TAXONOMY, PHYLOGENY AND BIOGEOGRAPHY OF MUSHROOM CORALS (SCLERACTINIA: FUNGIIDAE)

by

BERT W. HOEKSEMA

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Key words: Scleractinia, Fungiidae, mushroom corals, taxonomy, revision, fossil record, phylogeny, biogeography, Indo-Pacific, tropical, marine, benthic, shallow-water habitats, coral reefs, species diversity.

The Fungiidae are mushroom corals that live in sublittoral habitats in the tropical Indo-Pacific. Their habitats are part of coral reefs or other marine substrata, which usually can be found in the proximity of the reefs.

In the present taxonomic revision, the family is divided into 11 genera; one of which, *Fungia*, is subdivided into seven subgenera. A total of 40 species is described and figured, three of which are new to science. One species is renamed.

The stratigraphic distribution is given for all the species recorded in fossil state. A tentative phylogenetic reconstruction down to the species level is given. The cladogram that is provided should be considered a working hypothesis and not a sound basis for a completely revised classification and nomenclature of the Fungiidae.

For each species the presently known geographic range is mapped. The pattern of species richness in the Indo-Pacific is compared with that of some other taxa and discussed with respect to their distributional patterns. The ranges of the Fungiidae are analyzed with the use of approaches from both historical and ecological biogeography.

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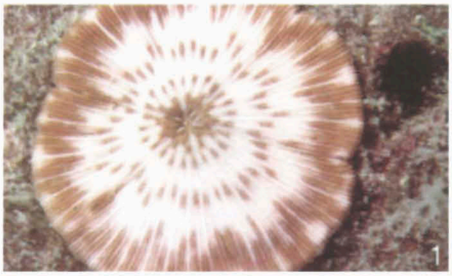
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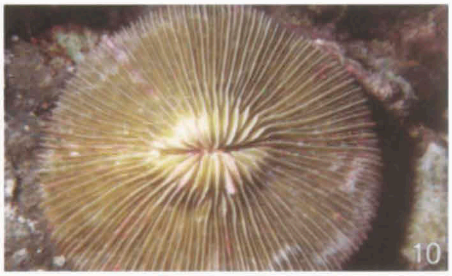
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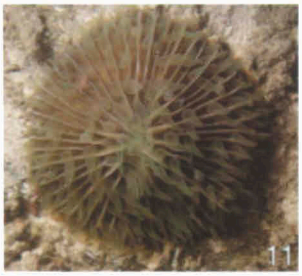
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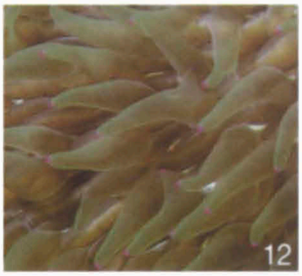
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Figs. 1-13 (opposite page). Fungiidae in their natural habitats on the reefs of the Spermonde Archipelago, SW Sulawesi, Indonesia. Fig. 1. *Fungia (Cycloseris) sinensis*; a non-zooxanthellate individual in the initial phase of fragmentation on the reef slope (15 m deep) at the W side of Bone Batang (RMNH 21830). Fig. 2. *Fungia (Cycloseris) somervillei* on the sandy bottom (30 m deep) at the W side of Kudingareng Keke (RMNH 22084). Fig. 3. *Fungia (Cycloseris) somervillei*; a fragmented and regenerated animal on the sandy bottom (27 m deep) at the W side of Kudingareng Keke. Fig. 4. *Fungia (Cycloseris) fragilis*; an unfragmented animal with three commensalistic shrimps, *Periclimenes magnificus*, Bruce, 1979 (identification by C.H.J.M. Fransen) on the sandy bottom (27 m deep) at the SW side of Kudingareng Keke. Fig. 5. *Fungia (Cycloseris) costulata* on the reef slope (12 m deep) at the W side of Bone Batang. Fig. 6. *Fungia (Cycloseris) tenuis* on the reef slope (9 m deep) at the W side of Samalona (RMNH 21755). Fig. 7. *Fungia (Cycloseris) vaughani* on the sandy bottom (30 m deep) at the W side of Kudingareng Keke (RMNH 22072). Fig. 8. *Fungia (Verrillofungia) scabra* on the reef slope (9 m deep) at the E side of Kudingareng Keke. Fig. 9. *Fungia (Verrillofungia) concinna* on the reef slope (18 m deep) at the W side of Badi. Fig. 10. *Fungia (Verrillofungia) repanda* on the reef slope (15 m deep) at the W side of Kudingareng Keke. Fig. 11. *Fungia (Danafungia) fralinae* on the reef slope (15 m deep) at the W side of Samalona. Fig. 12. *Fungia (Danafungia) fralinae*; close-up of tentacles showing the violet tips; note that some of the tentacles are bifurcated. Fig. 13. *Fungia (Danafungia) horrida* on the reef slope (12 m deep) at the W side of Kudingareng Keke.

INTRODUCTION

Mushroom corals (Fungiidae) are generally restricted to the shallow-water habitats of coastal areas, islands and shallow banks in the tropical Indo-Pacific. The mushroom-like appearance of the animals has attracted the attention of many people visiting the natural environments where they live. Most species are free-living and therefore easy to collect. Because of their attractiveness, stony corals are frequently brought home as souvenirs. It is not surprising, therefore, that they can also be purchased in souvenir and aquarium shops remote from the place where they were originally collected. It is obvious that they are common in the zoological collections of natural history museums all over the world. However, despite their conspicuous appearance and their abundant presence in collections, most individual species are not well known. The present study deals with the taxonomy, phylogeny and biogeography of these mushroom coral species.

The most recent previous revision of fungiid species was published by Gardiner (1909). It is considerably out of date and mainly based on a study of corals from the West Indian Ocean, with additional data from the literature. Compared to Gardiner's work, Döderlein's (1902) earlier revision of the genus *Fungia* had more impact on the more recent literature of the first half of the 20th century. Since the publication of these two studies, taxonomic information about fungiid species became mainly restricted to expedition reports and other publications dealing with coral faunas of limited geographic areas, such as the Maldives (Pillai & Scheer, 1976), the Great Barrier Reef (Veron & Pichon, 1979), Guam (Randall & Meyers, 1983), the Red Sea (Scheer & Pillai, 1983) and Western Australia (Veron & Marsh, 1988). Nevertheless, in the literature the taxonomic status of many nominal taxa remained uncertain or was interpreted incorrectly because most authors were unacquainted with the type material. Consequently, during the present revision many taxonomic changes had to be made.

A recent generic revision by Wells (1966) has had much impact on the systematics of the Fungiidae. His division of *Fungia* into subgenera was adopted by many coral taxonomists. He presented a hypothetical scheme with regard to the evolution of the Fungiidae down to the subgeneric level. Cairns (1984b) used basically the same characters as Wells to construct a cladogram of the Fungiidae.

In the present study a tentative phylogenetic reconstruction down to the species level is made. The cladogram that is provided should be considered a working hypothesis and not a sound basis for a completely revised classification and nomenclature of the Fungiidae. Several parts of it are still poorly founded, especially because of uncertainties caused by the abundance of homoplastic similarities. As long as this situation exists there are no good reasons to change the prevailing nomenclature, which would result in confusion. The systematic account of the Fungiidae as presented in the present study aims in the first place to be a tool for an easy recognition of its taxa.

ACKNOWLEDGEMENTS

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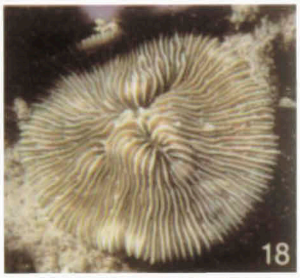
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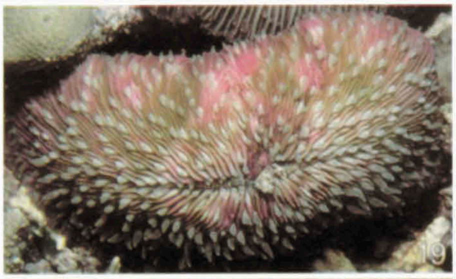
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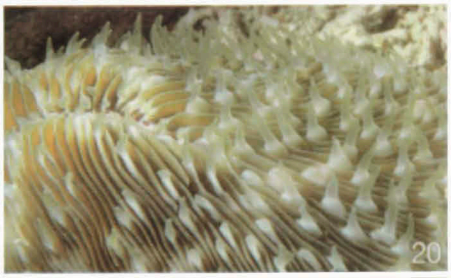
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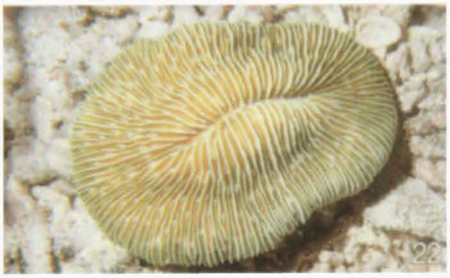
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research in the Spermonde Archipelago (SW Sulawesi). The research permission was granted by LIPI. I thank the rector of Hasanuddin University at Ujung Pandang (UNHAS) for sponsoring the research. The assistance supplied by the staff members of UNHAS, especially Mr. W. Moka, is gratefully acknowledged.

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Figs. 14-24 (opposite page). Fungiidae in their natural habitats on the reefs of the Spermonde Archipelago, SW Sulawesi, Indonesia (continued). Fig. 14. *Fungia (Fungia) fungites* on the reef flat (2 m deep) at the W side of Kudingareng Keke, where the animals are more brightly coloured and built coarser than those which live deeper. The pink colour around the damaged area at the part of the periphery below probably indicates the occurrence of healing. The colour pink in *F. (F.) fungites* can usually be observed at the whole periphery and then probably indicates the production of new material. Fig. 15. *F. (F.) fungites* on the reef slope (6 m deep) at the W side of Kudingareng Keke. The specimen is browner than the animal shown in fig. 14; its septa are thinner and the septal dentations are finer. Fig. 16. *Fungia (Danafungia) scruposa* on the reef slope (12 m deep) at the E side of Samalona. The five animals are still in the attached anthocaulus-stage. The small coral below is in a very early anthocaulus-stage, whereas the largest animal is in late anthocaulus-stage and probably due to become detached. The tentacles are almost contracted. Fig. 17. An anthocyathus of *Fungia (Danafungia) scruposa* with extended tentacles on the reef slope (12 m deep) at the E side of Samalona. Fig. 18. *Fungia (Wellsofungia) granulosa* on the reef slope (15 m deep) at the N side of Bone Tambung. The animal is irregularly built as a result of the fusion of two individuals during the anthocaulus stage (see fig. 42). Fig. 19. *Fungia (Lobactis) scutaria* on the reef slope (9 m deep) at the N side of Kudingareng Keke. Fig. 20. Close-up of tentacles of *F. (L.) scutaria*. Each tentacle is distinctly supported by the tentacular lobe on the septum underneath. Fig. 21. *Fungia (Pleuractis) moluccensis* on the reef slope (18 m deep) at the E side of Kudingareng Keke. This animal lives partly burried under the sediment, but its mouth is still uncovered. Fig. 22. *Fungia (Pleuractis) gravis* on the reef slope (15 m deep) at the W side of Kudingareng Keke. Fig. 23. *Fungia (Pleuractis) paumotensis* on the reef slope (9 m deep) at the W side of Kudingareng Keke. Fig. 24. *Heliofungia actiniformis* on the reef slope (15 m deep) at the NW side of Kudingareng Keke. The long tentacles and the fleshy body hide the skeleton at the inside.

Schuhmacher (HSC); Mr. Suharsono (PPPO); Dr. W. Decraemer (IRSNB/KBIN); Mr. J. De Vidts (MZS); Dr. K.W. Petersen (UZMK); Dr. L.M. Marsh (WAM); Dr. D. Kühlman (ZMB); Dr. J.W. Wells (Cornell Univ., Ithaca, N.Y.); Dr. N.E. Chadwick (H. Steinitz Mar. Biol. Lab., Eilat).

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METHODS

The research was started with an introductory study of collections present in two Dutch museums (i.e. the RMNH and the ZMA; see list of abbreviations). Part of this material was previously described by Van der Horst (1919; 1921), Boschma (1923; 1925; 1929) and Umbgrove (1939; 1940). The rest was sampled during the Snellius Expedition (1929-1930) and collected by Moll (1983). Most of the examined specimens came from Indonesia.

After the initial study of museum specimens, fieldwork was performed to collect additional material. The field studies were performed in Indonesia at NW Java (1983), the Flores Sea region (Snellius-II Expedition, 1984) and SW Sulawesi (1984-1986). The main purpose was to collect specimens for samples of each species with the widest possible ranges of body size and morphological variation. Special attention was paid to poorly known species. With the help of SCUBA corals were collected down to depths where no Fungiidae could be observed anymore, which was usually not deeper than 40 m.

Finally, museum collections were restudied to investigate the stratigraphic and biogeographic ranges of the species. Only if no representative specimens were available for study, illustrations in the literature were used. Published records without accompanying illustrations are neglected. Methods used for the phylogenetic and biogeographic analyses are explained in the chapters dealing with the phylogeny and the biogeography of the Fungiidae.

LIST OF ABBREVIATIONS

AIMS – Australian Institute of Marine Science, Townsville
AMNH – American Museum of Natural History, New York
ANSP – Academy of Natural Sciences of Philadelphia
BMNH – British Museum (Natural History), London
GPC – G. Paulay collection
HLM – Hessisches Landesmuseum, Darmstadt
HMG – Hunterian Museum, Glasgow
HSC – H. Schuhmacher collection
IGPTU – Institute of Geology and Paleontology, Tohoku University, Sendai
IRSNB – Institut Royal des Sciences Naturelles de Belgique, Bruxelles
KBIN – Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussel
LSL – Linnean Society of London
MCZ – Museum of Comparative Zoology, Cambridge (Mass.)
MGH – Museum Godeffroy, Hamburg
MNHN – Muséum National d'Histoire Naturelle, Paris
MZS – Musée Zoologique, Strasbourg
NHMW – Naturhistorisches Museum, Wien
NS – Tel Aviv University
NTM – Northern Territory Museum, Darwin
PPPO – Pusat Penelitian dan Pengembangan Oseanologi, Jakarta
QMB – Queensland Museum, Brisbane
QMT – Queensland Museum, Townsville
RGM – Rijksmuseum van Geologie en Mineralogie, Leiden
RMNH – Rijksmuseum van Natuurlijke Historie, Leiden
SLR – Hebrew University Jerusalem
SMNS – Staatliches Museum für Naturkunde, Stuttgart
UB – Universität Basel
ULB – Université Libre de Bruxelles
UMZC – University Museum of Zoology, Cambridge
UPMSI – University of the Philippines, Marine Sciences Institute, Quezon City
UPZD – University of the Philippines, Zoology Department, Quezon City
USNM – U.S. National Museum of Natural History, Washington
UZMK – Universitetets Zoologisk Museum, København
WAM – Western Australian Museum, Perth
YPM – Yale Peabody Museum of Natural History, New Haven


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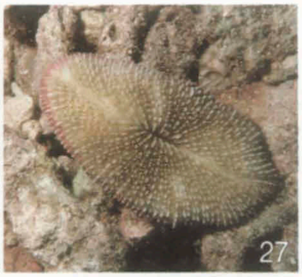
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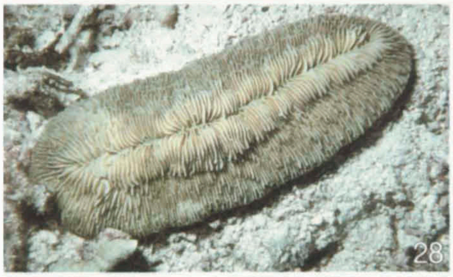
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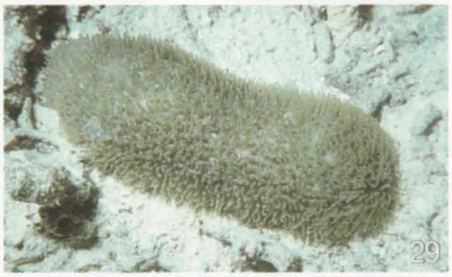
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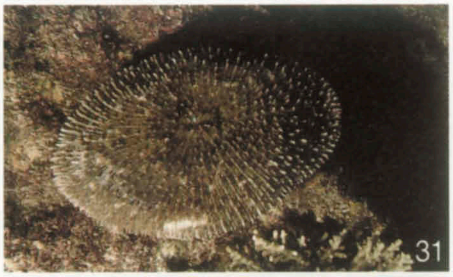
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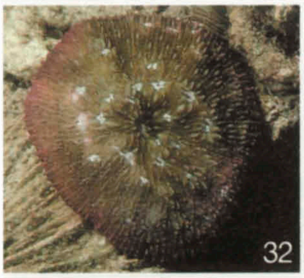
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ZMA – Instituut voor Taxonomische Zoölogie (Zoölogisch Museum), Amsterdam
ZMB – Museum für Naturkunde der Humboldt-Universität (Zoologisches Museum), Berlin
ZSI – Zoological Survey of India, Calcutta

CRITERIA AND TERMINOLOGY USED IN THE TAXONOMY

Taxonomic position. — Within the order of the Scleractinia the Fungiidae form a conspicuous family of shallow-water corals, restricted to the tropical Indo-Pacific. According to Wells (1956) the Fungiidae can be traced back to the Mid Cretaceous, when it separated from the now extinct Synastreidae, a family of hermatypic corals, which were either solitary or colonial (fig. 38). The Fungiidae and the Micrabaciidae (a family of solitary, free-living deep-sea corals) were since Wells' (1956) revision of the Scleractinia the only accepted

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Figs. 25-37 (opposite page). Fungiidae in their natural habitats on the reefs of the Spermonde Archipelago, SW Sulawesi, Indonesia (continued). Fig. 25. A small coral of *Ctenactis albitentaculata* spec.nov. in early anthocyathus-stage on the reef slope (15 m deep) at the W side of Bone Tambung (RMNH 16054). The white tentacles are still distinct despite their contracted condition. Fig. 26. A small coral of *Ctenactis echinata* in early anthocyathus-stage on the reef slope (6 m deep) at the W side of Kudingareng Keke (RMNH 20172). Fig. 27. A small coral of *Ctenactis crassa* in early anthocyathus-stage on the reef slope (15 m deep) at the W side of Bone Batang (RMNH 20199). The animal has still one mouth. The pink colour at the periphery of the coral probably indicates growth. Fig. 28. *Herpolitha limax* on the reef slope (6 m deep) at the N side of Kudingareng Keke. Fig. 29. *Polyphyllia talpina* on the reef flat (3 m deep) at the W side of Kudingareng Keke. Fig. 30. *Sandalolitha robusta* on the reef slope (12 m deep) at the W side of Kudingareng Keke. Fig. 31. *Zoopilus echinatus* on the reef slope (18 m deep) at the W side of Badi (RMNH 22113). The animal is in early anthocyathus-stage, recently detached from its stalk. Figs. 32. *Halomitra pileus* on the reef slope (12 m deep) at the W side of Badi. The animal is in early anthocyathus-stage. The periphery has a pink colour probably indicating growth. The area around each mouth is distinctly white. Fig. 33. A paratype of *Halomitra clavator* spec. nov. on the reef slope (25 m deep) at the W side of Badi (RMNH 22111). Like the holo- and the paratype from Komodo, it could easily be distinguished from neighbouring animals of *Halomitra pileus*, by its evenly coloured, ochre tissue. The animal lacks a pink margin and has the stomatal "lips" not distinctly white as in *H. pileus*. Fig. 34. *Podabacia crustacea* on the reef slope (12 m deep) at the SE side of Samalona. Fig. 35. *Lithophyllon undulatum* on the western reef slope of Bone Baku (RMNH 22127). The animal is a juvenile with the periphery distinctly loose from the substratum. The margin around the (still) single mouth is typically blueish grey. Fig. 36. An adult of *L. undulatum* on the reef slope (15 m deep) at the SW side of Kudingareng Keke. This animal has several stomata almost regularly arranged in a concentric pattern around the larger primary mouth. Fig. 37. *Lithophyllon mokai* spec. nov. on the reef slope (15 m deep) at the SW side of Kudingareng Keke. This adult coral is slightly smaller than the juvenile of *L. undulatum* in fig. 35. The peripheral margin is still attached to the substratum what is typical for the encrusting habit of the animal. The stomata are irregularly arranged and the stomatal margins are dark brown.

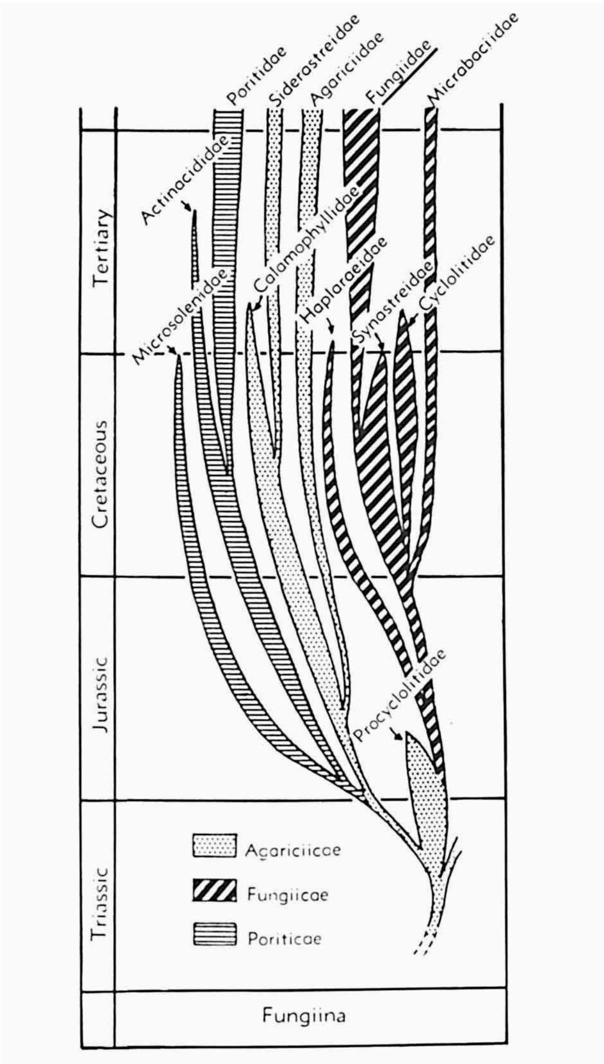


Fig. 38. An evolution scheme of the families within the Fungiina (after Wells, 1956). The Fungiacyathidae, which have recently been separated from the Fungiidae (Chevalier & Beauvais, 1987), are not included in the scheme, since their taxonomic position is not yet clear.

extant families in the superfamily Fungiicae. Only recently the Fungiacyathidae (Chevalier & Beauvais, 1987) were split from the Fungiidae, as a monogeneric, cosmopolitan family of non-zooxanthellate, solitary, deep-sea corals with a skeleton structure different from that of the Fungiidae. At present it is not very clear how the scleractinian families are related to each

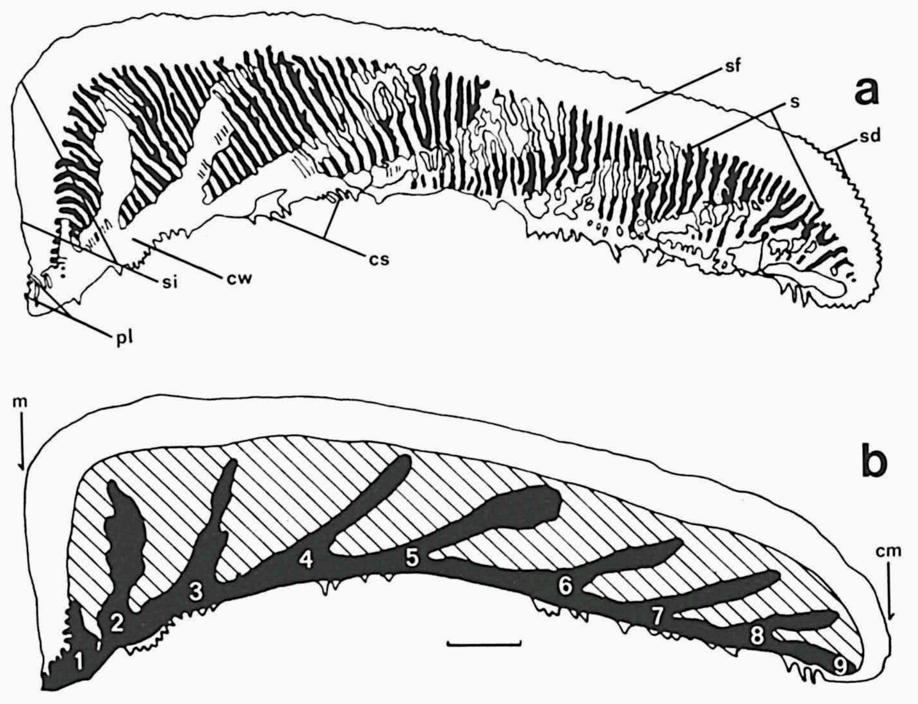


Fig. 39. Lateral view of a septo-costal unit. Fig. 39a. Several structures displayed when a coral is broken cross-wise: si = inner edge of septum; pl = paliform lobes; cw = corallum wall in cross-section; cs = costal spines; s = compound synapticulae; sf = septal fringe; sd = septal dentations. Fig. 39b. Orientation of some parts of a septo-costal unit after several phases of growth: m = the present location of the mouth (in the living animal) or fossa (in the skeleton); cm = the present location of the corallum margin; 1-9 = successive locations of the corallum wall (black). Scale bar: 1 cm. (Modified after Gill, 1980).

other. A phylogenetic analysis is needed to solve this problem. This, however, is not within the scope of the present revision.

