fig. 1) and *Manicina areolata* (L., 1758) (fig. 10) have obtained a similar growth form in the adaptation to live on sand. *Cynarina lacrymalis* (fig. 8) and *Scolymia lacera* (Pallas, 1766) (fig. 11) are two solitary mussids and both adapted to live on a soft bottom, but occur in different geographical areas. In respect to the free-living faviid corals *M. areolata* and *T. geoffroyi* we can speak of a convergent evolution and the same holds for the mussid corals *S. lacera* and *C. lacrymalis.*

The subfamily Trachyphyllinae Wells, 1956, becomes rather doubtful as a separate group once observed that: *Indophyllia* is a mussid (this paper), *Antillophyllia* is a faviid fossil genus from the western Atlantic of which the

taxonomic status is doubtful (this paper), *Wellsophyllia* is synonymous with *Trachyphyllia* (this paper), *Callogyra* is synonymous with *Trachyphyllia* (Pichon, 1980) and *Moseleya* is probably part of *Favites* (Veron e.a., 1977). This all makes the subfamily Trachyphyllinae monogeneric, including only *Trachyphyllia.* We propose – also because of its resemblance to the W. Atlantic faviid genus *Manicina* – to regard *Trachyphyllia* as an Indo-Pacific genus in the subfamily Faviinae instead of the Trachyphyllinae and to disregard the latter.

About the Anthemiphylliidae, Wells (1956: 367) stated that its paleontological history is unknown, "but the septal structure suggests a rhizangiid ancestry". While examining the specimens from Indonesia of *Anthemiphyllia dentata* we do agree with this statement. *Anthemiphyllia* contains the only free-living non-zooxanthellate faviid species and must be regarded as a relict group.

Other unattached corals in soft bottom communities belong in general to the suborder Caryophyllina, a very successful group of corals in adapting to extreme environments, and the much younger suborder Dendrophylliina. Most of these are non-zooxanthellate deep-sea corals. Some genera, like *Catalaphyllia, Euphyllia* and *Heterocyathus* of the Caryophylliina and *Turbinaria* and *Heteropsammia* of the Dendrophyllina are zooxanthellate and well adapted to reject sediment. Problems dealing with these genera will be treated in following papers.

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