An autapomorph character state in the corallum architecture of the Fungiidae, is the presence of interseptal bar-like structures (fig. 39), which are currently indicated as "compound synapticulae" (Wells, 1956; 1966). According to Gill (1980: 301) these compound synapticulae are not homologous with the "simple synapticulae" that occur in other coral families and therefore he introduced the term "fulturae" to be used instead of "compound synapticulae". In the present study the latter term is used. Up to now, there has been no confusion when coral systematists used the term "compound synapticulae" to indicate that the bar-like structures uniquely observed in the Fungiidae differ from the simple trabeculae.

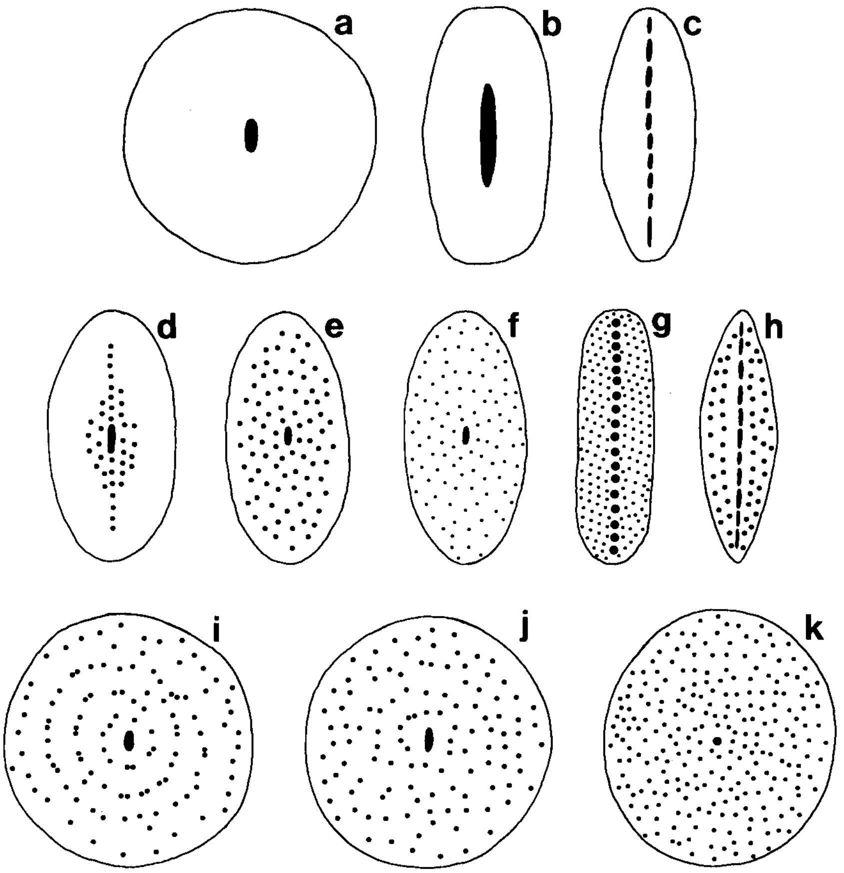


Fig. 40. Corallum outlines and stomatal distribution patterns of the Fungiidae. When intrastomadaeal and circumoral budding dominate over peripheral budding, the stomata are distributed in an either aggregated or irrelar pattern. When peripheral budding dominates, the secondary stomata are more evenly arranged. Examples: (a) a round and monostomatous animal (*Fungia*, *Heliofungia*); (b) an oval animal with a long mouth (*Fungia*); (c) intrastomadaeal budding along the central axis in an elongate animal (*Ctenactis crassa*); (d) circumoral budding, predominantly along the long axis of an oval animal (*Sandalolitha dentata*); (e) evenly distributed secondary stomata developed by peripheral and circumoral budding in an oval animal (*Sandalolitha robusta*); (f) as the former, with smaller secondary stomata (*Zoopilus*); (g) an elongate animal with relatively large stomata arranged along the central axis, and smaller ones evenly distributed alongside it by peripheral and circumoral budding (*Polyphyllia*); (h) an elongate animal with large stomata developing along the central axis by intrastomadaeal budding, and in irregularly formed rows alongside the axis by circumoral and peripheral budding (*Herpolitha*); (i) a round animal with a large mouth at the centre of the polyp and secondary stomata spaced in an clustered pattern by circumoral and peripheral budding (*Halomitra*); (j) a round coral with small secondary stomata developing in a slightly irregular pattern by peripheral and circumoral budding (*Lithophylon*); (k) an animal with a slightly oval outline and secondary stomata developing in an evenly distributed pattern by peripheral and circumoral budding (*Podabacia*).

In the taxonomy of the Fungiidae, the main criteria to separate taxa are based on differences in the life-cycles and on incongruences in the architecture of the skeletons. In the field, it is relatively easy to distinguish the fungiid genera based on such characters, whereas this is more difficult for subgenera and species. For these lower taxa differences in the micro-architecture of the coralla are important (e.g. the morphology of the corallum wall, the septa and the costae). The skeleton can most easily be observed if the soft tissue of the animal is removed. Much training is needed to identify animals in the field, when the soft tissue is still intact.

Soft body parts. — In general, mushroom coral polyps show too much intraspecific variation in exterior shape for use in the Fungiidae classification. Only a few species can easily be recognized by their characteristically shaped or coloured tentacles, whereas most fungiids have small translucent tentacles in mature stage (i.e. shorter than 1 cm when extended).

The morphology of the nematocysts has never been used in the taxonomy of the Fungiidae. Observations by Abe (1938) indicate that within single species a variety of nematocyst types may exist. According to Den Hartog (1980: 67), the differences in shape and size of the various types of nematocysts observed in the Scleractinia strongly suggest to be of importance at higher taxonomic levels.

The skeleton. — In the Fungiidae solitary and colonial forms exist. Because the terms "solitary" and "colonial" may lead to confusion (Rosen, 1979b), the terms "monostomatous" (or "monocentric") and "polystomatous" (or "polycentric") are preferred. A mushroom coral becomes polystomatous by means of either intrastomatous, circumstomatous or peripheral budding, or by a combination of these processes (Fig. 40). Intrastomatous (= intra-oral) budding is initiated by crosswise division of the first stoma, by fusion of two opposite septa. Each of the newly developed stomata may divide likewise. In circumstomatous (= circumoral) budding new stomata appear around older ones, by invagination of the septa. Peripheral budding is a process of successive invagination of the septa at the coral margin. Actually this is a special form of circumoral budding because it always occurs around at least the primary stoma. It is mentioned specifically because in contrast to the usual circumoral budding, it does not occur on the whole corallum upper surface, but in a more restricted part of it.

Intrastomatous, circumstomatous and peripheral budding are kinds of intratentacular budding. In the Fungiidae, extratentacular budding is a means of asexual reproduction and not a way to achieve coloniality (see below). Septa

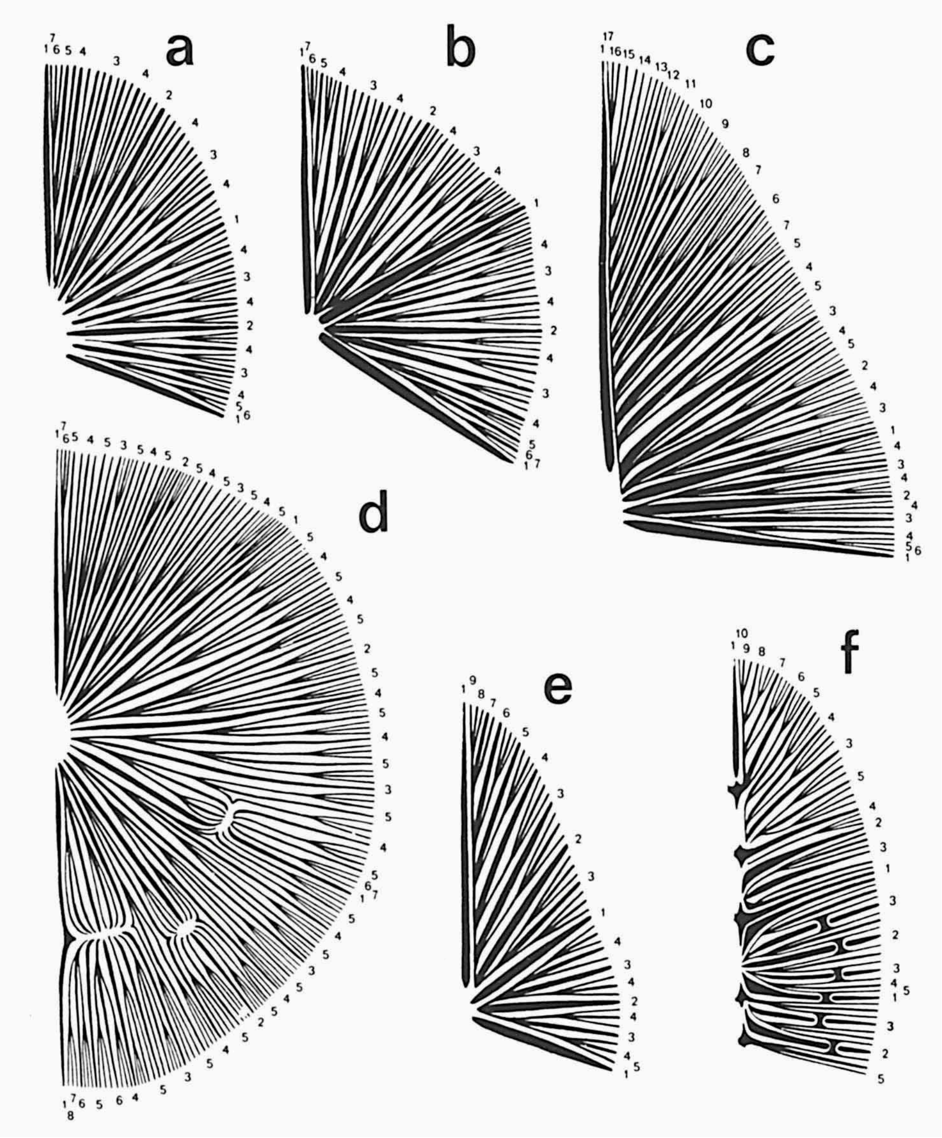


Fig. 41. Schematical presentation of the septal arrangement in young polyps of some species of Fungiidae: (a) up to 7 cycli in *Fungia (Cycloseris) cyclolites*, (b) up to 7 cycli in *F. (C.) hexagonalis*, (c) up to 17 cycli in *Ctenactis echinata*, (d) up to 8 cycli in *Halomitra pileus*, (e) up to 9 cycli in *Herpolitha limax*, (f) up to 10 cycli in *Polyphyllia talpina*. In figs. 40a, b, c, e, f septa in a third part of the corals are shown; in fig. 40d this is done for a half part. The figures are not to scale. (After Boschma, 1934).

which become divided by the forming of new stomata are therefore not homologous with the septo-costae found between the calices of colonial corals in most other scleractinian families. Septo-costae are homologous with costae. In the mushroom corals, costae are situated at the lower side of the coralla. For the fungiid morphology, instead of "septo-costae", the term "interstomatous septa" is proposed.

A septo-costal unit is the complete lamellar structure, composed of a septum and a costa, laterally connected to adjacent septo-costal units by compound synapticulae and the corallum wall (fig. 39). The septa and costae are radial structures which appear in cycles (fig. 41). The septa and costae of the first cycle are also called those of the lowest order; consequently the ones of later cycles are indicated as higher order septa and costae (Bourne, 1887; Boschma, 1929).

In general the septa and costae are straight, but in some species they are wavy. Their arrangement may differ as well; in some species they are more densely packed than in others. If the septa are thick and densily packed, it is more difficult to discern the compound synapticulae. The septa and costae of lower orders are usually larger in size, i.e. thicker and more protruding, than those of later origin, although in some species, their sizes are almost equal. In some species the higher order costae remain rudimentary.

An important criterion in the classification of fungiid taxa, is the form of the corallum outline. The corals may be round (discoidal), oval (elliptical) or elongate in shape (fig. 40). Further, the species may have corals of varying thickness, which can be flat, arched (with the upper side convex) or cup-shaped (with the upper side concave).

Some characters may change during the ontogeny. Up to now several "species" have been distinguished, based upon the shapes of corals which were actually successive ontogenetic phases within only a single species. Therefore, in the present study the range of the diameter (c.q. length) of the studied specimens is given for each species. This is relevant if the state of a character depends at least partly on the size of the animal. Furthermore, the maximum length found per species may be of taxonomic importance.

In monostomatous species particularly the length of the fossa (the skeleton part containing the mouth or stoma) may be a distinctive character. Because the length of the fossa depends on the corallum size, it is only useful as a taxonomic criterium when it is related to the corallum length (the diameter measured in the extension of the fossa).

Inside the fossa a distinct columella is usually present, consisting of trabeculae and paliform lobes, which protrude from the bottom of the fossa and from the inner edges of the septa, respectively. The structure of the columella may vary in the arrangement of the trabeculae and the paliform lobes.

The size and shape of the septal and costal ornamentations (dentations and spines, respectively) are very useful characters in the classification of the Fungiidae. The dentations on the septal margin are either small and granulate, large and lobate, or angular. On the septal sides granulations occur which are irregularly distributed or arranged in patterns, such as rows and ridges either perpendicular or parallel to the septal margin. The costal protuberances vary from small, granular spines in some species, to short and club-shaped or long and thorn-like projections in others. Large costal spines may have either a smooth surface, or be covered by granulations.

The lower-order septa are usually solid, but in some species they are perforated at the margin; those of higher orders are almost always perforated. There may occur relatively large holes in the septa, which then are called fenestrate. One species can be recognized by the consistent presence of tentacular lobes on the septa. These tentacle-supporting projections are situated just above the inner edge of each septum. In other species tentacular lobes occur only occasionally.

The structure of the corallum wall is also important for the classification. In several species, this wall remains solid, while in others perforations develop between the costae. In some species the corallum wall is completely covered by small granulations, whereas their distribution is limited to the costal projections in others.

FUNGIID LIFE-CYCLES

The life-cycle of a fungiid coral species consists of sexual and asexual reproduction phases (fig. 42). The asexual reproduction is always the result of regeneration; it may occur in each species, but not necessarily in each individual coral. The following generalized scenario of the fungiid life-cycle is composed of phases which were observed in different species. Basically there are no interspecific differences in the life-cycles, otherwise than a few mentioned in the text below; the species may differ only in the timing of the successive phases.

The development of larvae, in the sexual part of the life-cycle, has been studied in detail by Abe (1937) and by Krupp (1983). Their observations suggest that mushroom coral species are either hermaphroditic and viviparous, or gonochoristic and oviparous. As planula larvae (fig. 42a) the animals become infected by zooxanthellae (Krupp, 1983) and after a planktonic period, which may last up to two weeks (Abe, 1937), they seek a suitable hard substratum for settlement.

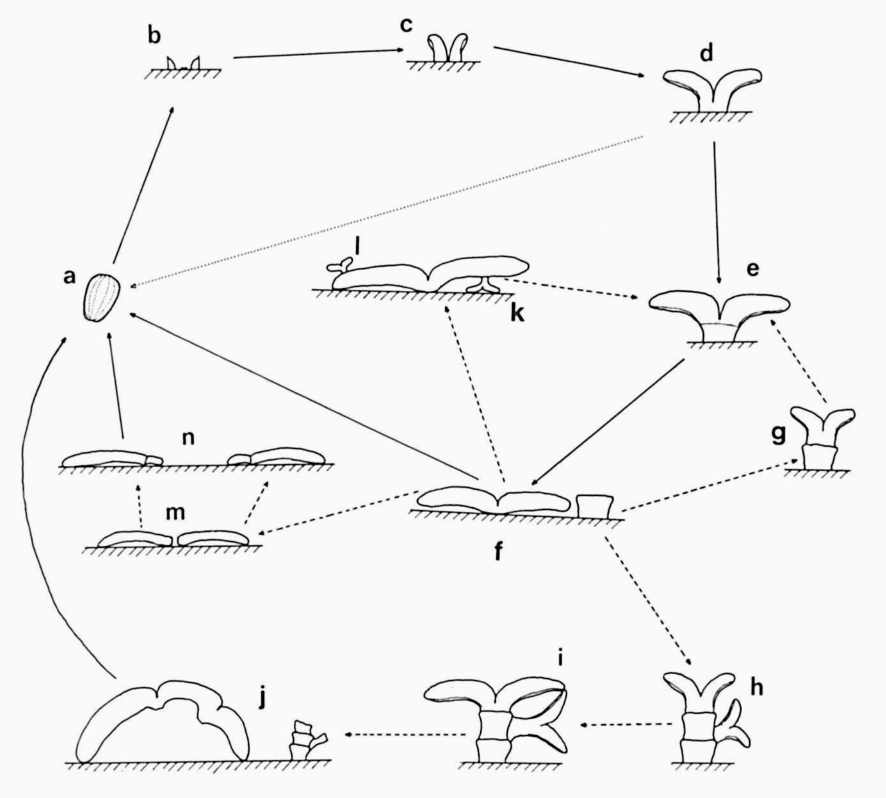


Fig. 42. Scheme of fungiid life cycles. Solid arrows indicate phases in the sexual reproduction; broken arrows mark possible stages of asexual reproduction; the dotted arrow symbolizes a short-cut: (a) planula larva; (b-d) settlement and development of an early anthocaulus; (e) advanced anthocaulus developing a fissure between the disc and the stalk; (f) mature anthocyathus, now separated from its stalk and able to produce planulae; (g) new anthocaulus regenerated from a previously empty stalk; (h) regeneration of several anthocauli from an empty stalk; (i-j) fusion of anthocauli and the development of a polystomatous polyp in an otherwise monostomatous animal; (k) new anthocaulus generated at the aboral surface of a mature animal;(l) new anthocaulus developed at a diseased, damaged part of the coral, either the upper surface or the periphery; (m-n) regeneration of an anthocyathus after fragmentation. In the scheme a usually monostomatous species has been used as an example. Most polystomatous species have the same life cycles. The sedentary species of *Cantharellus*, *Lithophyllon* and *Podabacia* remain in anthocaulus stage (d) when reaching fertility and consequently short-cut several stages in the life cycle (e-f, g, l-n). Two or more individuals of these species may undergo coalescence (h-i). Occasionally, sedentary species may break off the substratum by accident, with the stalk remaining attached to the animal. In this way the usually attached polyps become free-living. (Partly after Wells, 1966).

During the early anthocaulus-stage, which is the beginning of the sessile phase (fig. 42b), the calyx of the corallum develops as a short cylinder, with six septa of the first order inside (Boschma, 1923a). Septa of higher orders start to develop inside the corallum wall and corresponding costae on the outside (fig.

42c). During the advanced anthocaulus-stage the corallum wall grows towards the substratum, until it is almost parallel to it (fig. 42d). At the end of the anthocaulus-stage (also called anthoblast), the animal has a mushroom-like appearance. Animals of some genera (*Cantharellus*, *Lithophyllon* and *Podabacia*) remain in this stage and if they reach maturity, they may produce eggs and sperm; after fertilization new planulae may develop.

In the other genera the animals become free-living; they reach the anthocyathus-stage. In the transitional phase between anthocaulus and anthocyathus, the calcium carbonate becomes dissolved in a narrow, transverse zone at the base, which becomes the plane of detachment (fig. 42e). In this plane the lime dissolves gradually from the centre toward the outside: i.e. the columella and the septa first, then the corallum wall and the costae (Yamashiro & Yamazato, 1987a; 1987b; see also fig. 173). If the corallum breaks, the larger part, the disc, becomes separated from the base, the stalk, which remains attached to the substratum (fig. 42f). In some species a detachment scar remains visible at the aboral corallum side, but it heals completely in the majority of free-living species. After maturation, the reproductive organs in the free-living disc develop gametes, thus making the sexual part of the cycle complete.

From the empty stalk, new polyps may regenerate (Lister, 1888; Bourne, 1893), which eventually also break off, leaving the stalk empty and ready to regenerate again (fig. 42g). When the process is repeated, the stalk grows in height, each new disc that is formed being detached at a level above that from which its stalk springs.

Occasionally, two or more anthocauli grow from one stalk at the same time (fig. 42h). Because there is not much space on the single stalk, the genotypically identical discs may grow against each other and fuse (fig. 42i). When the fused discs are loosed from the stalk, a free-living coral with two or more stomata results (fig. 42j). This fusion process has been described by Boschma (1922; 1923b) as the coalescence of buds.

Some animals grow buds at the aboral side of their skeleton (fig. 42k), usually near the margin, but sometimes at the detachment scar. If the soft tissue at the oral side of the polyp has been damaged, the animal may regenerate new buds at the upper side or near the margin (fig. 42l). This may also occur when the mouth cannot receive food anymore (Boschma, 1922; 1923a; 1923b; 1924). All young buds may develop into free-living individuals.

Another way in which asexual reproduction can take place, is by means of fragmentation. In some species this process is regulated by the animals themselves, i.e. by autotomy (Yamashiro et al., 1989: fig. 3). Divisions of the discs occur after slits have grown in the corallum wall which make the animals brittle. This auto-fragmentation process resembles the detachment mechanism by dissolving the calcium carbonate, but it is directed in the opposite way, i.e. from the corallum periphery towards the centre. The loose fragments (fig. 42m) usually regenerate into new individuals (fig. 42n), which subsequently may split again. Whether these individuals are able to develop mature gonads producing gametes, is not clear.

Fragmentation may also occur accidentally, especially in thin corals. When the fragments survive, each one may regenerate into a new individual. If the original coral was monostomatous, each of the fragments without the original mouth may grow a new one. In fragile polystomatous corals, the large centrally located primary mouth will after fragmentation remain in only one of the many fragments; all fragments will continue to produce the smaller secondary stomata.

IDENTIFICATION

A key is provided to facilitate the identification of the Fungiidae. Due to the variety in shape, a species may key out more than once. For instance, when a coral breaks, its regenerating fragments differ in shape from the original specimen. In some species a character may appear very uniform, whereas in others it may be much more variable. As a consequence, the specimens of some species are more easily identifiable than those of others. The identity of the specimens has to be checked with the help of the elaborate description and the illustrations.

Most characters used in this key concern the skeleton. Sometimes a species is easier to recognize by means of characters seen in the living animal, such as a very specific coloration of the tentacles. Therefore these characters are mentioned as well.

Key to the Fungiidae

1\. Corals free-living in adult stage 2
– Corals remain sedentary 38
2\. Each coral with usually one, centrally located mouth 3
– Each coral with several mouths 28
3\. Corallum wall solid 4
– Corallum wall perforate 19
4\. Septal dentations fine (density > 10 / cm) 5

– Septal dentations coarse (density ≤ 10 / cm) 18

5\. Granulations on septal fringe predominantly arranged in rows, perpendicular to septal margin 6

– Granulations on septal fringe arranged in rows or ridges, parallel to septal margin, possibly in zigzag patterns 16

6\. Costae fine; adjacent ones (almost) equal 7

– Lower order costae distinctly larger than other ones 14

7\. Septa densely packed and (almost) equal in height 8

– Septa loosely packed; septa of lower orders more exsert than others 9

8\. Central fossa short (length $< 1/10$ diameter of corallum); septa almost equal in thickness and very tightly packed, with almost no space in between them .... *Fungia (Cycloseris) sinensis* (p. 31)

– Length of fossa $\geq 1/10$ diameter of corallum; septa of lower orders thicker than adjacent septa; septa compact with distinct space in between them .... *Fungia (Cycloseris) distorta* (p. 37)

9\. Outline of corallum oval (in unbroken specimens) 10

– Outline of corallum (irregularly) round (in complete specimens) ... 11

10\. Coralla thick; septa of succeeding orders slightly alternating in height .... *Fungia (Cycloseris) cyclolites* (p. 41)

– Coralla convex around fossa (humped); lower order septa higher than other ones .... *Fungia (Cycloseris) somervillei* (p. 50)

11\. Coralla with undulating or folded margin 12

– Coralla with regular, smooth periphery (in unbroken specimens) 13

12\. Coralla thin; length of fossa $< 1/10$ diameter of corallum; margin of adult specimens undulating; outline of juvenile specimens hexagonal; septa of first two orders higher than others .... *Fungia (Cycloseris) hexagonalis* (p. 59)

– Coralla thick; corallum margin irregularly folded; septa of low orders thicker and higher than adjacent septa of higher orders .... *Fungia (Cycloseris) curvata* (p. 47)

13\. Coralla and septa thin; adjacent costae slightly alternating in height .... *Fungia (Cycloseris) fragilis* (p. 54)

– Coralla moderately thick; first order septa thicker than others; costae not distinctly alternating in height .... *Fungia (Cycloseris) costulata* (p. 64)

14\. Maximum length of corallum > 10 cm; septa thin and loosely packed; density of septal dentations < 25 / cm; spines on lower order costae sharp, those on higher order costae rudimentary (density < 22 / cm); tentacles long (up to 2 cm) with violet tips . *Fungia (Danafungia) fralinae* (p. 97)

– Length of corallum ≤ 10 cm; septa densely packed; number of septal dentations > 30 / cm; costal spines granular (density > 20 / cm); tentacles short (< 1.5 cm) and without violet tips 15

15\. Coralla thick and slightly arched; lower order costae thick and irregularly ornamented .... *Fungia (Cycloseris) tenuis* (p. 70)

– Coralla flat and thin; lower order costae thin and finely ornamented; sides of costae covered by rows of granulations, perpendicular to costal margin .... *Fungia (Cycloseris) vaughani* (p. 74)

16\. Costae (almost) equal in size; septa thin and high; corallum thick and arched .... *Fungia (Verrillofungia) scabra* (p. 83)

– Lower order costae distinctly larger than others; septa moderately thick and not high 17

17\. Coralla round and flat; density of septal dentations ≥ 30 / cm .... *Fungia (Verrillofungia) spinifer* (p. 79)

– Coralla slightly concave; outline slightly oval; density of septal dentations < 33 / cm .... *Fungia (Verrillofungia) concinna* (p. 87)

18\. Septal dentations lobate; costae equal in size; detachment scar distinct; density of costal spines ≥ 20 / cm; tentacles long (> 2.5 cm) with usually white acrospheres .... *Heliofungia actiniformis* (p. 149)

– Septal dentations angular; costae very unequal in size; detachment scar not distinct in adult specimens; number of costal spines < 20 / cm; tentacles short .... *Fungia (Danafungia) horrida* (p. 101)

19\. Outline of corallum round 20

– Outline of corallum varies from oval to elongate 23

20\. Density of septal dentations ≥ 30 / cm .... *Fungia (Wellsofungia) granulosa* (p. 125)

– Density of septal dentations ≤ 25 / cm 21

21\. Costal spines club-shaped and granulate; granulations on septal sides arranged in zigzagged ridges, parallel to septal margin .... *Fungia (Verrillofungia) repanda* (p. 92)

– Costal spines acute with small granulations concentrated at the tip; granulations on septal fringe arranged in rows perpendicular to septal margin or not in a distinct pattern 22

22\. Septa are usually densely packed; septal dentations are regularly angular; granulations on septal sides form rows perpendicular to septal margin; costae equal to subequal in size and ornamentation .... *Fungia (Fungia) fungites* (p. 116)

– Septa loosely arranged; septal dentations irregularly angular and unequal in size; granulations on septal fringe not distinctly patterned; costae of higher orders relatively small .. *Fungia (Danafungia) scruposa* (p. 108)

23\. Density of septal dentations > 12 / cm; costal spines echinose; length of corallum ≤ 25 cm 24

– Density of septal dentations ≤ 12 / cm; costal spines granulate or blunt; maximum length of corallum > 25 cm 27

24. Upper surface of corallum convex around fossa (humped); septal dentations granular; granulations on septal fringe irregularly arranged ... 25

– Upper surface of corallum not convex around fossa; septal dentations angular; granulations on septal fringe arranged in rows, either perpendicular or parallel to septal margin, or zigzagged 26

25. Density of costal spines > 40 / cm; costae are unequally sized; septa of lower orders may be perforate at septal fringe .... *Fungia (Pleuractis) moluccensis* (p. 135)

– Number of costal spines < 40 / cm; costae (almost) equal in size; septa of lower orders solid .... *Fungia (Pleuractis) gravis* (p. 140)

26. Tentacular lobes present; density of septal dentations ≥ 30 / cm; granulations on septal fringe arranged in rows perpendicular to septal margin .... *Fungia (Lobactis) scutaria* (p. 130)

– Tentacular lobes absent; density of septal dentations < 30 / cm; granulations on septal fringe arranged in distinct zigzagged rows, parallel to septal margin .... *Fungia (Pleuractis) paumotensis* (p. 143)

27. Corallum outline varies from oval to elongate; septa are loosely arranged; septal dentations long and tapering towards their tips; tentacles white .... *Ctenactis albitentaculata* (p. 154)

– Corallum outline elongate; septa densely packed; septal dentations short and lobate; tentacles colourless .... *Ctenactis echinata* (p. 158)

28. Coralla elongate; stomata in distinct row over central axis 29

– Outline of coralla varies from round to oval; stomata distributed over whole upper surface 33

29. Stomata in central furrow; septal dentations coarse 30

– Largest stomata arranged in central furrow, smaller ones alongside it; septal dentations small 31

30. Number of stomata up to 3; septal dentations slightly lobate; septa not densely arranged .... *Ctenactis echinata* (p. 158)

– Number of stomata up to 11; septal dentations coarse and angular; septa densely packed .... *Ctenactis crassa* (p. 163)

31. Stomata alongside central axis unevenly arranged; length interstomatous septa > 1 cm; septa oriented parallel to each other; granulations on septal fringe arranged in rows, perpendicular to septal margins .... *Herpolitha limax* (p. 168)

– Stomata alongside central furrow almost evenly distributed; length interstomatous septa < 1 cm; granulations on septal fringe irregularly arranged 32

32. Coralla thin and fragile; septa remote from central furrow oriented parallel to each other; central axis may be absent after fragmentation .... *Polyphyllia novaehiberniae* (p. 177)
– Coralla thick; most septa diverging from stomata; central furrow usually present .... *Polyphyllia talpina* (p. 181)
33. Outline of coralla oval 34
– Outline of coralla round 36
34. Primary, central stoma distinct in complete specimens (usually absent in regenerated fragments); secondary stomata not distinct; density of septal dentations < 8 / cm .... *Zoopilus echinatus* (p. 195)
– All stomata distinct; density of septal dentations ⩾ 8 / cm 35
35. Secondary stomata concentrated around larger central, primary stoma; septa unequal in height; septal dentations irregularly shaped, long and sharp .... *Sandalolitha dentata* (p. 187)
– Stomata almost evenly distributed; septa nearly equal in height; septal dentations blunt and lobate .... *Sandalolitha robusta* (p. 191)
36. Density of septal dentations ⩾ 15 / cm; length interstomatous septa varying little .... *Polyphyllia novaehiberniae* (p. 177)
– Density of septal dentations < 15 / cm; interstomatous septa of unequal length 37
37. Coralla usually thick; all stomata distinct; septal dentations sharp .... *Halomitra pileus* (p. 200)
– Coralla extremely thin and fragile; secondary stomata less distinct than primary one; septal dentations club-shaped *Halomitra clavator* (p. 205)
38. Each corallum with one, centrally located mouth 39
– Each corallum with several mouths 40
39. Outline of corallum varies from round to slightly oval; corallum margin without folds; septa thick; septal dentations small .... *Cantharellus doederleini* (p. 209)
– Corallum margin round with folds; septa thin; septal margins frayed or with small dentations .... *Cantharellus noumeae* (p. 212)
40. Corallum wall perforate .... *Podabacia crustacea* (p. 226)
– Corallum wall solid 41
41. Corallum foliaceous; maximum diameter > 10 cm .... *Lithophyllon undulatum* (p. 216)
– Corallum encrusting; maximum diameter < 10 cm .... *Lithophyllon mokai* (p. 222)

SYSTEMATIC ACCOUNT

In the systematic part of this revision the genera and the species are arranged according to the principle of more or less subjectively determined similarity to facilitate the comparison of their descriptions and illustrations for identification.

In the enumerations of the examined material, per species first the type specimens are treated in chronological order. The additional material is arranged geographically according to locality, in principle from west to east and from north to south. For each locality the specimens are arranged in alphabetical order according to museum or collection name. If specimens in a collection are catalogued, the order of numbering is followed. If a catalogue number represents more than one specimen, the number of specimens is given between brackets. Some catalogue numbers are shortened by omitting for exemple the prefix "Coel." or the code letter "C", which only indicate that the corals can be found in the coelenterate collection.

The localities of examined specimens are indicated by dots on geographical distribution maps. Localities which are only known from well illustrated specimens are indicated by asterisks, whereas those only known from published records are not indicated.

Order **SCLERACTINIA** Bourne, 1900
Suborder **FUNGIINA** Verrill, 1856
Superfamily **FUNGIICAE** Dana, 1846
Family **FUNGIIDAE** Dana, 1846

Characters. — The animals are mono- or polystomatous (i.e. they have either one mouth or more). Most species have a free-living phase in their life-cycle; a minority remains sedentary. The corallum wall is either solid (imperforate) or perforated. The septa of highest orders are perforated. Adjacent septa are connected by compound synapticulae. The septal and costal ornamentations vary considerately in size and form. At generic and subgeneric level they are usually less variable, thus more diagnostic in shape.

Remarks. — The geographical distribution of the family is limited to the tropical waters of the Indo-Pacific, where the species live in shallow water, usually in the vicinity of coral reefs.

Fungia Lamarck, 1801

Type species: *Fungia agariciformis* Lamarck, 1801 [= *Fungia fungites* (Linnaeus, 1758)]. Designated by Leuckart, 1841.

Fungia Lamarck, 1801: 369; 1815, 1816: 234-235; Oken, 1815: 74; Eschscholtz, 1825: 746; Blainville, 1830: 302-303; Ehrenberg, 1834: 48; Lamarck, 1836: 369-370; Leuckart, 1841: 42; Dana, 1846: 287-289; Milne Edwards & Haime, 1849: 71; 1850: xlvi; 1851: 76; 1860: 5-7; Klunzinger, 1879: 59-60; Duncan, 1885: 141-142; Quelch, 1886: 130-132; Ortmann, 1889: 518-519; Döderlein, 1902: 11-57; Gardiner, 1905: 938; Vaughan, 1907a: 110-128; 1907b: 380-383; Gardiner, 1909: 263-268; Vaughan, 1918: 127; Matthai, 1924: 38; Boschma, 1925: 186-188; Montanaro, 1932: 176; Vaughan & Wells, 1943: 140; Wells, 1956: 338-389; 1966: 237; Veron & Pichon, 1979: 128-129; Ditlev, 1980: 54-55; Nemenzo, 1981: 186; Scheer & Pillai, 1983: 78; Nemenzo, 1986: 142; Veron, 1986b: 330-334; Chevalier & Beauvais, 1987: 706.
Fongia Blainville, 1820: 215-216.

Characters. — Adult animals are monostomatous and free-living. They have either a solid or a perforated corallum wall. The outline of unbroken specimens varies from circular to oval; regenerating fragments may be irregularly formed. The septa and costae vary from equal to unequal and their ornamentations from fine to coarse. The tentacles remain relatively small.

Remarks. — *Cycloseris* and *Diaseris*, which are either considered synonymous (see e.g. Vaughan & Wells, 1943; Wells, 1956; 1966) or separate genera (see e.g. Veron & Pichon, 1979), are re-united under the senior name *Cycloseris* as only one of the seven subgenera of *Fungia*. Following Veron & Pichon (1979), *Heliofungia* is given generic status. *Ctenactis*, up to now considered by many authors a subgenus of *Fungia* (following Wells, 1966), in the present study is referred to as a separate genus, with *Herpetoglossa* as a junior synonym.

Most of the least evolved character states found within the Fungiidae can be observed in *Fungia*, particularly in the subgenus *F. (Cycloseris)*. Wells (1966) regarded *Cycloseris* and *Fungia* as distinct genera on paleontological and structural grounds. According to him *Cycloseris*, with an older paleontological record, is the predecessor of *Fungia* because its species have (1) smaller dimensions, (2) a solid wall, (3) septa with minute dentations reflecting their simpler trabecular and perforate structure and (4) fine, lightly granulated or dentate costae. As a result of the present revision, in which the species have been studied in more detail, it has become more difficult to separate the two taxa from each other. The characters mentioned above are not exclusively shown by *Cycloseris*.

The subgenera of *Fungia* can be distinguished from each other only by different combinations of characters concerning: (1) the corallum outline, which is either circular or oval-elongate, (2) the size and form of the septal dentations and the costal spines, (3) the granulation patterns on the septal sides, and (4) high order costae almost as large as the other ones or distinctly reduced in size.

Fungia is the most widespread genus of the family. In the fossil record it is the oldest one known (table 2). In total 23 species are recognized. None of them are new to science, although the last one was described only recently (Claereboudt & Hoeksema, 1987). One species has to be renamed because of homonymy.

Subgenus **Cycloseris** Milne Edwards & Haime, 1849

Type species: *Fungia cyclolites* Lamarck, 1815. By monotypy.

Cycloseris Milne Edwards & Haime, 1849: 72; 1850: xlix; 1851: 111-112; 1860: 49; Tenison-Woods, 1878: 328; Duncan, 1885: 149-150; Quelch, 1886: 119-120; Gardiner, 1899: 171; 1905: 944; Vaughan & Wells, 1943: 139; Wells, 1956: 388; 1966: 235-236; Veron & Pichon, 1979: 107-108; Ditlev, 1980: 54; Nemenzo, 1981: 182; Scheer & Pillai, 1983: 74; Nemenzo, 1986: 140; Pillai, 1986: 153; Veron, 1986b: 320-321; Chevalier & Beauvais, 1987: 710.

Diaseris Milne Edwards & Haime, 1849: 72; 1850: xlix; 1851: 117; 1860: 54-55; Duncan, 1885: 150; Gardiner, 1905: 945; Veron & Pichon, 1979: 119, 121; Veron, 1986b: 326-327. (Type species: *Fungia distorta* Michelin, 1842. By monotypy.)

Characters. — Adult animals are free-living; their outline varies from circular to oval. In almost all species the coralla may fracture repeatedly into regenerating wedge-shaped pieces. In general the animals remain monostomatous but after fragmentation, or if animals grow relatively large, they may produce extra stomata. The corallum wall is solid. The septal margins are ornamented by fine, sharp dentations. The costae are covered by fine spiny protuberances which, when they grow large, may become granular in appearance. The animals are not known to exceed a diameter of 15 cm. The tentacles remain very small, compared to those in other subgenera.

Remarks. — The species group was at first recognized by Döderlein (1901: 354; 1902: 58) who called it the " *Patella* -Gruppe". *Cycloseris* and *Diaseris* cannot be considered separate taxa. The fragmented *Diaseris* -form of each species corresponds in its septo-costal form and arrangement exactly with that of the unbroken *Cycloseris* -form. This relationship was recognized by taxonomists like Döderlein (1902), Gardiner (1909) and Boschma (1925), but not by e.g. Veron & Pichon (1979). The latter authors consider *Diaseris* distinct from *Cycloseris* referring to only the fragmentation.

In this study fragmentation is regarded as a process which may occur during the free-living phase in the life cycle of most *Cycloseris* species. It might be related to a lack of water circulation or the presence of fine sediment (see Hoeksema & Moka, 1989). During fragmentation fissures appear in the corallum wall from the periphery towards the centre, but not necessarily along the primary septa in contrast to what is stated by Vaughan & Wells (1943). After fragmentation only wedge-shaped, regenerating fragments remain (Yamashiro et al., 1989). The slits in the corallum wall and the lobate corallum margin only rarely occur in species belonging to other subgenera in *Fungia*. As a consequence of the interruptions in the corallum margin, the outline becomes lobate.

Diaseris cannot be considered a separate taxon, because each of its supposed species would resemble a *Cycloseris* species, except that the latter would lack the ability of auto-fragmentation. Acceptance of *Diaseris* as a genus would imply that the fragmented forms of several *Cycloseris* species have to be described as new *Diaseris* species.

Among the subgenera of *Fungia*, *F. (Cycloseris)* has the most widespread distribution. Its boundaries almost completely determine the range of *Fungia*. In total ten species are distinguished, one of which is renamed because of homonymy.

Fungia (Cycloseris) sinensis (Milne Edwards & Haime, 1851)
(figs. 1, 43-54, 611, 616)

Cycloseris sinensis Milne Edwards & Haime, 1851: 112-113 ("les mers de la Chine"); 1860: 51-52; Tenison-Woods, 1878: 329; 1879: 19-20; Quelch, 1886: 122; Bassett-Smith, 1890: 446; Döderlein, 1902: 62; Pillai, 1972: 202; Pillai, 1983: 85; Veron & Kelley, 1988: 31, figs. 9c-d. Not: Gardiner, 1905; Nemenzo, 1971; 1981; 1986; Veron & Marsh, 1988.

Diaseris freycineti Milne Edwards & Haime, 1851: 118 ("patrie inconnue"); 1860: 55; Semper, 1872: 269, pl. 21 fig. 1; Alcock, 1893: 147-148; Döderlein, 1902: 64. (New synonymy).

Diaseris distorta — Alcock, 1893: 147; Gardiner, 1905: 945; Harrison & Poole, 1909a: 901-902, pl. 85 figs. 2b, 3a; 1909b: 914; Veron & Pichon, 1979: 121-123, figs. 194-196; Veron, 1986b: 326-327 (partim); Veron & Marsh, 1988: 82 (partim).

Diaseris mortoni Tenison-Woods, 1880: 460-461 (partim).

Cycloseris freycineti — Quelch, 1886: 121-122; Bassett-Smith, 1890: 447; Döderlein, 1902: 62.

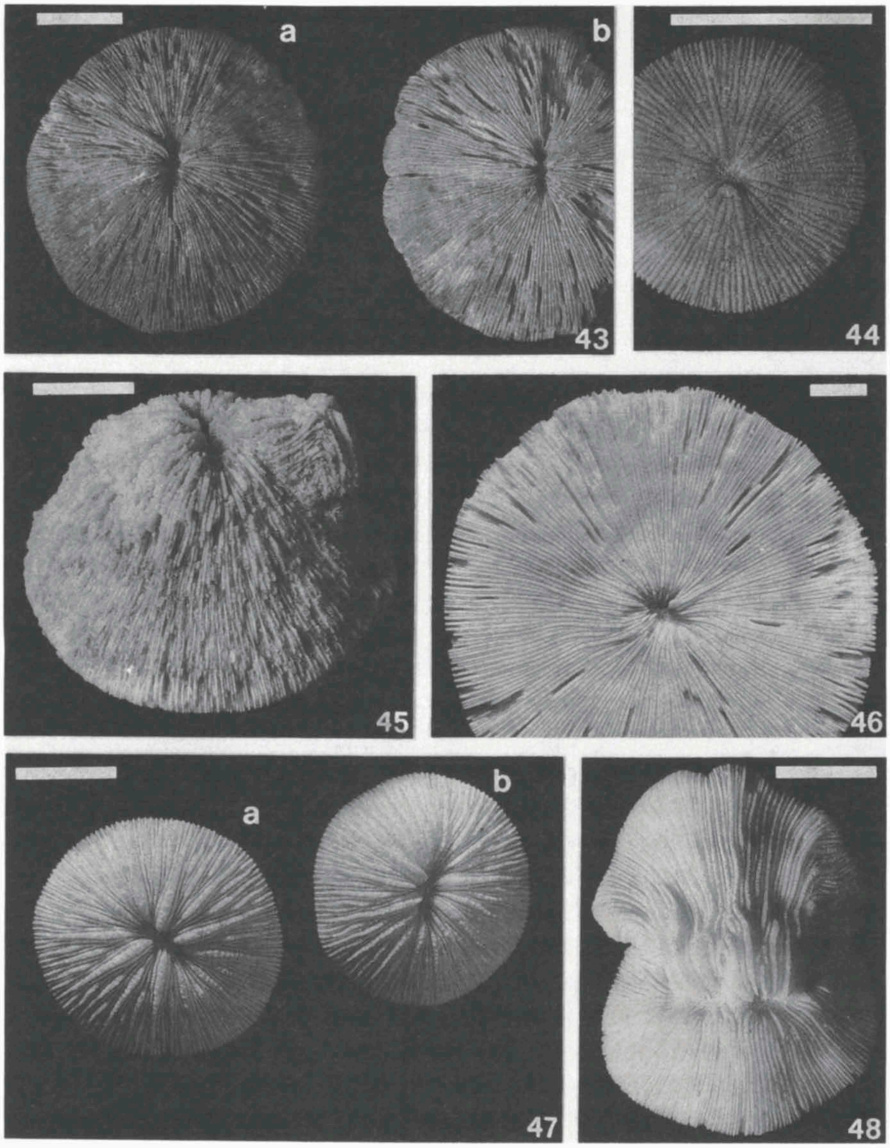
? *Cycloseris discus* Quelch, 1886: 122, pl. 6 figs. 3-3a ("Santa Cruz Major Island, off Samboangan, Philippines, 10 fathoms"); Döderlein, 1902: 63.
Not *Fungia discus* Dana, 1846.

Cycloseris mycoides Alcock, 1893: 147, pl. 5 fig. 10 (Andaman Sea); Döderlein, 1902: 63. (New synonymy).

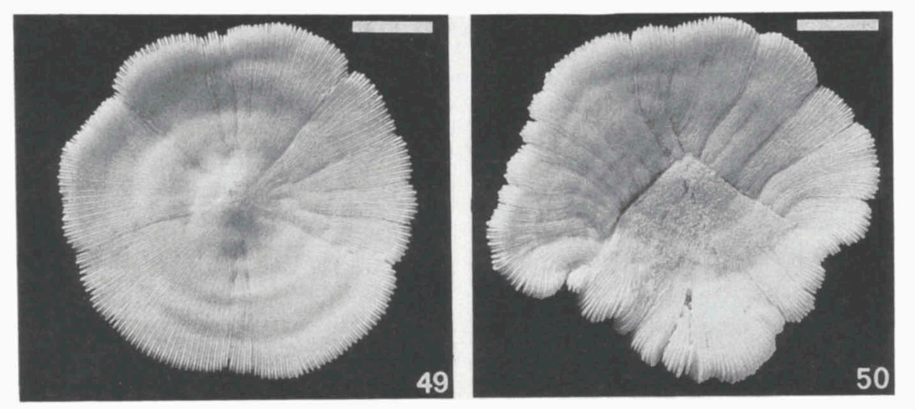
Cycloseris distorta — Quelch, 1886: 120; Bassett-Smith, 1890: 447; Ortmann, 1892: 653; Wells, 1954: 447 (partim); Pillai, 1972: 203; Pillai & Scheer, 1976: 43; Ditlev, 1976: 6; Rosen, 1979: 11; Pillai, 1983: 85.

Fungia patella — Döderlein, 1902: 65-73 (partim; including var. *filigrana* Döderlein, 1902 ["Ralum 59-73 m Tiefe"]), pl. 1 figs. g, o, pl. 2 figs. r-s'.

Fungia distorta — Von Marenzeller, 1907: 88; Gardiner, 1909: 268; Boschma, 1923c: 142-143



Figs. 43-48. Upper surface of corals (anthocyathi) of *Fungia (Cycloseris) sinensis*. Scale bars: 1 cm. Fig. 43. The two syntypes of *Fungia sinensis* (MNHN 234; Chinese Sea); the lobate margin in (b) indicates that autotomy has set in. Fig. 44. A juvenile (RMNH 8282; Sulu Is., Philippines). Fig. 45. An arched, thin coral (RMNH 8284; Sulu Is.). Fig. 46. A large, flat coral (ZMA 1238; Paternoster Is., Indon.). Fig. 47. Arched, thick corals (RMNH 21828; SW Sulawesi, Indon.) with unequally exsert septa similar to those in a syntype of *Cycloseris mycoides*. Fig. 48. A multiple fragmented and regenerated coral with four fossae along the last fracture line; in the original fragment (above) septa are unequally exsert, but in the regenerated part (below) septa are evenly high (RMNH 8281; Kei Is., Indon.).



Figs. 49-50. Aboral surface of two corals (anthocyathi) of *Fungia (Cycloseris) sinensis* (RMNH 21834; SW Sulawesi, Indon.). Scale bars: 1 cm. Fig. 49. A complete coral with a lobate margin and several clefts along which fragmentation may take place; the detachment scar is still visible. Fig. 50. A once broken coral with new clefts in the regenerated part.

(partim), pl.9 fig. 10; 1925: 203-204 (partim); Faustino, 1927: 170, pl. 46 fig. 3; Boschma, 1929: 43.

Fungia fragilis — Vaughan, 1907a: 130-131, pl. 28 figs. 1-1a; Gardiner, 1909: 268; Boschma, 1923c: 10-12 (partim), pl.10 figs. 17-23; Boschma, 1925: 196-198 (partim), pl. 5 figs. 18-19; Vaughan & Wells, 1943: pl. 17 fig. 9.

? *Fungia (Cycloseris) martini* Felix, 1921; 37-38, pl. 141 figs. 3-3a (Miocene, "Britisch Ost-Borneo").

? *Fungia (Cycloseris) subcyclolites* Felix, 1921: 38, pl. 143 figs. 5-5a (Miocene, "Britisch Ost-Borneo").

Fungia sinensis — Faustino, 1927: 171-172; Yabe & Sugiyama, 1935: 396. Not: Gardiner, 1909; Ma, 1937.

Fungia freycineti — Faustino, 1927: 185, pl. 60 fig.3.

Cycloseris fragilis — Wells, 1954: 447; Pillai, 1972: 202.

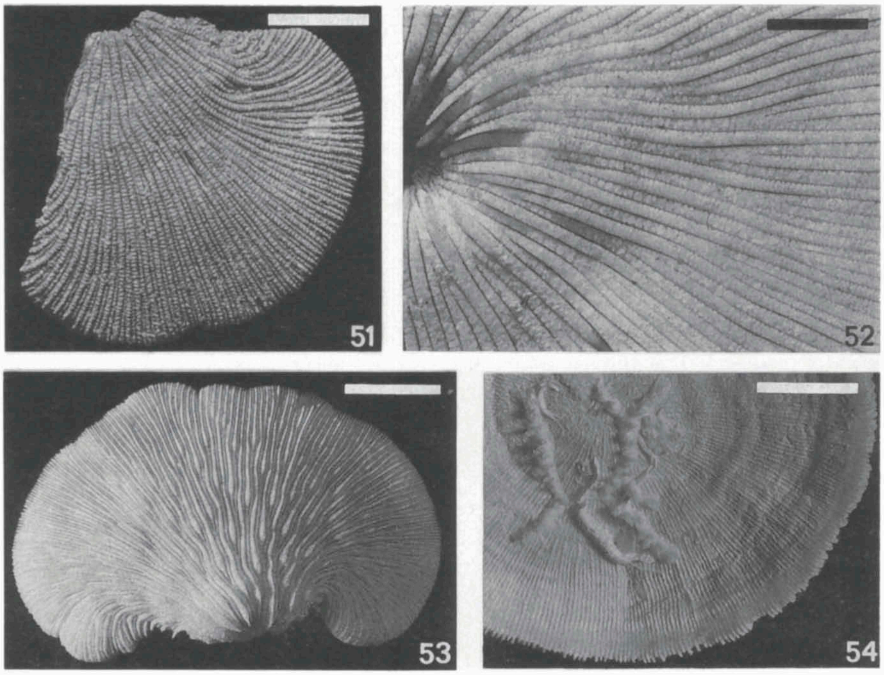
Diaseris fragilis — Cairns, 1984a: 8, pl. 1 fig. C; Veron, 1986b: 327 (partim); Veron & Marsh, 1988: 82 (partim).

Cycloseris patelliformis — Veron & Marsh, 1988: 81 (partim).

Type material examined. — MNHN 234 (2 syntypes of *Cycloseris sinensis*; type loc. CHINA SEA); MNHN 482 (2 syntypes of *Diaseris freycineti*; type loc. unknown); QMB G10018 (3 paralectotypes of *Diaseris mortoni*; Holborn I., Queensland, AUSTRALIA).

Other material. — S MOZAMBIQUE: USNM 77956 (2). MALDIVES: BMNH 1950.1.11.18, MCZ 3579. S CHINA SEA. Macclesfield Bank: BMNH 1889.9.24.39 (2), 1892.10.17.105/131, 1893.9.1.172. Tizard Bank: BMNH 1889.9.24.37-38. JAPAN. Okinawa: USNM 77787. PHILIPPINES. SW Luzon: USNM 77943 (3). E Burias: USNM 77945 (3). Romblon: USNM 78090 (many frags.). NE Leyte: USNM 78092 (3). SW Mindanao: BMNH 1880.11.25.137 (10), USNM 78080 (6 frags.). Sulu Is.: RMNH 8282-8284 (7), 16003 (3), USNM 77944, 77946-77947 (many specimens), 78082-78083 (7), 78085 (many frags.), 235540, 235897, 235943, UZMK (5), ZMA 721b-c (6). INDONESIA. Lombok: ZMA 720a (3). E Kalimantan: RMNH 22100 (3). SW Sulawesi: RMNH 8303 (2), 15235, 20897 (16), 20962 (8), 21702 (2), 21712 (8), 21715-21718 (37), 21812 (32), 21816-21818 (9), 21828 (9), 21830 (2), 21833, 21844 (5), 21848 (6), 21856-21857 (31). Tiger Is.: ZMA 721a/d (4). Postillon Is.: ZMA 720b. Paternoster Is.: ZMA 1238 (2). Tukang Besi Is.: RMNH 22049. N Sumbawa: RMNH 21628 (many frags.), ZMA 721e-f. Komodo: RMNH 21413 (many frags.), 21417 (8), 21586 (2). Ambon: RMNH 8298 (2), ZMA 720c (6), UZMK (4). Banda: RMNH 8299-8300 (7), 8302 (12), UZMK (32). Kei Is.: 8281 (2), 8301, 8304, 8325 (4), 8329 (4), 16004, UZMK (14). AUSTRALIA. Houtman Abrolhos Is.: WAM 161.78 (10), 217.78, 508.81, 199.85, 218.85, 81.88. N Great Barrier Reef: QMB G7659, USNM 78278 (many frags.). C Great Barrier Reef: QMB G3625, G3627, G3629, G3636, G7242, G8062 (8). PAPUA NEW GUINEA. Bismarck Sea: ULB. Gulf of Papua: AIMS 24. PALAU IS.: USNM 78031 (2). NEW CALEDONIA: RMNH 16263, USNM 81086. FIJI: USNM 81087 (3). MARSHALL IS.: USNM 44838. HAWAII IS.: USNM 20837, 77301, 78053 (2), 78116-78160 (many frags.). SOCIETY IS.: RMNH 8985 (4), 15795-15796 (13).

Characters. — The adult animals are free-living. Unfragmented animals are usually monostomatous (solitary), whereas fractured specimens may have supernumerary mouths (fig. 48). The coralla are either discoidal or regenerated, wedge-shaped fragments with a lobed outer margin. In the corallum wall, from the margin towards the centre, there may be fissures along which fragmentation can take place (figs. 49-50). The coralla vary from thin to thick



Figs. 51-54. Close-ups of *Fungia (Cycloseris) sinensis* corals. Fig. 51. Upper surface of a fragment showing details of evenly exsert septa (RMNH 8298; Ambon, Indon.). Scale bar: 0.5 cm. Fig. 52. Septa of the coral in fig. 46. Scale bar: 0.5 cm. Fig. 53. Upper surface of a fragment with tentacular lobes on unequally exsert septa (RMNH 15795; Tahiti, Society Is.). Scale bar: 1 cm. Fig. 54. Costae and epibiontic bryozoans on the aboral surface of a small coral (RMNH 8283; Sulu Is., Philippines). Scale bar: 0.5 cm.

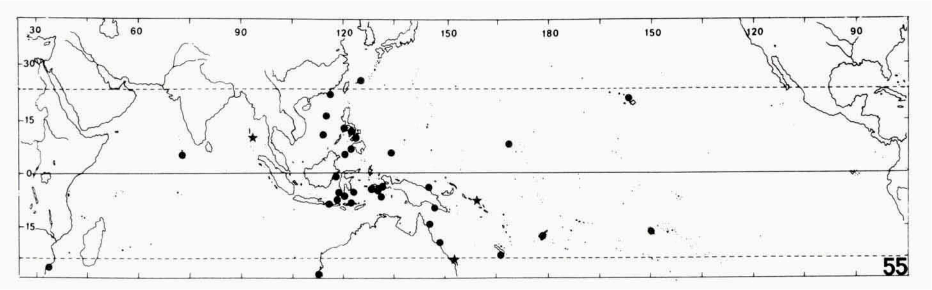


Fig. 55. The range of *Fungia (Cycloseris) sinensis*. Records are from examined material (●) and published illustrations (★).

and from flat to highly arched. The diameter of the specimens varies between 0.5 and 8.5 cm.

The central fossa is very short; its length, measured at the bottom, is only 1/15 to 1/12 of the corallum diameter. All septal edges around the fossa stand almost upright. The columella is formed by radiating rows of simple, tightly packed trabeculae and paliform lobes with the tips distinctly pointing upwards. In broken specimens the regenerating columella often remains incomplete.

The septa are densely packed and usually straight. The septa of lower order cycles are higher and thicker than those of higher orders, although this may not always be clear. In full-grown coralla the lower order septa are solid and those of higher orders perforated; in small specimens all septa are perforated. Tentacular lobes may be present (fig. 53). The septal margins are ornamented with fine and sharp granular dentations. Their number varies from 50 to 90 per cm. The septal sides are densely covered by fine granulations, which are regularly arranged, in rows perpendicular and parallel to the septal margin (fig. 611). Because of the tight septal arrangement, the compound synapticulae connecting the septa laterally cannot easily be detected.

The corallum wall is solid and ungranulated; it may show a detachment scar at the aboral side of specimens in anthocyathus-stage (fig. 49). It may partly be covered by epibionts (fig. 54). The costae are equal in size; they are straight and fine but distinctly discernible from the centre to the corallum margin. All costae are finely ornamented with granular, acute spines (fig. 616). Their number varies from 50 to 100 per cm.

The living animal is usually brown or ochre-like yellow, but non-zooxanthellate specimens coloured red and white have also been observed (fig. 1). In some animals the area around the mouth is bright green. The tentacles are very small.

Geographical distribution (fig. 55). — The species has a distribution which ranges from Mozambique, the Maldive Islands and W Australia (Houtman

Abrolhos Islands) in the Indian Ocean towards southern Japan (Ryukyu Islands), the Hawaiian Islands and the Society Islands in the Pacific Ocean.

Remarks. — The two syntypes of *Cycloseris sinensis* are slightly abraded but still useful as reference for the species; one specimen shows the initial phase of fragmentation (fig. 43). *F. (C.) sinensis* is poorly known. Apparently most authors did not recognize specimens of this species because they were unacquainted with its syntypes and as well with its various forms. The corals, in particular the fragmented specimens, were often misidentified. Although Döderlein (1902: 62) listed *C. sinensis* as one of the *Cycloseris* -forms in his *patella* -group, he did not discuss it in his revision, except that he mentioned to be unsure about its taxonomic position ("... vermag ich kein Urteil abzugeben", p. 65). Since then the name remained more or less neglected.

The syntypes of *Diaseris freycineti* and some of the paralectotypes of *D. mortoni* are similar to the fractured (*Diaseris* -) form of *Fungia sinensis*. The holotype of *Cycloseris discus*, from SW Mindanao (Philippines), is probably lost; it is not in the BMNH with the other types of Quelch. The vaguely illustrated specimen (Quelch, 1886: pl. 6 figs. 3-3a) resembles most closely a coral of *F. sinensis*.

Whether the syntypes of *Cycloseris mycoides*, are still at the ZSI (the former Indian Museum) is not known. They were not mentioned by Matthai (1924), who studied the coral collection of the Indian Museum, and my request for a loan in order to examine them was not answered. The syntype illustrated by Alcock (1893: pl. 5 fig. 10) seems to be thick and has very prominent low order septa, like some of the specimens of *F. sinensis* from SW Sulawesi (see fig. 47). According to Alcock (1893: 147), *C. mycoides* appears to be "near *Cycloseris sinensis*, Edw. & H., and *Cycloseris discus*, Quelch". Döderlein (1902: 63, 65) was not sure about the taxonomic status of this species. According to the descriptions given by Felix (1921), both Miocene species *F. martini* and *F. subcyclolites* are most probably synonymous with *F. sinensis*. Their type specimens are not clearly enough illustrated to determine their synonymy definitely.

The species is most similar to *F. distorta*. Its septa are thicker and more tightly packed than those of the latter species, resulting in broader septal dentations. Diagnostic characters of *F. sinensis* are: (1) the short length of the central fossa compared to the corallum diameter; (2) the simple, erect trabeculae and paliform lobes, which are arranged in a distinct radial pattern; (3) the tight arrangement of the septa; (4) the high degree of septal perforation.

Fungia (Cycloseris) distorta Michelin, 1842

(figs. 56-70)

Fungia distorta Michelin, 1842: 316 (no locality given); 1843: pl. 5 ("Habite....."); Boshoff, 1981: 21. Not: Döderlein, 1902; Von Marenzeller, 1907; Gardiner, 1909; Boschma, 1923c; Matthai, 1924; Boschma, 1925; Faustino, 1927; Boschma, 1929; Umbgrove, 1946b.

Diaseris distorta — Milne Edwards & Haime, 1851: 118; 1860: 55, pl. D12 figs. 4a-4b; Semper, 1872: 269, pl. 21 fig. 2; Pichon, 1974: 176, fig. 1; Wood, 1983: 114; Hamilton & Brakel, 1984: 252; Wallace, 1984: 38, fig. 22.2; Wells, 1984: 205. Not: Alcock, 1893; Gardiner, 1905; Harrison & Poole, 1909a; 1909b; Veron & Pichon, 1979; Ditlev, 1980; Cairns, 1984a; Veron, 1986b; Veron & Marsh, 1988.

Diaseris pulchella Verrill, 1866: 48-49, pl. 1 fig. 3 ("Foukow Bay, Island of Ousima, in 20 fathoms on a hard sandy bottom"); Döderlein, 1902: 64. (New synonymy).

Fungia patella var. *dubia* Döderlein, 1902: 73, pl. 2 figs. t-t', v-v' ("Ralum 24-30 m Tiefe").

Fungia (Cycloseris) fragilis — Gerth, 1925: 34.

Cycloseris distorta — Wells, 1954: 447 (partim). Not: Quelch, 1886; Bassett-Smith, 1890; Ortmann, 1892; Pillai, 1972; Pillai & Scheer, 1976; Ditlev, 1976; Rosen, 1979a; Nemenzo, 1980; Pillai, 1983; Scheer & Pillai, 1983.

Cycloseris mexicana Durham, 1947: 24-25, pl. 9 figs. 4, 7-10 ("Albatross sta. 2824, Gulf of California"); Durham & Barnard, 1952: 52-53, pl. 4 fig. 21; Squires, 1959: 414-415; Durham, 1962: 46; 1966: 125; Brusca, 1980: 64; Wells, 1983: 230, pl. 11 figs. 4, 6. (New synonymy).

Fungia fragilis — Reed, 1971: 38, fig. 4.

Cycloseris patelliformis — Scheer & Pillai, 1974: 35, pl. 17 fig. 4.

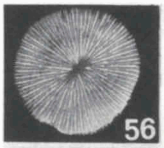
Cycloseris fragilis — Maragos, 1977: 209, 212, figs. 5, 84-85.

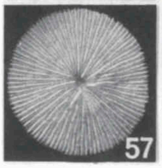
Diaseris fragilis — Veron & Pichon, 1979: 123-125, figs. 197-201; Veron, 1986b: 327 (partim).

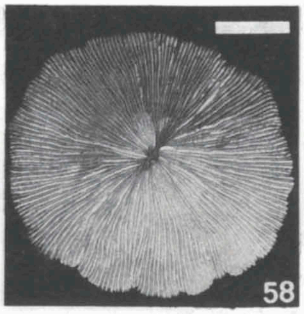
Type material examined. — MNHN 235-236 (3 syntypes of *Fungia distorta*; type loc. unknown); USNM 74695, YPM 768 (2 syntypes of *Diaseris pulchella*; type loc. Ousima I., JAPAN); USNM 547369 (holotype of *Cycloseris mexicana*; type loc. Gulf of California, MEXICO); USNM 547372 (paratype of *C. mexicana*; Agua Verde Bay, Lower California).

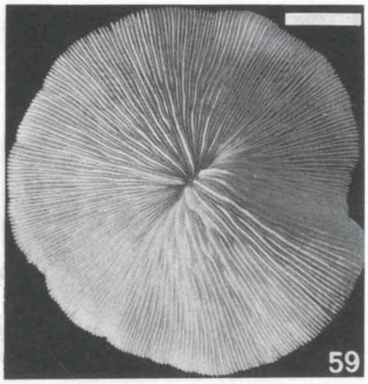
Other material. — ZANZIBAR: USNM 78237 (many frags.). S MOZAMBIQUE: USNM 77723-77724. MALDIVES: MCZ 3579. PHILIPPINES: USNM 77952 (2), 77965-77966 (20), 77987 (many frags.), USNM 78240 (2). Cebu: USNM 77941. Bohol: MCZ 5409 (6), USNM 77987 (many frags.). SW Mindanao: BMNH 1880.11.25.137 (2). Sulu Is.: USNM 77950-77951 (6), 78081 (7), 78084 (4 frags.). INDONESIA. Nias: RGM 125809 (fossil); SW Sulawesi: RMNH 22060. Komodo: RMNH 22044-22045 (23), 22048 (13). N Sumbawa: RMNH 22042-22043 (3). Timor: RMNH 9487. PAPUA NEW GUINEA. Bismarck Sea: ULB. PALAU IS.: USNM 78030 (6). MARSHALL IS.: USNM 44835-44837. HAWAII IS.: USNM 78097-78115 (many frags.). MEXICO. Gulf of California: AMNH (many frags.), USNM 78332 (many frags.), 547369-547372 (47), YPM 8230 (4). COCOS I.: USNM 80084. GALAPAGOS IS.: USNM 46957 (3), 77272 (many frags.).

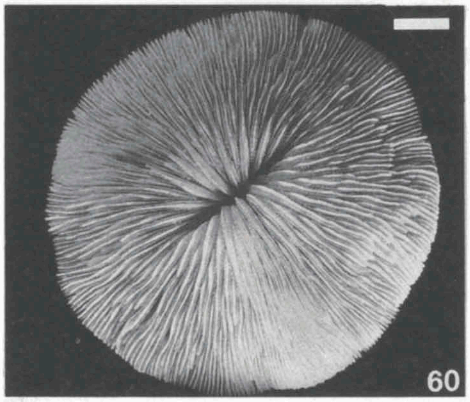
Characters. — Adult animals are free-living. Unbroken specimens are usually monostomatous (solitary), but large specimens may have grown supernumerary stomata by circumstomadaeal budding (figs. 60, 67). The coralla vary in outline from discoidal to slightly oval, or they consist of regenerated wedge-shaped fragments. In fragmenting specimens fissures can be observed in the corallum wall, which start to develop at the corallum margin (fig. 66). Along the fracture lines, where regeneration takes place, the fragmented coralla may grow additional stomata. The coralla vary in thickness; they are

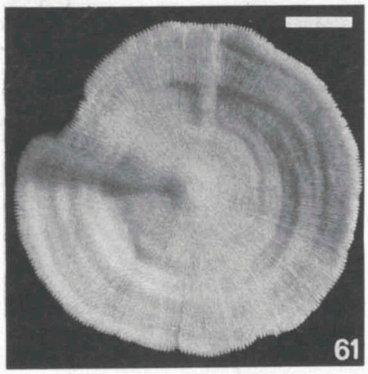


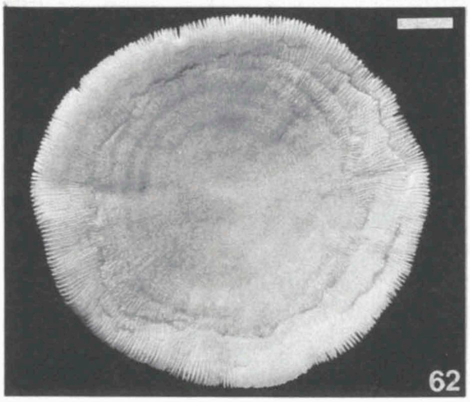


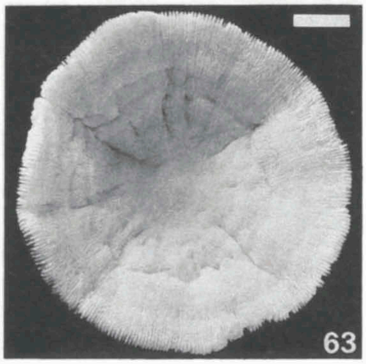




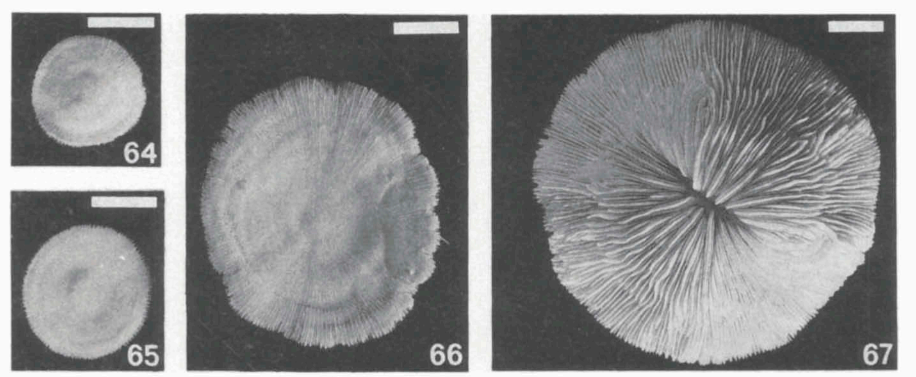








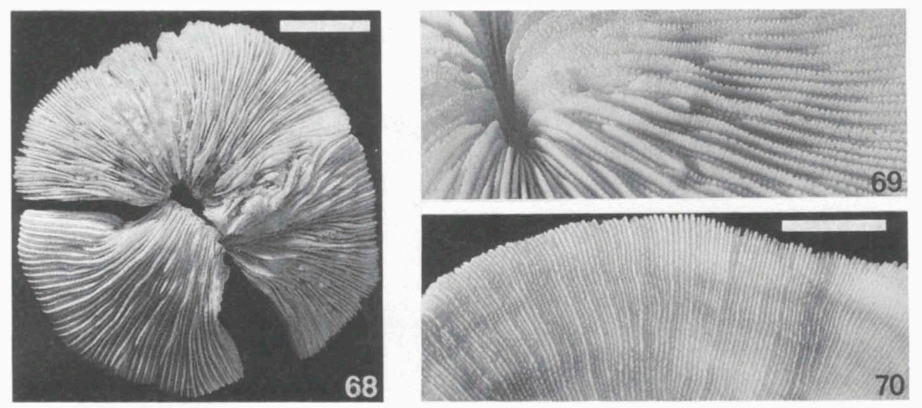
Figs. 56-63. Corals (anthocyathi) of *Fungia (Cycloseris) distorta* from Komodo, Indonesia. Scale bars: 1 cm. Figs. 56-57. Upper surface of juveniles (RMNH 22048); scale bar in fig. 58. Fig. 58. Upper surface of an immature specimen with a lobate margin in the initial phase of fragmentation (RMNH 22048). Fig. 59. Upper surface of a thin coral (RMNH 22048). Fig. 60. Oral surface of a full-grown thick coral with several secondary fossae near the margin (RMNH 22044). Fig. 61. Aboral surface of the coral in fig. 59. Fig. 62. Aboral surface of the coral in fig. 60 showing discontinuous costae. Fig. 63. Aboral surface of the coral in fig. 67 with folds in the corallum wall.



Figs. 64-67. Corals (anthocyathi) of *Fungia (Cycloseris) distorta* from Komodo, Indonesia. Scale bars: 1 cm. Figs. 64-65. Aboral surface of the juvenile corals in figs. 56-57. Fig. 66. Aboral surface of the coral in fig. 58 showing clefts in the lobate margin. Fig. 67. Upper surface of a mature specimen with interrupted septa and several secondary fossae (RMNH 22044).

usually flat but can also be slightly arched. The diameter of the specimens varies between 1.5 and 7.5 cm.

The central fossa is short; at its bottom, its length varies from 1/10 to 1/6 of the corallum diameter. The septal edges at both ends of the fossa are strongly diverging, making its opening appear longer. The edges of the septa at both sides of the mouth stand upright. The columella is formed by a mass of tightly packed trabeculae and paliform lobes with the tips more or less pointing upwards. In broken specimens the columella is usually lost or only partly regenerated.



Figs. 68-70. Corals (anthocyathi) of *Fungia (Cycloseris) distorta*. Fig. 68. Upper surface of a syntype of *Fungia distorta* (MNHN 235, loc. unknown); the incomplete coral has undergone at least two fragmentation cycles. Scale bar: 1 cm. Fig. 69. Septa of the coral in fig. 59. Scale bar: 0.5 cm. Fig. 70. Costae of the coral in fig. 61. Scale bar: 0.5 cm.

The septa are densely packed and usually straight. The septa of lower order cycles are flanked by pairs of higher order septa, which are thinner and less exsert. In full-grown coralla the septa of lower orders are solid and those of higher orders only partly perforated, whereas in small specimens all septa are perforated. The septa lack distinct tentacular lobes. The septal margins are ornamented with fine and sharp granular dentations, which are often fused in pairs. Their number varies from 40 to 60 per cm. The septal sides are densely covered by fine granulations, which are usually arranged in rows perpendicular to the septal margin. Because of the tight septal arrangement, the compound synapticulae (which connect the septa laterally) cannot be easily distinguished.

The corallum wall is solid, ungranulated and usually not covered by epibionts. A detachment scar may be distinctive at the aboral side of small specimens in anthocyathus-stage. In many specimens concentrical growth rings can be seen (figs. 61-63, 64-66). The costae are equal to subequal in size; they are straight and distinct from the centre towards the corallum margin, but may be interrupted in large specimens (figs. 62-63). All costae are finely ornamented with small, acute spines, the number of which varies from 50 to 100 per cm.

The living animal is usually brown; its mouth may have a different colour, such as bright green. The tentacles are small and transparent.

Geographical distribution (fig. 71). — The species is extremely widespread, it occurs from southern Mozambique in the western Indian Ocean towards the Gulf of Panama in the eastern Pacific. Its northernmost locality is southern Japan, at the Ryukyu Islands.

Remarks. — In the literature Michelin's (1842) original description of the species had been overlooked. The plate with two drawn illustrations of a specimen, published in the following year (Michelin, 1843: pl. 5), was usually referred to as being the first publication of *Diaseris distorta*. The drawings are

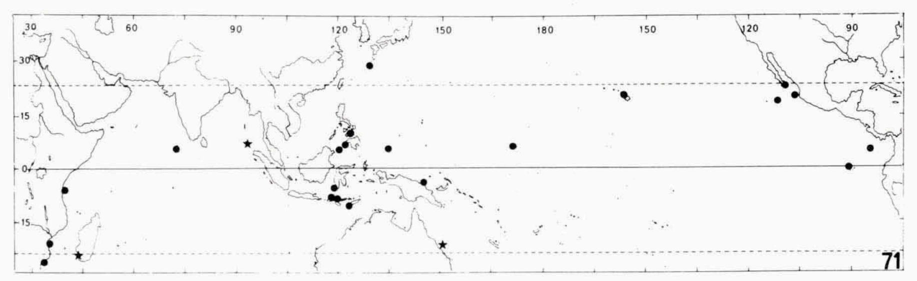


Fig. 71. The range of *Fungia (Cycloseris) distorta*. Records are from examined material (●) and published illustrations (★).

not clear enough to show the species' distinctive characters, and this probably caused much confusion about its identity (compare fig. 68). Several authors used the name *distorta* for coralla belonging to other species (see synonymy). Most of these authors were misguided by the fragmented shape of their specimens, not being aware that several species other than *F. distorta* are also able to break into fragments, and that *F. distorta* is also able to maintain an undistorted shape.

Diaseris pulchella and *Cycloseris mexicana* cannot be distinguished from *F. distorta*; they show the same septal arrangement and similar patterns of dentations and granulations at the septal margins. Their type localities are at the periphery of *F. distorta* 's range, in the North and East Pacific respectively. Döderlein (1902: 64-65), in his revision of *Fungia*, did not give his opinion about the taxonomic position of *Diaseris pulchella*, because he only knew it from the literature.

F. distorta is morphologically intermediate between *F. cyclolites* and *F. sinensis*. Its septa are thinner and less regularly arranged than those of *F. cyclolites*; its mouth is longer and the trabeculae of its columella are less clearly radially arranged than in *F. sinensis*. Like animals of the latter species, corals of *F. distorta* can be confused with juvenile specimens of *F. (Wellsofungia) granulosa*. In some specimens of *F. (Pleuractis) moluccensis* from Komodo, the septal arrangement resembles very much that of *F. distorta*.

Fungia (Cycloseris) cyclolites Lamarck, 1815
(figs. 72-84, 612, 617)

Fungia cyclolites Lamarck, 1815, 1816: 236 ("les mers Australes"); Blainville, 1830: 303; 1834: 337; Lamarck, 1836: 371-372; Leuckart, 1841: 46; Dana, 1846: 289-290; Döderlein, 1902: 61, 77-79, pl. 4 figs. 7-9, pl. 5 figs. 5-5a; Bedot, 1907: 218; Gravier, 1907: 342; Gardiner, 1909: 270-271; Harrison & Poole, 1909b: 914; Folkeson, 1919: 16; Van der Horst, 1921: 59, pl. 2 fig. 5; Matthai, 1924: 40-41; Umbgrove, 1924: 271; Boschma, 1925: 205-210 (partim), pl. 6 figs. 25-48; Umbgrove, 1926: 42; Yonge, 1930: 36-37; Boschma, 1934: 4200-4201, fig. 2; Faustino, 1927: 171, pl. 46 figs. 4-5; Montanaro, 1932: 178-179; Yabe & Sugiyama, 1935: 396; Ma, 1937: 129-130, pl. 56 figs. 2-3; Umbgrove, 1938: 271; Yabe & Sugiyama, 1941: 76-77, pl. 64 figs. 2-4c, pl. 65 figs. 1-3a; Umbgrove, 1946a: 88; Umbgrove, 1946b: 533.

Fongia cyclolites — Blainville, 1820: 216.

Fungia glans Dana, 1846: 290-291, pl. 18 fig. 2 (no locality given); Duncan, 1886: 15; Döderlein, 1902: 61. (New synonymy).

Cycloseris cyclolites — Milne Edwards & Haime, 1851: 112; 1860: 50, pl. D12 fig. 3; Studer, 1877: 644; Tenison-Woods, 1878: 328-329; Quelch, 1886: 121; Bassett-Smith, 1890: 446; Saville-Kent, 1893: 176, chromo pl. 6 figs. 15-16; Gardiner, 1905: 944-945 (partim); Vaughan, 1907b: 260; Gravier, 1911: 61; Vaughan & Wells, 1943: pl. 17 fig. 8; Crossland, 1952: 152; Nemenzo, 1955: 57; Wells, 1955: 11; 1964: 110, pl. 1 figs. 1-3; Boschma, 1959: 272; Eguchi, 1968: C15; Pillai, 1972: 202; Pichon, 1974: 176; Scheer & Pillai, 1974: 35, pl. 17 figs. 1-2; Utinomi, 1975: 71;

Ditlev, 1976: 6; Faure, 1977: 9; Rosen, 1979a: 11; Veron & Pichon, 1979: 108-110, figs. 171-174, 753; Nemenzo, 1981: 183, fig. 199; Pillai, 1983: 85; Scheer & Pillai, 1983: 76-77; Wallace, 1984: 38, fig. 22.1; Johnston, 1986: 159; Nemenzo, 1986: 205, fig. 161; Pillai, 1986: 153-154; Veron, 1986b: 321-322; Veron & Kelley, 1988: 26, 28, fig. 9a; Veron & Marsh, 1988: 81 (partim). Not: Schuhmacher, 1979; Nakamori, 1986.

Diaseris mortoni Tenison-Woods, 1880: 460-461 (partim), pl. 15 figs. 1-2 ("off Holborn Island"); Döderlein, 1902: 64. (New synonymy).

Fungia japonica Vaughan, 1906: 827-828, pl. 67 figs. 1-4 ("Tertiary", "Toshibetzt Valley, Yesso, Japan"). (New synonymy).

Fungia (Cycloseris) cyclolites — Felix, 1915: 32; Gerth, 1921: 422; 1923: 102.

Fungia adrianae Van der Horst, 1921: 60, pl. 2 figs. 6-7 ("Place of origin unknown, probably the indo-australian Archipelago"); Van Soest, 1979: 107. (New synonymy).

Fungia patelliformis Boschma, 1923a: 136-138 (partim), pl. 9 figs. 15-15a.

Fungia borneensis Gerth, 1925: 47 (Miocene, "Fluss Kabasian", Borneo). (New synonymy).

Cycloseris marginata — Scheer & Pillai, 1974: 35-36, pl. 17 fig. 3.

Cycloseris cyclolithes — Ditlev, 1980: 54, fig. 225. (Incorrect spelling).

Cycloseris costulata — Wijsman-Best, Faure & Pichon, 1980: 612, pl. 10 fig. 4.

Cycloseris distorta — Nemenzo, 1980: 288-289, fig. 4.

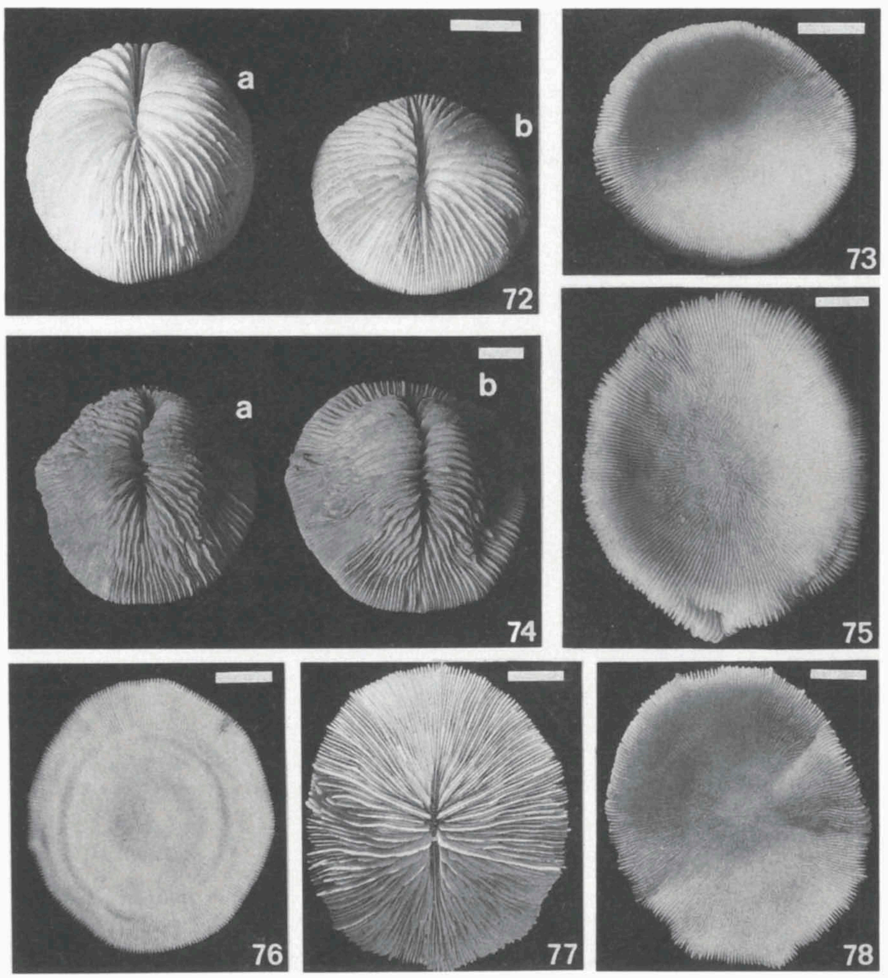
Diaseris distorta — Veron, 1986b: 321, 326 (partim); Veron & Marsh, 1988: 82 (partim).

Diaseris fragilis — Veron & Marsh, 1988: 82 (partim).

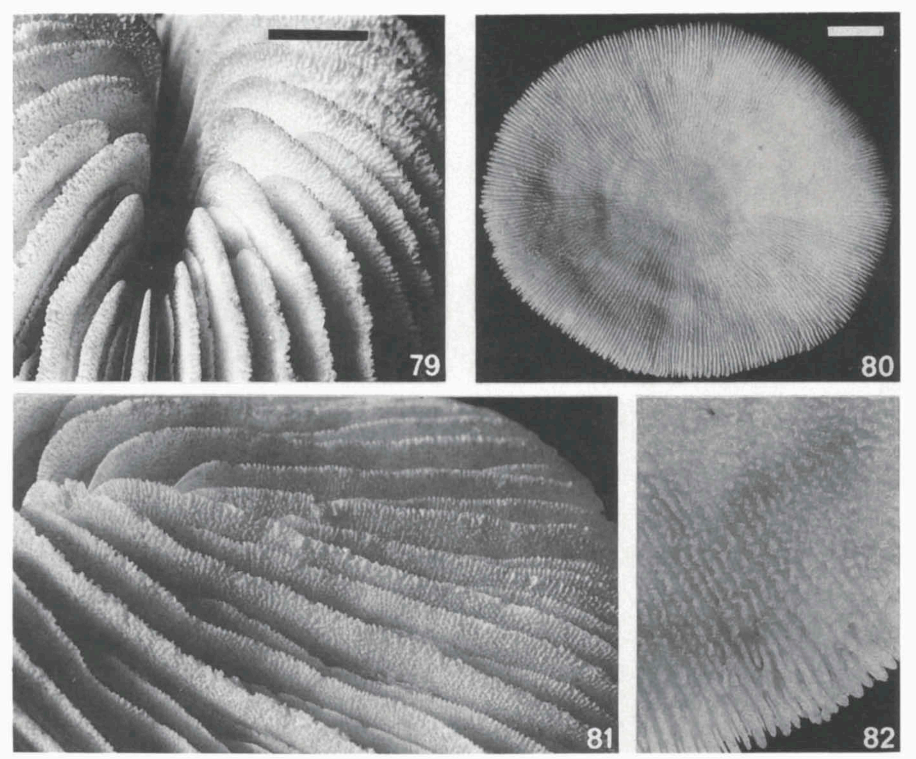
Type material examined. — MNHN 73-74 (syntypes of *Fungia cyclolites*; type loc. unknown); QMB G10018 (lectotype [present designation] of *Diaseris mortoni* [the syntype most similar to the one illustrated by Tenison-Woods, 1880: pl. 15 figs. 1-2] and 4 paralectotypes of *Diaseris mortoni*; type loc. Holborn I., off Pt. Denison, Queensland, AUSTRALIA); USNM 154426, 68280 (holotype and paratype of *Fungia japonica*; type loc. Yesso, JAPAN); ZMA 340 (holotype of *Fungia adrianae*; type loc. unknown); ZMA 1236 (paralectotype of *Fungia patelliformis*; Bay of Pidjot, E Lombok, INDONESIA); RGM 43122, 167801 (syntypes of *Fungia borneensis*; type loc. Kabasian, Kalimantan, INDONESIA).

Other material. — RED SEA: BMNH (6), 1928.4.23.1-2, 1937.11.17.379-382, ZMA 358 (7). DJIBOUTI: MNHN 1393. NE SOMALIA: USNM 78230. ZANZIBAR: ANSP 4524 (3). MOZAMBIQUE: BMNH 1934.8.5.9 (many frags.), RMNH 12060, 12081. ALDABRA: BMNH 1986.10.6.114 (11). N MADAGASCAR: USNM: 78227 (4). SRI LANKA: BMNH 1875.4.8.127 (3), USNM 77756 (3). INDIA. Madras: BMNH 1890.2.10.2-3. JAPAN: USNM 77786 (3), ZMA 1239. S CHINA SEA. Macclesfield Bank: BMNH 1893.9.1.206. PHILIPPINES: MCZ (3), USNM 77964 (2), 77988-77989 (7), 77994 (2). N Mindoro: MCZ 3973 (2), 3998 (3). S Masbate: USNM 77317 (3). SE Mindanao: USNM 77972 (4), 77977. MALAYSIA. Malacca: BMNH 1842.1.28.50-51, 1842.11.30.10. NE Borneo: RGM 41755, 43115 (both fossil). INDONESIA. Belitung (Billiton): RGM 18015 (3 ex., fossil), RMNH 9417 (2). Java: RGM 3877 (fossil), 40993 (3 ex., fossil), 77768-77769, 77992 (3). SW Sulawesi: RMNH 22061-22070 (19). Komodo: RMNH 21386 (10), 21416 (22), 21585 (51), 22040 (8). N Sumbawa: RMNH 20813 (3), 21627 (30), 22039 (2). NE Sumba: RMNH 20306 (4). Moluccas: ZMA 5500 (3). Ambon: RMNH 8349-8352 (50), UZMK (67). Banda: UZMK (2). Timor Sea: RMNH 9416 (4), 9419 (2). AUSTRALIA. Kimberley: WAM 16.78, 507.86. Pilbara: WAM 47.72 (5), 985.79, 453.86 (19), 454.86 (2), 460.86. Shark Bay: WAM 488.79 (4). Houtman Abrolhos Is.: WAM 217.78 (23), 218.78 (3). N Great Barrier Reef: QMB G7655, G8747-8754, G8270-8273, USNM 78226, 78277 (4). C Great Barrier Reef: MCZ 5407-5408 (14), QMB GBR304-319, GL3628 (2). S Great Barrier Reef: QMB G7120 (8), USNM 78276. PAPUA NEW GUINEA. Bismarck Sea: ULB. NEW CALEDONIA: ANSP 4523 (3), MNHN 1829, USNM 73773 (14), 78279, ZMA 6254-6256 (23). HAWAII IS.: AMNH 1670, 1674-1675, 3236 (8), MCZ (1 recent, 1 fossil).

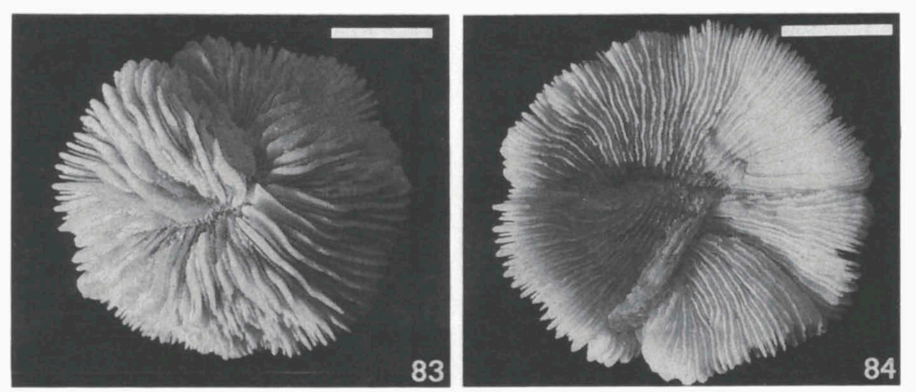
Characters. — Adult animals are free-living. If unfragmented, their outline varies from round to oval; they are usually monostomatous, but sometimes large specimens have grown supernumerary stomata by circumstomadaeal budding (fig. 74a). Fragmented, regenerating specimens have an outline which is usually irregular, varying from wedge-shaped to round; they may have



Figs. 72-78. Corals (anthocyathi) of *Fungia (Cycloseris) cyclolites* from Indonesia. Scale bars: 1 cm. Fig. 72. Upper surface of two corals of which (a) is arched (RMNH 9417; Belitung) and (b) is flat (RMNH 8352; Ambon). Fig. 73. The concave aboral surface of the coral in fig. 72a showing mainly straight costae. Fig. 74. Upper surface of two corals (RMNH 8352; Ambon) of which (a) has secondary fossae near the margin and (b) has interrupted septa around an arched centre. Fig. 75. Aboral surface of a coral with the costae intermingled at the centre (RMNH 8352; Ambon). Fig. 76. Aboral surface of a flat coral with straight costae (RMNH 8352; Ambon). Figs. 77-78. Upper and lower surface of a coral with almost equally thin septa and with folds in the corallum wall (RMNH 22067; SW Sulawesi).



Figs. 79-82. Corals (anthocyathi) of *Fungia (Cycloseris) cyclolites* from Indonesia. Fig. 79. Septa of the coral in fig. 72a with up-right margins alongside the fossa. Scale bar: 0.5 cm. Fig. 80. Aboral surface of a large coral with wavy costae (RMNH 8352; Ambon). Scale bar: 1 cm. Fig. 81. Septa of a coral from Ambon (RMNH 8352; Ambon); scale bar in fig. 79. Fig. 82. Costae of the same coral; scale bar in fig. 79.



Figs. 83-84. Upper and lower surface of a regenerated fragment of *Fungia (Cycloseris) cyclolites* (RMNH 12060; Inhaca I., S Mozambique). Scale bars: 1 cm.

grown several stomata along the former fracture lines (figs. 83-84). The coralla are relatively thick; they vary from flat to highly arched. The length of the specimens varies between 0.5 and 9.0 cm.

The length of the central fossa, measured at its bottom, is 1/9 to 1/4 of the coral length. Along the sides of the fossa the septal edges are erect, whereas at its ends they are diverging, making its opening appear longer (fig. 79). The columella is formed by a mingled mass of tightly packed, partly fused trabeculae and paliform lobes, which have their tips either pointing upwards or in various directions.

The septa are densely packed and usually straight, but sometimes wavy. The septa of lower order cycles are high, thick and solid; they are flanked by those of higher orders, which are thinner, lower and very often perforated. Tentacular lobes may be present. The septal margins are ornamented with small, sharp dentations. Their number varies from 40 to 80 per cm. The septal sides are covered by fine granulations which are arranged in rows or fused in ridges perpendicular to the septal margin (fig. 612). Because of a relatively loose septal arrangement, the compound synapticulae can easily be detected.

The corallum wall is solid and ungranulated. A detachment scar is usually only distinct at the aboral side of small specimens in anthocyathus-stage. In some specimens concentric growth rings can be discerned at the lower side (fig. 76); some specimens may show folds in the wall (fig. 78). The costae are equal to subequal in size. They are straight and prominent near the corallum margin, whereas at the centre they may become less distinct (fig. 73) and meandering (fig. 75). In very large specimens they may be wavy over their whole length (figs. 80, 82). The costae are ornamented with granular, small spines, which are usually acute (fig. 617), but may also be more or less blunt, especially in large specimens. Their number varies from 40 to 100 per cm.

The colour of the living animal usually varies from light to dark brown. The tentacles are small and transparent, sometimes showing vaguely white batteries of nematocysts.

Geographical distribution (fig. 85). — The species occurs in a range which extends from East Africa (Red Sea and Mozambique) eastward towards the Hawaiian Islands, in the Central Pacific. The northernmost distribution limit is located at Japan (Honshu) and the southern one at Western Australia (Houtman Abrolhos Is.).

Remarks. — In the literature *F. cyclolites* is relatively the best known species of *Cycloseris*, although this only refers to records of animals observed in complete shape. *Diaseris mortoni* and *Fungia japonica* are both names given to fragmented forms of *F. cyclolites*. Döderlein (1902: 65, 78) already suggested that *Diaseris mortoni* might be synonymous with *F. cyclolites*, but he

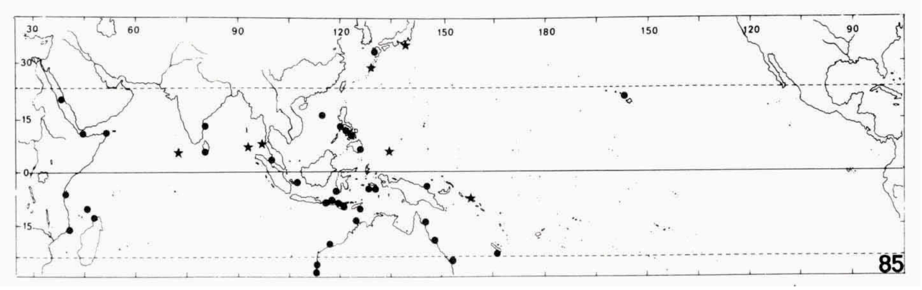


Fig. 85. The range of *Fungia (Cycloseris) cyclolites*. Records are from examined material (●) and published illustrations (★).

was not certain about this.

A fossil specimen from the Hawaiian Islands, which is almost identical to the holotype of *F. japonica*, is at the MCZ. Recent specimens from the Hawaiian Islands are present in the collections of the AMNH and the MCZ. *F. cyclolites* has not been recorded from Hawaii before, neither extant nor as a fossil.

The holotype of *Fungia glans* could not be located. According to Dana's (1846) description and figure it probably belongs to *F. cyclolites*. The holotype of *F. adrianae* is a very large specimen of *F. cyclolites*; it has wavy costae, resembling those of some of the larger specimens from Ambon (fig. 82). The syntypes of *F. borneensis*, which are in fossilized state, are similar to those of *F. cylolites*.

F. cyclolites is morphologically intermediate between *F. distorta* and *F. somervillei*, which makes it sometimes difficult to separate specimens of this species from those of the other two. In general coralla of *F. cyclolites* are more heavily built than those of the two other species; i.e. the septa and corallum of each individual are relatively thicker. Compared to *F. distorta* the septa are more loosely packed, the septal dentations are sharper and the granulations on the septa are more distinctly arranged in rows. It differs further from *F. somervillei*, with which it may have a humped oral surface in common, by not having a relatively thin corallum margin.

In the most common shape, coralla of *F. cyclolites* are oval and highly arched, but at some localities they resemble slightly those of *F. costulata*, by being more round and oval. They still can easily be recognized as belonging to *F. cyclolites* because of their longer fossal opening, resulting from the stronger divergence of the septal edges at both ends of the mouth. Besides this, the costae of *F. cyclolites* are sharper, more distinct and more regularly alternating in height than those of *F. costulata*.

At some locations *F. cyclolites* may be confused with *F. curvata*. The former may be distinguished from the latter by its more oval, more regular corallum outline, its flatter shape, and its thinner first order septa.

Fungia (Cycloseris) curvata nom. nov.
(figs. 86-95)

Fungia elegans Verrill, 1870a: 100 (La Paz, California); 1870b: 542, pl. 10 figs. 1-2; Rehberg, 1892: 27; Döderlein, 1902: 62, 79-80, pl. 4 figs. 3-6, pl. 5 fig 6; Van der Horst, 1921: 59.

Not *Fungia elegans* Bronn, 1837: 900-901, pl. 36 figs. 7a-d. (Type species of *Stephanophyllia* Michelin, 1841; designated by Milne Edwards & Haime, 1850).

Cycloseris elegans — Vaughan, 1907b: 115-116, 127-128; Durham, 1947: 24, pl. 9 figs. 1-3, 5-6, 11-12; Durham & Barnard, 1952: 52, pl. 4 figs. 20a-b; Squires, 1959: 414; Durham, 1962: 52; 1966: 125; Brusca, 1980: 64, pl. 4; Wells, 1983: 229-230, pl. 11 figs. 3, 5; Veron & Kelley, 1988: 28.

Cycloseris cyclolites — Boschma, 1925: 205-210 (partim).

Fungia sp. — Burchard, 1979: 20, pl. 28.

Type material examined. — YPM 3989a-b (lectotype and paralectotype of *Fungia curvata* [= *Fungia elegans* Verrill]; type loc. La Paz, Gulf of California, MEXICO [designation by Durham, 1947; for illustrations of lectotype see Verrill, 1870b]).

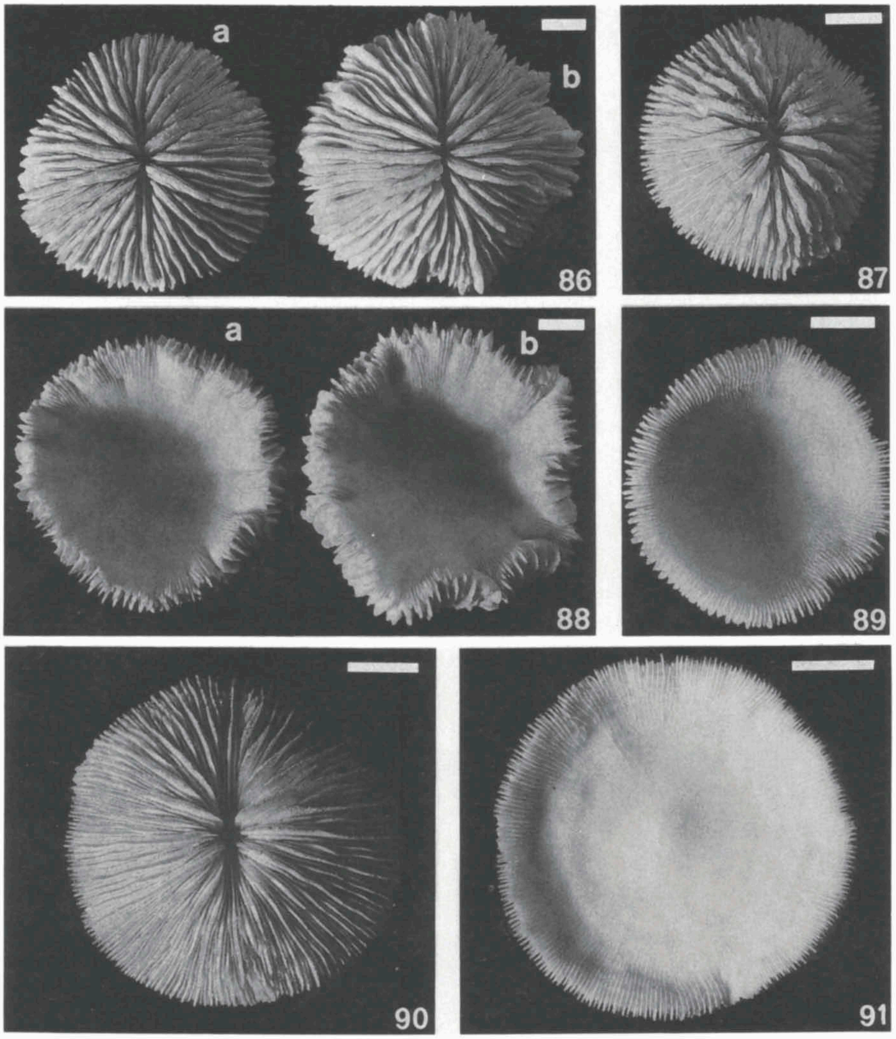
Other material. — RED SEA. Gulf of Aqaba: USNM 78268. ZANZIBAR: USNM 78236 (3). PERSIAN GULF: MCZ 5405 (4). PHILIPPINES: MNHN 233. INDONESIA. E Kalimantan: RMNH 22099. Ambon: RMNH 8347. PAPUA NEW GUINEA. Bismarck Sea: ULB. GALAPAGOS IS.: USNM 46956. MEXICO: MNHN Fun14. Gulf of California: AMNH 546 (11), 1873 (2), BMNH 70.8.22.8 (4), MCZ 5288 (7), RMNH 9445 (3), USNM 8979 (7), YPM 3963-3965 (503), 3977-3978 (19), 3980-3988 (25), ZMA 439. Three Maria Is.: AMNH (11). COCOS I.: USNM 80083. S COSTA RICA: USNM 77890. PANAMA. Gulf of Panama: MCZ 5416 (16).

Characters. — Adult animals are monostomatous and free-living. The outline of immature coralla is regularly discoidal, but later it becomes folded. Fragmented coralla are wedge-shaped and get an irregularly formed outline after regeneration (Wells, 1983: pl. 11 figs. 3, 5; USNM 46956). The coralla are relatively thick; small specimens are relatively flat but when they grow larger, they become highly arched. The diameter of the specimens varies between 1.5 and 8.5 cm.

The length of the central fossa, measured at its bottom, is 1/12 to 1/7 of the corallum diameter. The septal edges stand upright, except at both ends of the fossa, where they are diverging, making the fossal opening appear longer. The columella is formed by a mingled mass of loosely packed, partly fused trabeculae and paliform lobes with the tips pointing in various directions.

The septa are densely packed; they are straight, except where they fuse at the corallum margin. They are very unequal in thickness and height, especially in full-grown animals. The very thick and solid septa of lower orders are flanked by thinner and lower, perforated septa of higher orders. Tentacular lobes are absent. The septal margins are ornamented with fine, sharp dentations which become indistinct on the very thickened lower order septa (fig. 94). Their number varies from 40 to 80 per cm. The septal sides are thinly covered by fine granulations which are arranged in rows, or fused in ridges, perpendicular to the septal margin. The compound synapticulae connecting the septa laterally can easily be detected, in spite of the tight septal arrangement.

The solid corallum wall is not granulated and may still show a detachment

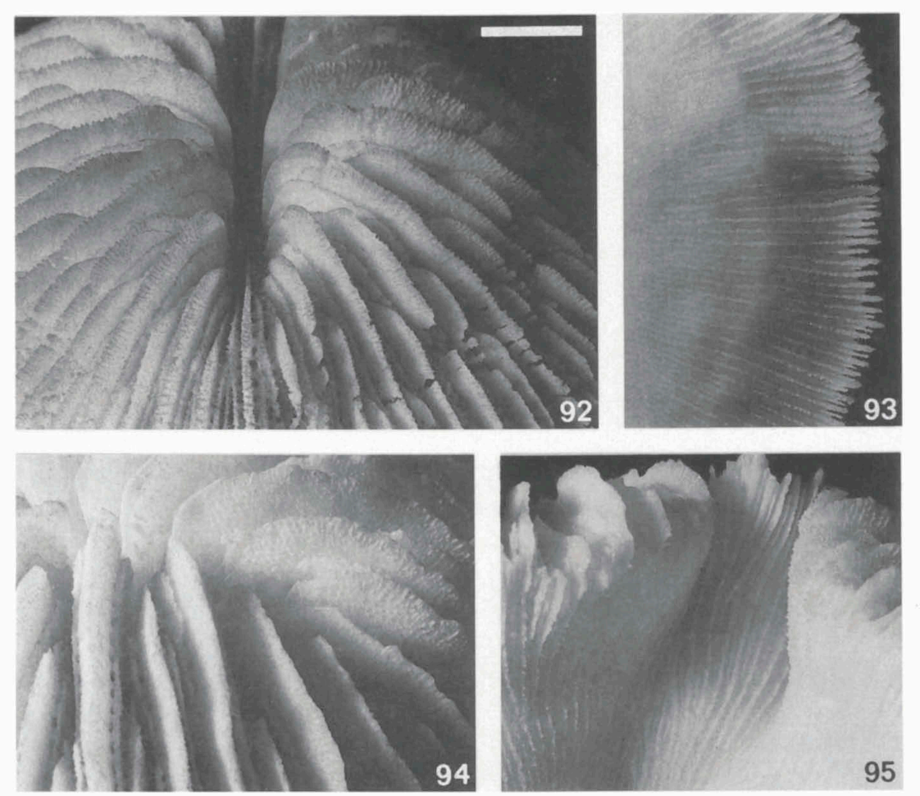


Figs. 86-91. Corals (anthocyathi) of *Fungia (Cycloseris) curvata*. Scale bars: 1 cm. Fig. 86. Upper surface of two large corals showing the thick first two order septa (RMNH 9445; Gulf of California, Mexico). Fig. 87. Upper surface of a small coral (RMNH 22099; Bontang, E Kalimantan, Indon.). Fig. 88. Aboral surface of the corals in fig. 86 with large folds in the coral margin. Fig. 89. Aboral surface of the coral in fig. 87 with slightly developed folds. Figs. 90-91. Upper and lower surface of a juvenile with poorly developed folds in the coral margin and a slightly visible detachment scar (RMNH 8347; Ambon, Indon.).

scar at the aboral side of small specimens in anthocyathus-stage (fig. 91). The costae are almost equal in size. At the corallum margin they are distinct; they are straight where the margin is still undisturbed, but they may become disarranged where it is folded (fig. 95). They are less distinct near the centre, where they are intermingled. All costae are ornamented with small and acute, granular spines. Their number varies from 40 to 80 per cm.

The living animal is brown. Its tentacles are small and transparent.

Geographical distribution (fig. 96). — Originally the species was supposed to be endemic for the west coast of Mexico (see e.g. Ekman, 1953: fig. 4). Later the Galapagos Islands were added to its known distribution in the East Pacific (Wells, 1983). At present specimens are known to occur in the West



Figs. 92-95. Close-ups of *Fungia (Cycloseris) curvata* corals. Scale bar: 0.5 cm. Fig. 92. Septa of the coral in fig. 90; some of them have partly frayed margins. Along the fossa the margins are vertical. Fig. 93. Detail of the coral in fig. 91 showing a small fold and the fine, sharp spines on the unequally exsert costae. Fig. 94. Septa of the coral in fig. 86b; the compound synapticulae reach almost as high as the septa of the last cycles. Fig. 95. Costae of the coral in fig. 88b bearing very fine spines.

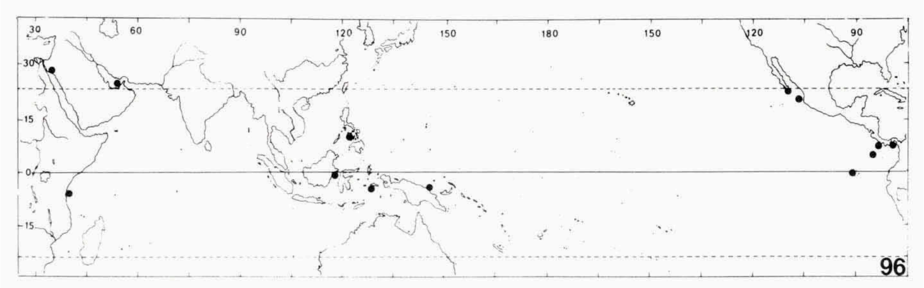


Fig. 96. The range of *Fungia (Cycloseris) curvata*. Records are from examined material (●).

Indian Ocean (Red Sea, Persian Gulf and Zanzibar) and in the Central Indo-Pacific as well.

Remarks. — *Fungia elegans* Verrill, 1870 is a junior homonym of *Fungia elegans* Bronn, 1837. Because no other synonym is available, a new name is given to Verrill's species.

An immature specimen from Ambon (figs. 90-91), which Boschma (1925) identified as *F. cyclolites*, is too round to belong to that species. Besides, it already shows the development of a marginal fold which is typical of *F. curvata*. The opening of the fossa is not as long as that of *F. cyclolites*. In very early anthocyathus stage the species lacks the marginal folds and resembles *F. costulata*. Adult corals of *F. curvata* are usually thicker and more arched than those of the latter species. Further, its lower order septa are thicker, adjacent costae alternate more in height and the septa at both ends of the fossa diverge more.

Etymology. — The name curvata has been used to indicate the strongly arched or curved shape in which the animal usually occurs.

Fungia (Cycloseris) somervillei Gardiner, 1909
(figs. 2-3, 97-108)

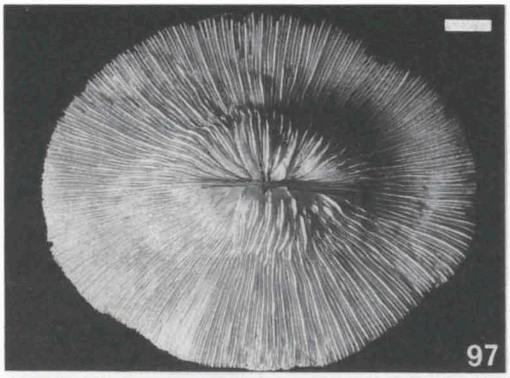
Fungia somervillei Gardiner, 1909: 269, pl. 34 figs. 5-6 ("Seychelles, F 5, 44 fms."; "A second specimen in a dead and rather broken condition was dredged in the Amirante Group, E, 20 fms."); Matthai, 1924: 41 (partim); Boschma, 1925: 204-205, pl. 6 fig. 65; Umbgrove, 1946a: 90, pl. 1 figs. 3-4; Pichon, 1974: 176; Faure, 1977: 9; Pillai, 1983: 86 (partim). Not: Van der Horst, 1921; Schuhmacher, 1979.

Cycloseris somervillei — Pillai, 1971a: 323; 1972: 203 (partim); Veron & Pichon, 1979: 113-115, figs. 180-183; Nemenzo, 1980: 293-294, fig. 3; Tribble & Randall, 1986: 158; Veron, 1986b: 323; Veron & Kelley, 1988: 26, 28.

Fungia (Pleuractis) somervillei — not: Scheer & Pillai, 1974; Ditlev, 1976; 1980.

Fungia paumotensis — Veron & Marsh, 1988: 84 (partim).

Type material examined. — UMZC (lectotype [present designation] of *Fungia somervillei*; type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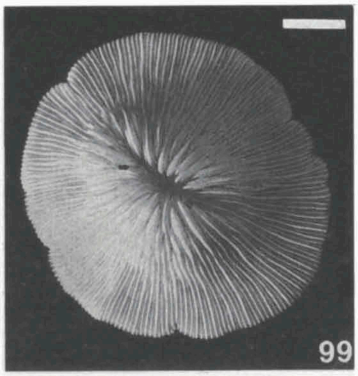
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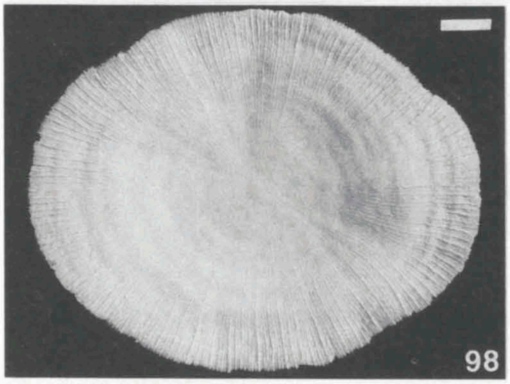
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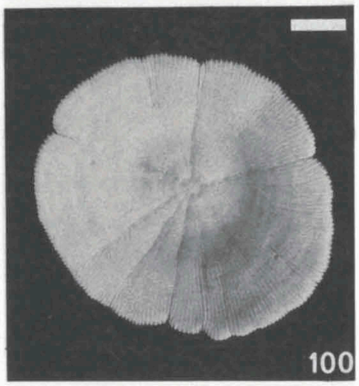
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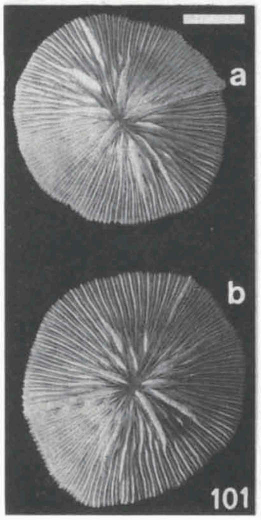

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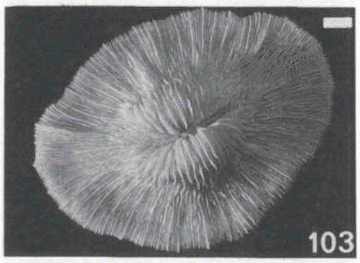
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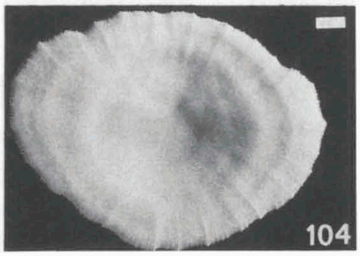
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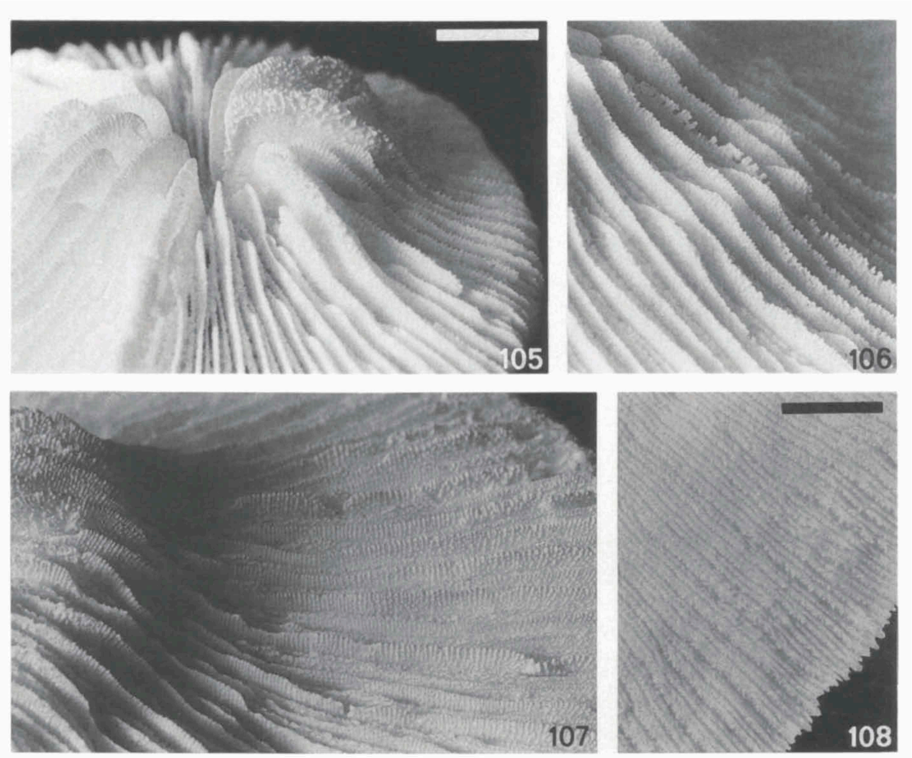
Figs. 97-104. Corals (anthocyathi) of *Fungia (Cycloseris) somervillei*. Scale bars: 1 cm. Figs. 97-98. Upper and lower surface of a large coral with a distinctly convex centre, showing clearly unequal costae (UZMK; Sulu Is., Philipp.). Figs. 99-100. Upper and lower surface of a medium-sized coral with a lobate margin and distinct clefts, indicating that it is in the initial phase of fragmentation (RMNH 22084; SW Sulawesi, Indon.). Figs. 101-102. Upper and lower surface of two juveniles, each with a slightly protruding fossa, some of the lower order septa extremely exsert and the costae only slightly alternating in size (RMNH 22084; SW Sulawesi). Figs. 103-104. Upper and lower surface of an adult with relatively exsert lower order costae (RMNH 22084; SW Sulawesi).

loc. SEYCHELLES; illustrated by Gardiner, 1909: pl. 34 figs. 5-6); BMNH 1983.8.12.1 (paralectotype of *F. somervillei*; loc. AMIRANTE IS.).

Other material. — PHILIPPINES: USNM 77968 (2). Cebu: UPMSI 344. S Mindanao: BMNH 1886.12.9.198, USNM 77778, 77969 (2). Sulu Is.: USNM 77781, UZMK (1). INDONESIA. Java: RGM 77771 (fossil). SW Sulawesi: RMNH 22080-22091 (62). Komodo: RMNH 21419 (6), 22041 (4). AUSTRALIA. Kimberley: WAM 208.85. PAPUA NEW GUINEA. Bismarck Sea: ULB. MARIANA IS. Guam: USNM 80446 (3).

Characters. — Adult animals are free-living and remain usually monostomatous (solitary). In unbroken form their outline is oval, whereas after fragmentation they may consist of wedge-shaped pieces (fig. 3). If they regenerate, their outline becomes irregular. Some specimens show clefts in the corallum wall, along which fragmentation can take place (fig. 100); they originate at the periphery and penetrate towards the centre. The coralla are convex and thick around the central fossa, whereas their margin is relatively



Figs. 105-108. Close-ups of *Fungia (Cycloseris) somervillei* corals. Scale bars: 0.5 cm. Fig. 105. Septa of the juvenile shown in fig. 101b. Fig. 106. Septa of the coral in fig. 98 showing clear tentacular lobes and the partly frayed septal margin. Fig. 107. Septa of the coral in fig. 97 showing clear rows of granulations on the septal fringe. Fig. 108. Costae of the coral in fig. 98 with small granulate spines.

thin; they vary from flat to arched. The length of the specimens varies between 3.0 and 12.5 cm.

The length of the central fossa, measured at its bottom, is 1/15 to 2/9 of the coral length. The septal edges at its sides stand upright, while they diverge strongly at both ends. The columella is formed by a mingled mass of tightly packed trabeculae and paliform lobes with the tips pointing upwards.

The septa are thin, straight and densely packed. The thickest and highest septa are those of lower order cycles, which are solid. They are flanked by those of higher order cycles, most of which are partly fenestrate. In many of the small specimens some of the low order septa are extremely high (figs. 101, 105). Tentacular lobes are present on the septa of some specimens (fig. 106). The septal margins are ornamented with fine and sharp granular dentations. Their number varies from 40 to 70 per cm. The septal sides are densely covered by fine granulations which are arranged in rows perpendicular to the septal margin (fig. 107). The compound synapticulae, which connect the septa laterally, cannot always easily be detected, because of the tight septal arrangement.

The solid corallum wall is ungranulated; it may show a detachment scar in juvenile specimens in anthocyathus-stage (fig. 100). The costae are almost equal in size. They are straight and distinct near the corallum margin, while they become vague and wavy near the centre. All costae are finely ornamented with acute, granular spines. Their number varies from 40 to 90 per cm.

The living animal is brown, often in a pattern of dark and light coloured radiating patches (fig. 2). The tentacles are small and transparent.

Geographical distribution (fig. 109). — Specimens have been collected in an area which ranges from the Indian Ocean (Seychelles) towards the Central Indo-Pacific (including the Philippines, Indonesia, N Australia and the Bismarck Sea) and the Mariana Is. (Guam). Maybe the area appears disjunct because the animals have not sufficiently well been collected in the deeper reef

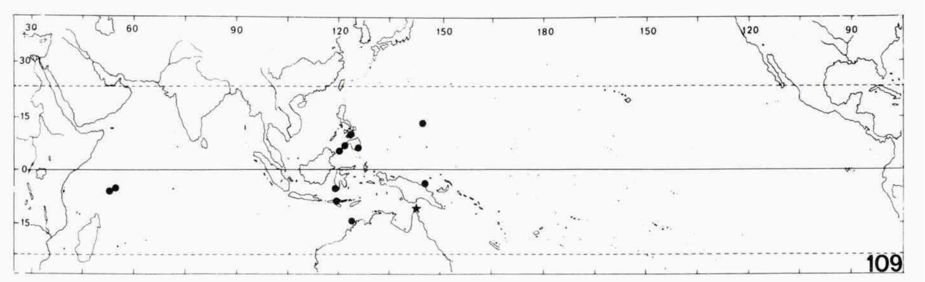


Fig. 109. The range of *Fungia (Cycloseris) somervillei*. Records are from examined material (●) and published illustrations (★).

zones where they usually live.

Remarks. — The specimen illustrated by Gardiner (1909) is designated lectotype because the only other type specimen is not complete.

Gardiner (1909) states that his species is a close ally of *F. sinensis*, a species he mixed with *F. fragilis*. Specimens of *F. somervillei* and *F. fragilis* may look like each other, especially in fragmented condition, but those of *F. somervillei* have a more elongate outline and a thicker centre.

F. somervillei can also be confused with *F. cyclolites*, because of its oval outline and long mouth. Adult corals of the latter species lack the relatively thin corallum margin around a thick centre and they cannot grow as large as mature specimens of the first species.

In the literature the species has often been confused with *F. moluccensis*, with which it has the oval outline and convex centre in common. The two species differ distinctly in their septal and costal ornamentations. Corals of *F. somervillei* lack the perforated corallum wall. Another diagnostic character of this species is the arrangement of the granulations on its septal sides in clear rows; those of *F. moluccensis* are more irregularly distributed.

Fungia (Cycloseris) fragilis (Alcock, 1893)
(figs. 4, 110-121, 614)

? *Cycloseris decipiens* Martin, 1880: 143-144, pl. 25 figs. 3-6, pl. 26 fig. 6 (Miocene, "Liotji-tjangkang", Java).

Diaseris fragilis Alcock, 1893: 148, pl. 5 fig. 11 ("Dredged in the Andaman Sea"); Döderlein, 1902: 64; Veron & Marsh, 1988: 82 (partim); Yamashiro, Hidaka, Nishihira & Poung-in, 1989: figs. 1-5, 7, 10-11. Not: Veron & Pichon, 1979; Cairns, 1984a; Veron, 1986b.

Fungia patella — Döderlein, 1902: 65-73 (partim), pl. 1 figs. d-d', h-i', k-m', q, pl. 2 figs. e-i', k-q', t-v'; Harrison, 1911: 1036; Van der Horst, 1921: 57-58 (partim); Yabe & Eguchi: 271-272, figs. 10-12.

Fungia distorta — Döderlein, 1902: 74-77 (partim), pl. 3 figs. a-i, k-z, aa-cc; Matthai, 1924: 39-40, pl. 10 figs. 2-4.

Cycloseris sinensis — Gardiner, 1905: 944, pl. 91 figs. 14-16.

Fungia fragilis — not: Vaughan, 1907a; Gardiner, 1909; Boschma, 1923c; 1925; Reed, 1971; Boshoff, 1981.

Fungia sinensis — Gardiner, 1909: 269, pl. 33 figs. 1-2.

Fungia (Cycloseris) patella — Gerth, 1921: 423-424 (including f. *hemispherica* Gerth, 1921 [Miocene, "Tji Boerial", Java]); 1923: 101-102, pl. 9 fig. 1.

? *Fungia (Cycloseris) decipiens* — Gerth, 1921: 424; 1923: 103; 1925: 34.

Fungia patelliformis Boschma, 1923c: 136-138 (partim), pl. 9 figs. 9, 11, 13-14b, 16-16a (Siboga Exped. "Stat. 311. Sapeh-bay, East Coast of Sumbawa"); 1925: 192-195, pl. 5 figs. 12-14, 21; Hoffmeister, 1925: 35; Umbgrove, 1938: 271; Crossland, 1952: 154, pl. 16 fig. 1; Van Soest, 1979: 107; Lamberts, 1983: 9. (New synonymy).

Fungia laciniosa Boschma, 1925: 198-199 (partim), pl. 5 figs. 15-17, 23 ("Banda, between Neira and Goenoeng Api, 20-30 m, 26 ex."). (New synonymy).

Fungia (Cycloseris) fragilis — not: Gerth, 1925.

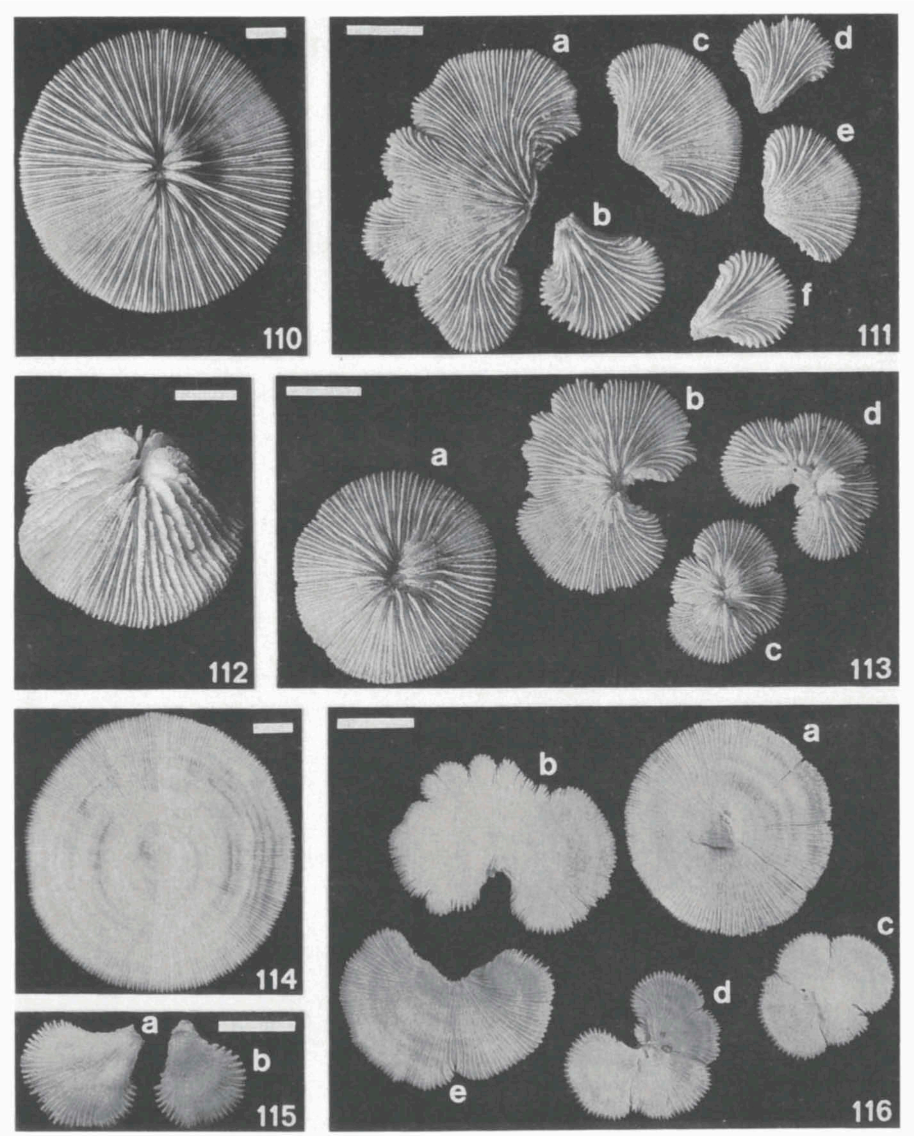
Fungia (Cycloseris) patelliformis — Gerth, 1925: 33-35.
Cycloseris fragilis — not: Vaughan & Wells, 1943; Wells, 1954; Pillai, 1972; Maragos, 1977.
Cycloseris patelliformis — Pillai, Vine & Scheer, 1973: 459; Ditlev, 1976: 6; Veron & Pichon, 1979: 115-116, figs. 184-187; Ditlev, 1980: 54, figs. 38, 226; Faure, 1982: 96-97; Fricke & Schuhmacher, 1983: 172; Scheer & Pillai, 1983: 74-75, pl. 16 fig. 1; Veron, 1986b: 324; Veron & Kelley, 1988: 26, 28, 31, fig. 9b; Veron & Marsh, 1988: 81 (partim). Not: Wells, 1954; Scheer & Pillai, 1974; Nemenzo, 1980.
Cycloseris distorta — Ditlev, 1980: 54, fig. 227.
Cycloseris c.f. *fragilis* — Randall & Myers, 1983: 17, figs. 337-338.
Cycloseris c.f. *patelliformis* — Hamilton & Brakel, 1984: 252.
Diaseris distorta — Veron & Marsh, 1988: 82 (partim).

Type material examined. — RGM 3878-3881, 3883-3884, 16752-16755, 17985 (syntypes of *Cycloseris decipiens*; type loc. Java, INDONESIA); ZMA 5507 (lectotype [present designation] of *Fungia patelliformis*; type loc. E Sumbawa, INDONESIA; for illustration, see Boschma, 1923a: pl. 9 fig. 11); ZMA 605, 724b (3 paralectotypes of *F. patelliformis*; Postillon Is., INDONESIA); ZMA 724a (4 paralectotypes of *F. patelliformis*; SW Sulawesi, INDONESIA; ZMA 5508 (paralectotype of *F. patelliformis*; Paternoster Is., INDONESIA); ZMA 5509 (paralectotype of *F. patelliformis*; Waigeo Is., INDONESIA); ZMA 5521 (2 paralectotypes of *F. patelliformis*; Banda, INDONESIA); UZMK (lectotype [present designation] of *Fungia laciniosa*; type loc. Banda, INDONESIA; for illustration, see Boschma, 1925: pl. 5 figs. 15-16); UZMK (7 paralectotypes of *F. laciniosa*; Banda, INDONESIA).

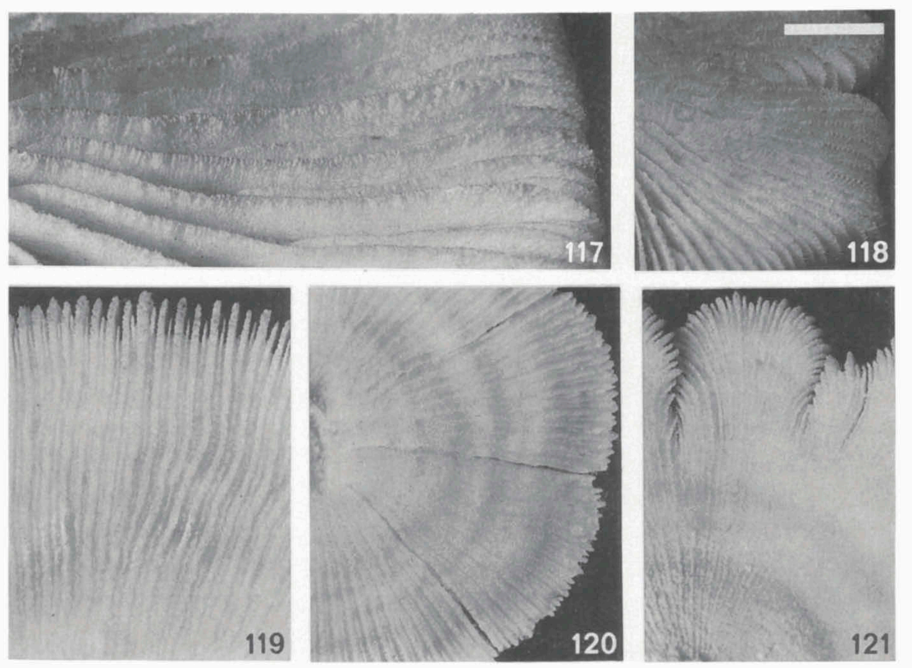
Other material. — RED SEA. Gulf of Aqaba: USNM 78251 (7). S MOZAMBIQUE: USNM 77955 (4). SEYCHELLES: BMNH 1981.3.5.459-461/467. ALDABRA: BMNH 1986.10.6.114D. MALDIVES: MCZ 3598 (many frags.). S CHINA SEA. Macclesfield Bank: BMNH 1893.9.1.207. JAPAN. Okinawa: USNM 77788. THAILAND. Koh Kahdat: RMNH 8270 (13), 8278 (4). PHILIPPINES: USNM 77775. Cebu: BMNH 1903.4.5.5. Bohol: MCZ 5409 (5). SW Mindanao: BMNH 1886.12.9.170, 1890.12.13.12 (7), USNM 77999, 78079 (many frags.). Sulu Is.: RMNH 8273, 8276-8277, 8317, USNM 77779 (15), 77948 (many frags.), 78086 (many frags.), 78228 (2). INDONESIA. Nias: RGM 125810 (6 frags., fossil). SE Sumatra: RMNH 10484. NW Java: RMNH 8314 (2), 8321, 16035 (11). Lombok: RMNH 10485. E Kalimantan: RMNH 22098. SW Sulawesi: RMNH 8316, 15711 (2), 20896 (5), 22053-22056 (82), 22058-22059 (8); 22092-22095 (25 + many frags.), UZMK (1). Halmahera: RMNH 16001 (22). N Sumbawa: RMNH 21590, 21625 (many frags.). Komodo: RMNH 21414 (46 ex. many frags.), 21517 (74), 21558, 21583 (9). Ambon: RMNH 8326 (2), 8328, 15800 (17), UZMK (3). Banda: RMNH 8275 (13), 8305, 8307-8308 (3), 8331, 16034, USNM 78338, UZMK (58). Kei Is.: RMNH 8311-8313 (4), 8315 (3), 8318, 8320, 8322 (8), 16002 (5), UZMK (9). Saparua: RMNH 8348. AUSTRALIA. Shark Bay: WAM 465.86 (2). Houtman Abrolhos Is.: WAM 161.78, 219.78. Great Barrier Reef: BMNH 1897.3.9.168 (2), 1934.5.14.610 (5). PALAU IS.: USNM 78029 (15). MARIANA IS. Guam: USNM 79988. NEW CALEDONIA: ZMA 6257 (4), 6259 (2), 6262-6263 (20). MARSHALL IS.: USNM 77826. SAMOA IS.: USNM 77836-77837 (8).

Characters. — Adult animals are free-living and usually monostomatous. They are either discoidal or they consist of regenerating fragments with a lobed outer margin. In fragmenting corals clefts can be observed along which fragmentation can take place; they originate at the periphery and penetrate further towards the centre (figs. 116, 120-121). The coralla are thin; they vary from flat to highly arched. The diameter of the specimens varies between 1.0 and 15.0 cm.

The length of the central fossa, measured at its bottom, is 1/12 to 1/9 of the



Figs. 110-116. Corals (anthocyathi) of *Fungia (Cycloseris) fragilis* from Indonesia. Scale bars: 1 cm. Fig. 110. Upper surface of a large flat coral (UZMK; Banda). Fig. 111. Upper surface of loose fragments (UZMK; Banda). Fig. 112. Upper surface of an arched coral (RMNH 16034; Banda). Fig. 113. Upper surface of corals in the initial phase of fragmentation: (a) a complete coral with slits in the wall and a partly lobate margin (RMNH 8270; Kei Is.); (b-d) not all parts are separated yet (RMNH 16001; W Halmahera). Fig. 114. Aboral surface of the coral in fig. 109 showing concentric growth-rings in the corallum wall. Fig. 115. Aboral surface of the fragments in fig. 111b-c. Fig. 116. Aboral surface of the corals (a-d) in fig. 113 and of a fragment (e) (RMNH 16001; W Halmahera).



Figs. 117-121. Close-ups of *Fungia (Cycloseris) fragilis* corals. Scale bar: 0.5 cm. Fig. 117. Septa of a large coral showing distinct rows of granulations (RMNH 8308; Banda). Fig. 118. Septa of the coral in fig. 111a. Fig. 119. Costae of the coral in fig. 112. Fig. 120. Costae and clefts in the corallum wall of the coral in fig. 116a. Fig. 121. Costae of the coral in fig. 116b.

corallum diameter. The septal edges at the sides of the fossa stand upright, while those at both ends diverge slightly. The columella is formed by a mingled mass of tightly packed and partly fused trabeculae and paliform lobes with the tips pointing in various directions. In broken specimens the columella may be absent or may only be partly regenerated.

In unbroken coralla the septa are loosely packed and straight. In regenerating specimens the septa are not straight, but bend towards the clefts in the lobed corallum margin (fig. 111). The septa are thin and almost equal in thickness. The septa of lower order cycles are solid and more exsert than those of higher orders, which can be perforated. Tentacular lobes are absent. The septal margins are ornamented with fine and sharp granular dentations. Their number varies from 50 to 120 per cm. The septal sides are densely covered with fine granulations which are arranged in irregular rows or fused in ridges perpendicular to the septal margin (fig. 614). The compound synapticulae, which connect the septa laterally, can easily be distinguished, because of the loose septal arrangement.

The solid corallum wall is ungranulated. It shows a detachment scar at the aboral side of small specimens in anthocyathus-stage. The aboral side may partly be covered by epibionts. Concentric growth-rings may occur, which give the corallum wall an undulating appearance (fig. 114). The costae are alternating in height and thickness; the lower order cycle costae are flanked by younger ones. The costae are normally straight and always distinct near the corallum margin, but sometimes less distinct at the centre. In regenerating fragments the costae are not straight, but bend towards the corallum margin (fig. 121). All costae are ornamented with fine costal spines which are granulate and acute. Their number varies from 50 to 70 per cm.

The colour of the living animal varies from light to dark brown or from olive green to yellow (fig. 4). The small tentacles are transparent (sometimes showing distinct white batteries of nematocysts) or they are of the same colour as the rest of the animal.

Geographical distribution (fig. 122). — In the western Indian Ocean the species occurs from the Gulf of Aqaba towards southern Mozambique. The southernmost location is at the Houtman Abrolhos Islands off Western Australia. In the Pacific Ocean specimens have been collected from Okinawa (Ryukyu Islands) towards Nouméa (New Caledonia). Its most eastward location is at the Samoa Islands.

Remarks. — In the literature there is much confusion about the identity of this species. Whether the types are still available for research remains unclear. (My request for a loan at the ZSI was not answered). Matthai (1924), while studying Alcock's material in the Indian Museum (at present ZSI), thought that the species could not be distinguished from *Diaseris distorta*. This may be the reason why he did not mention that the specimens he illustrated (Matthai, 1924: pl. 10 figs. 2-4) actually are syntypes of *D. fragilis*. One of the specimens he studied (Matthai, 1924: pl. 10 fig. 2) is even the same coral as the one which was illustrated by Alcock (1893: fig. 11). The photographs given by Matthai

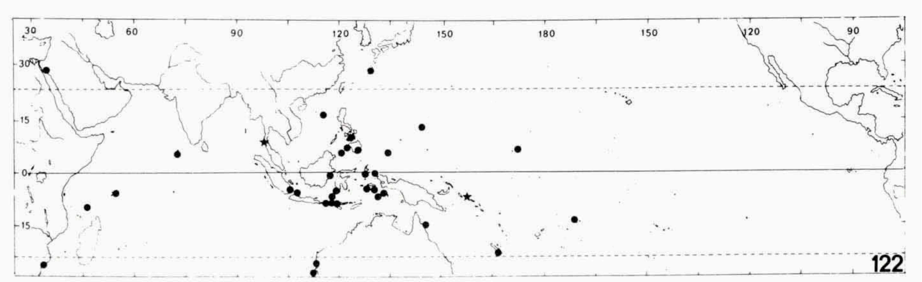


Fig. 122. The range of *Fungia (Cycloseris) fragilis*. Records are from examined material (●) and published illustrations (★).

are clearer than Alcock's drawing and are therefore more useful for a study of the types.

Döderlein (1902: 66), in his revision of *Fungia*, erroneously synonymized *Diaseris fragilis*, together with some other species, with *F. patella* Ellis & Solander (= *F. fungites*). Since his revision the taxonomic status of *F. fragilis* has remained unclear in the literature.

Whether *Cycloseris decipiens* is synonymous with *D. fragilis* is not clear. Although its syntypes resemble most specimens of *F. fragilis*, they are too much abraded to consider *C. decipiens* as a senior synonym of *D. fragilis*.

Boschma (1923c) identified specimens of *F. sinensis* erroneously as *F. fragilis*. Coralla of the latter species he described as *F. patelliformis*. The syntypes of *F. patelliformis* are from several localities. A lectotype is designated because one of the other type specimens belongs to *F. cyclolites*.

The type specimens of *F. laciniosa* belong to several species. The specimen presently designated as lectotype has irregularly frayed septal margins, an anomaly not uncommon in *Fungia*. Boschma (1925) considered the frayed septal margin a diagnostic character.

Especially in the field, corals of *F. fragilis* can easily be confused with those of *F. costulata*. They can be distinguished, however, because they are more fragile, i.e. their septa and their corallum margin are thinner. The costae of *F. costulata* are more equal in size, whereas those of *F. fragilis* are distinctly alternatingly exsert.

Of all fragmenting species in *Fungia*, *F. fragilis* has the most fragile coralla. Specimens of this species show some similarities with those of *F. cyclolites* and *F. somervillei*, especially in the septal form and arrangement, but the coralla are rounder and thinner than those of the other two species.

Fungia (Cycloseris) hexagonalis Milne Edwards & Haime, 1848
(figs. 123-135, 613)

Fungia hexagonalis Milne Edwards & Haime, 1848: 89, pl. 6 figs. 2-2f ("les Philippines"); Döderlein, 1902: 61-62; Boschma, 1925: 188-192, pl. 5 figs. 1-11, pl. 11 figs. 136-137.

Cycloseris hexagonalis — Milne Edwards & Haime, 1851: 113; 1860: 51; Pillai, 1972: 203; 1983: 85. Not: Gardiner, 1899a; 1899b; Wells, 1954; Maragos, 1977; Nemenzo, 1980.

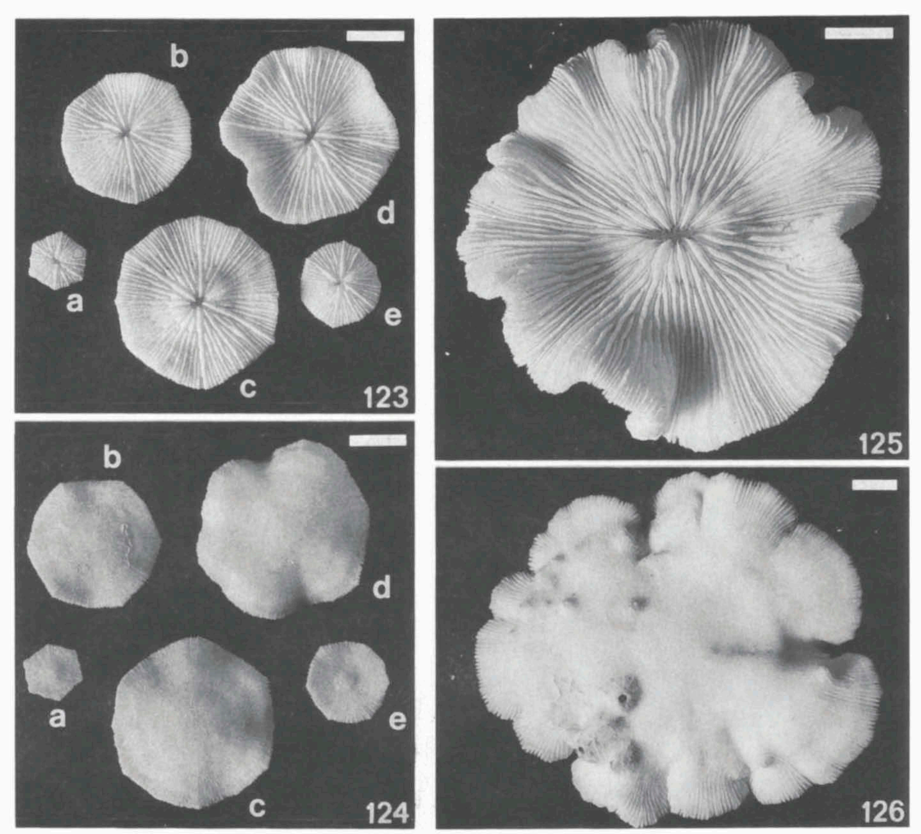
Cycloseris tenuis — Moseley, 1881: 190, pl. 10 figs. 6-6a; Bassett-Smith, 1890: 446.

Fungia patella — Döderlein, 1902: 65-73 (partim); Van der Horst, 1921: 57-58 (partim), pl. 1 fig. 1; Faustino, 1927: 168-169 (partim).

Fungia tenuis — Boschma, 1923c: 133-135, pl. 9 figs. 1-7a, 12.

Fungia distorta — Boschma, 1925: 203-204, pl. 6 figs. 55-64.

Cycloseris cyclolites — Nakamori, 1986: pl. 24 fig. 1.



Figs. 123-126. Corals (anthocyathi) of *Fungia (Cycloseris) hexagonalis*. Scale bars: 1 cm. Figs. 123-124. Upper and lower surface of juveniles (RMNH 16005; Banda, Indon.). Fig. 125. Upper surface of the neotype of *Fungia hexagonalis* (ANSP CN4521 SW Luzon, Philipp.). Fig. 126. Aboral surface of a large coral (RMNH 8291; Banda).

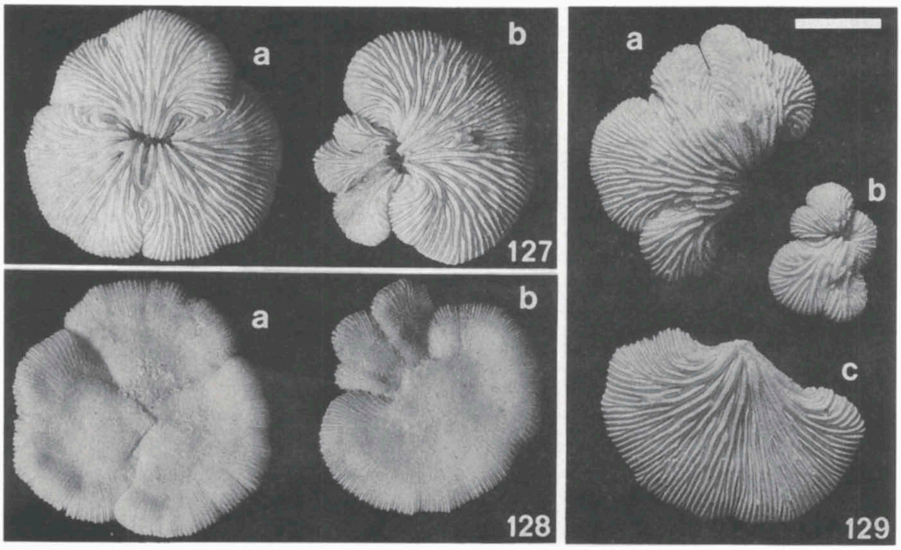
Type material examined. — ANSP CN4521 (neotype [present designation] of *Fungia hexagonalis*; type loc. Corregidor I., Manila Bay, SW Luzon, PHILIPPINES; see fig. 125).

Other material. — S CHINA SEA. Tizard Bank: BMNH 1889.9.24.44 (2). PHILIPPINES. SW Luzon: ANSP CN4522. Masbate: USNM 77949. INDONESIA. Paternoster Is.: ZMA 5519. Komodo: RMNH 21418 (70), 21518 (4). Banda: RMNH 8267 (253), 8287 (9), 8289-8297 (70), 8332 (2), 9486 (2), 15798-15799 (72), 16005 (13), ZMA 722, 5505-5506 (13). Kei Is.: RMNH 8268-8269 (58), 8327 (4), 8330 (2), 15797 (19). PAPUA NEW GUINEA. Bismarck Sea: ULB. TONGA IS.: BMNH 1880.11.25.138.

Characters. — Adult animals are free-living and usually monostomatous. Small specimens have a hexagonal outline, whereas larger ones become irregularly circular with an undulating or even crinkled margin. The coralla may also consist of regenerating wedge-shaped fragments (figs. 127-129). In the wall of some specimens clefts can be observed along which fragmentation may take place (fig. 128). The coralla are thin and usually flat. In particular the larger corals are concave near the margin and a little convex around the central fossa. The diameter of the specimens varies between 1.0 and 8.5 cm.

The central fossa is very small: its length, measured at its bottom, is 1/13 to 1/9 of the corallum length. The septal edges around the fossa stand upright. Those at both ends, however are slightly diverging. The columella is formed by a mingled mass of tightly packed trabeculae and paliform lobes with the tips pointing in various directions.

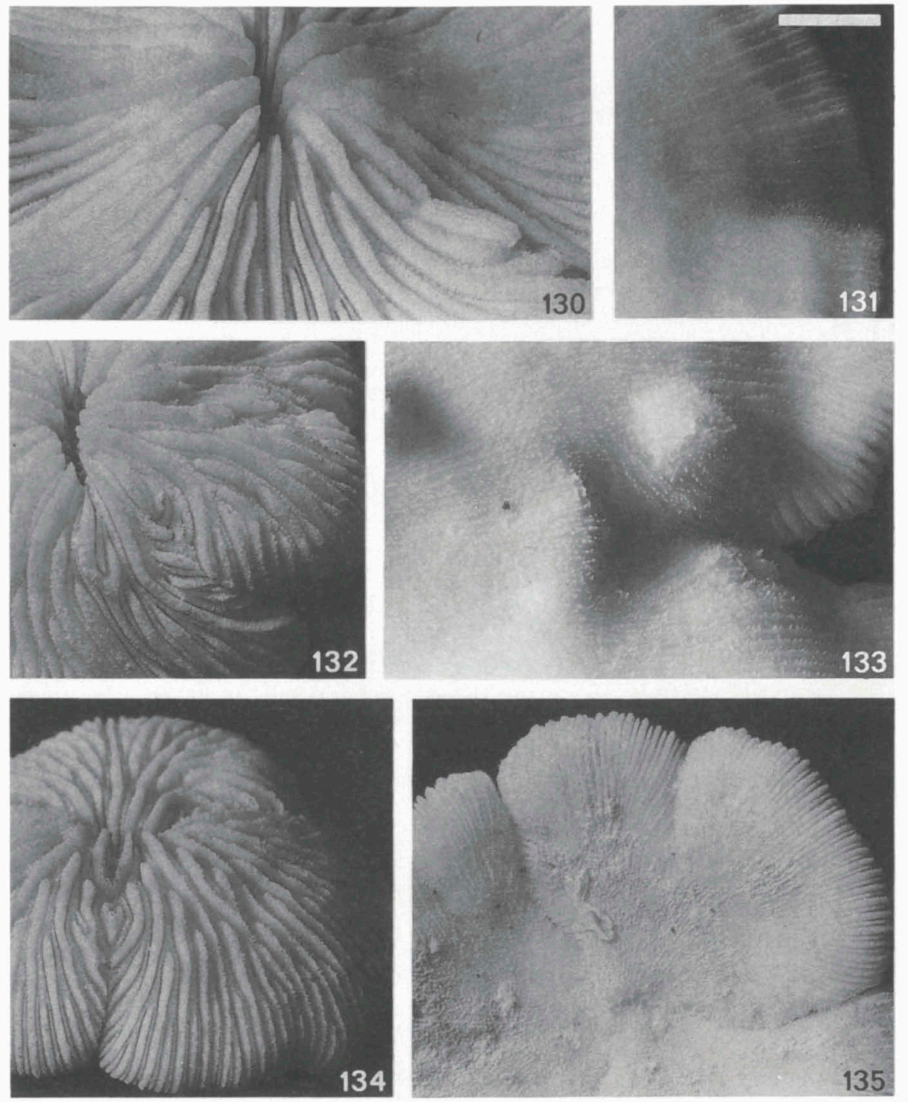
The septa are densely packed and straight in small specimens. In the larger specimens they bend where the corallum margin is undulating or folded. The septa of lower orders are thick, exsert and solid; those of higher orders thin and often fenestrate. The septa of the first two cycles are more prominent than the other ones, and this feature is most distinct in immature specimens (fig. 123). Tentacular lobes are absent. The septal margins are ornamented with small, sharp granular dentations. Their number varies from 50 to 100 per cm. In the largest specimens the septal margins are broad and the dentations less conspicuous which gives the margins a smooth appearance (figs. 130, 132, 134). The septal sides are densely covered by fine granulations which are evenly dispersed or arranged in rows perpendicular to the septal margin (fig. 613). The compound synapticulae, which connect the septa laterally, can



Figs. 127-129. Fragments of *Fungia (Cycloseris) hexagonalis* from Banda, Indonesia. Scale bar: 1 cm. Figs. 127-128. Upper and lower surface of two corals (RMNH 15798) of which (a) has regenerated almost completely and (b) has grown a new part that is splitting again. Fig. 129. Upper surface of three corals (RMNH 8267) of which (b) has regenerated a half disc.

easily be detected in spite of the tight septal arrangement.

The solid corallum wall is ungranulated and may show a detachment scar at



Figs. 130-135. Close-ups of *Fungia (Cycloseris) hexagonalis* corals from Banda, Indonesia. Scale bar: 0.5 cm. Fig. 130. Septa of an unfragmented coral (RMNH 15799) showing fine dentations on the septal margin and a dense granulation pattern on the septal sides. Fig. 131. Costae of the same coral showing fine, needle-like spines. Fig. 132. Septa of a partly regenerated fragment (RMNH 15798). Fig. 133. Costae of the coral in fig. 126. Fig. 134. Septa of the coral in fig. 127a. Fig. 135. Costae of the same coral showing thin acute spines.

the aboral side of small specimens in anthocyathus-stage. The corallum wall may partly be covered by epibionts (fig. 126). The costae are of almost equal thickness. They are straight and distinct near the corallum margin, but more vague at the centre. All costae are finely ornamented with small, acute granular spines (fig. 133). Their number varies from 50 to 100 per cm.

The colour of the living animal varies from brown to green or yellow. The small tentacles have the same colour as the rest of the animal or are transparent.

Geographical distribution (fig. 136). — The species is known from a few localities in the Central Indo-Pacific and from the Tonga Islands. Westward the range borders the Indian Ocean at Komodo. Its Pleistocene location at the Ryukyu Islands is not indicated (Nakamori, 1986: pl. 24: fig. 1).

Remarks. — The type specimens of *F. hexagonalis* were part of the collection of Stokes (Milne Edwards & Haime, 1848). At present this collection is at the BMNH, although it is no longer complete. The only specimens that remained are two small unnamed mushroom corals from unknown locality (BMNH 1855.12.27.30). They actually belong to *F. vaughani* and do not resemble any of the syntypes illustrated by Milne Edwards & Haime (1848: pl. 6 figs. 2-2f). In the Milne Edwards & Haime collection at the MNHN a specimen of *Fungia curvata*, labelled as *Fungia hexagonalis*, is found (MNHN 233). It does not resemble any of the illustrated syntypes and it is neither mentioned in the text, nor in the captions of the figures given by Milne Edwards & Haime (1848: 89). Because none of the syntypes of *F. hexagonalis* can be retraced and because there is some confusion about the identity of this species, a neotype from the type locality has been designated (fig. 125), which resembles the largest syntype figured by Milne Edwards & Haime (1848: pl. 6 fig. 2).

Döderlein (1902: 66) erroneously synonymized *Fungia hexagonalis*, together with some other species, with *F. patella* Ellis & Solander (= *F. fungites*). As a result of Döderlein's revision the identity of *F. hexagonalis*

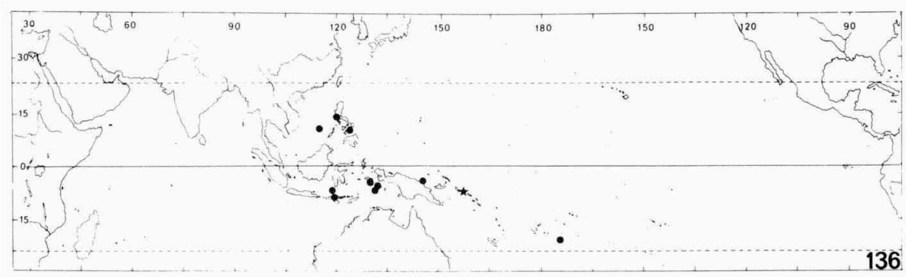


Fig. 136. The range of *Fungia (Cycloseris) hexagonalis*. Records are from examined material (●) and published illustrations (★).

became temporarily less clear until Boschma (1925: 188) redescribed the species.

F. hexagonalis has a fossa which is almost as short as that of *F. sinensis*. It can be distinguished from the latter species by its protruding first and second order septa and by its hexagonal or undulating margin. A hexagonal outline can also be seen in small specimens of *F. vaughani* and *F. costulata*. Corals of these two species are thicker and have longer fossae.

Fungia (Cycloseris) costulata Ortmann, 1889
(figs. 5, 137-156)

Fungia costulata Ortmann, 1889: 519, pl. 14 fig. 8 ("von der Südküste Ceylons"); Döderlein, 1902: 81, pl. 4 figs. 2-2a, pl. 5 figs. 7-7a; Gardiner, 1909: 271-272, pl. 35 fig. 9; Yabe & Sugiyama, 1935: 396; Umbgrove, 1946a: 91, pl. 1 figs. 5-6; Hoeksema & Moka, 1989: fig. 12.

Fungia patella — Vaughan, 1907a: 128-130 (partim); Van der Horst, 1921: 57-58 (partim); Faustino, 1927: 168-170, pl. 46 figs. 1-2; Montanaro, 1932: 177-178, pl 21 figs. 1-2.

Cycloseris cyclolites — Gardiner, 1905: 944-945 (partim); Schuhmacher, 1979: fig. 3.

Fungia (Cycloseris) halophila Felix, 1915: 32-33, pl. 38 figs. 4-4b (Plio-Pleistocene, "aus der Umgebung von Basleo bei Niki Niki auf Timor"). (New synonymy).

Fungia (Cycloseris) patella — Felix, 1921: 39-40.

Fungia (Cycloseris) wanneri Felix, 1921: 36-37, pl. 141 figs. 3-3a (Miocene, "Britisch Ost-Borneo"). (New synonymy).

Fungia sibogae Van der Horst, 1921: 59-60, pl. 1 figs. 3-4 (Siboga Exped., "Stat. ? 2 ex."); Nemenzo, 1971: 155-156, pl. 5 fig. 1; Van Soest, 1979: 107; Nemenzo, 1981: 184, fig. 201; 1986: 141, fig. 162. (New synonymy). Not: Umbgrove, 1946a.

Fungia marginata Boschma, 1923c: 141-142 (partim), pl. 9 figs. 8-8a, pl. 10 figs. 24-26 ("Siboga Exped. Sta. 315", "Anchorage East of Sailus Besar", Paternoster Islands, Indonesia); Boschma, 1925: 199-202 (partim), pl. 5 fig. 22, pl. 6 figs. 50-54; Van Soest, 1979: 107. (New synonymy).

Fungia döderleini Yabe & Sugiyama, 1941: 77 (partim; Solomon Is.); Shirai, 1980: 527. (New synonymy). Not: Nemenzo, 1971.

Not *Fungia döderleini* Von Marenzeller, 1907.

Cycloseris marginata — Vaughan & Wells, 1943: pl. 18 fig. 3; Ditlev, 1976: 6; Scheer & Pillai, 1983: 77. Not: Scheer & Pillai, 1974; Veron & Pichon, 1979; Nemenzo, 1980; Veron, 1986b.

Cycloseris patelliformis — Wells, 1954: 447, pl. 157 figs. 1-3.

Cycloseris costulata — Pillai, 1972: 203; Pillai & Scheer, 1976: 42; Veron & Pichon, 1979: 110-112, figs. 175-177; Pillai, 1983: 85; Scheer & Pillai, 1983: 77, pl. 17 figs. 1-5; Randall & Myers, 1983: 17, figs. 333-334; Wood, 1983: 111, 144; Johnston, 1986: 159; Veron, 1986a: 31; Veron, 1986b: 323; Veron & Kelley, 1988: 26, 28; Veron & Marsh, 1988: 81 (partim). Not: Wijsman-Best, Faure & Pichon, 1980.

Cycloseris erosa — Veron & Pichon, 1979: 113, figs. 178-179; Veron, 1986b: 323; Veron & Kelley, 1988: 28.

Cycloseris c.f. *costulata* — Wood & Tan, 1987: 197.

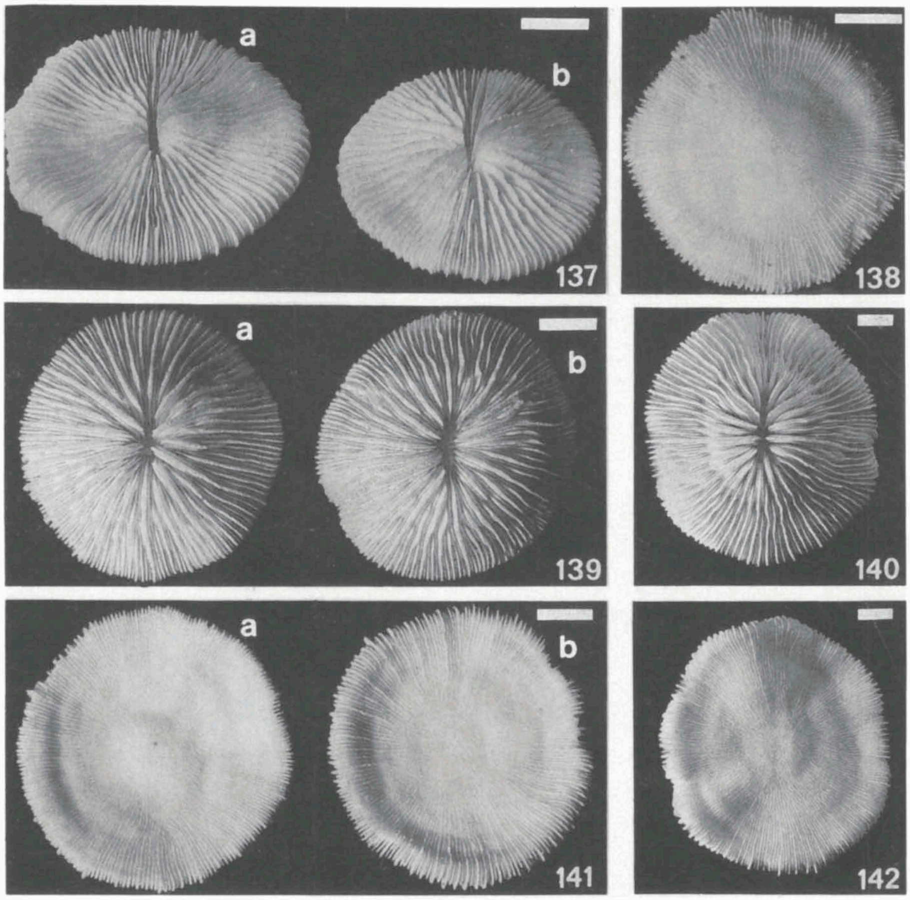
Cycloseris vaughani — Veron, 1986a: 31 (partim); Veron & Marsh, 1988: 81 (partim).

Cycloseris sinensis — Veron & Marsh, 1988: 82 (partim).

Type material examined. — UMZC (neotype [present designation] of *Fungia costulata*; type loc. Pearl Banks, SRI LANKA; see Gardiner, 1905: pl. 91 fig. 19; 1909: pl. 35 fig. 9); ZMA 485 (holotype of *Fungia sibogae*; type loc. unknown); ZMA 604, 723 (syntypes of *Fungia marginata*;

type loc. Paternoster Is., INDONESIA).

Other material. — RED SEA. Gulf of Aqaba: HSC 2/4 (1), RMNH 18065 (6), USNM 78253 (2), 78256, 78267, 78269-78271. DJIBOUTI: USNM 21985 (3). N MADAGASCAR: USNM 77731 (5). SRI LANKA: USNM 77757 (2). MALAYSIA. Sabah: BMNH (1). PHILIPPINES: USNM 77963, 77984. INDONESIA: ZMA 477. N Sumatra: RMNH 9544 (3). Java: RGM 77772 (fossil). NW Java: RMNH 16122. E Kalimantan: RMNH 20927 (3), ZMA 451. SW Sulawesi: RMNH 15712-15714 (4), 20837-20838 (7), 20890 (3), 20910 (5), 20912-20915 (498), 20924 (2), 20938 (27), 20988 (3), 21007-21008 (29), 21017, 21030-21031 (23), 21066 (3), 21082-21084 (14), 21089 (8), 21091 (3), 21101 (6), 21129 (54), 21140 (84), 21228 (30), 21232 (29), 21245 (36), 21254 (7), 21260 (10), 21279 (13), 21331-21333 (31), 21388-21391 (24), 21397, 21447-21448 (6). Tiger Is.:

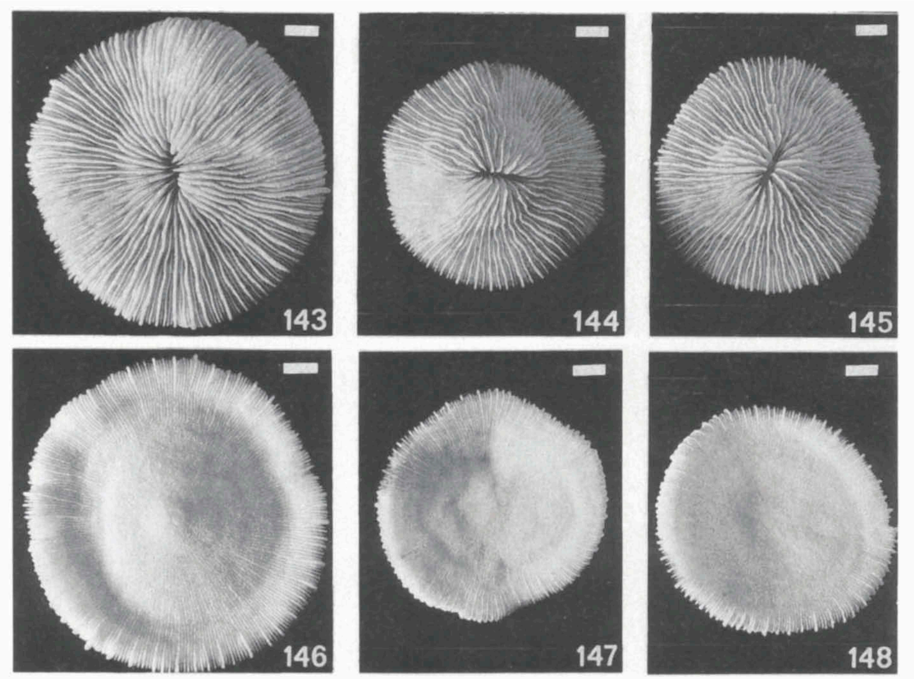


Figs. 137-142. Corals (anthocyathi) of *Fungia (Cycloseris) costulata*. Scale bars: 1 cm. Fig. 137. Upper surface of two syntypes of *Fungia marginata* (ZMUC; Banda, Indon.). Fig. 138. Aboral surface of the coral in fig. 137b. Fig. 139. Upper surface of two thick arched corals (RMNH 15714, 15713; SW Sulawesi, Indon.). Fig. 140. Upper surface of a thick flat coral (RMNH 20915; SW Sulawesi). Fig. 141a. Aboral surface of the coral in fig. 139a. Fig. 141b a coral from the same sample (RMNH 15714). Fig. 142. Aboral surface of the coral in fig. 140.

RMNH 20322 (6), 20593-20594 (7), 21168 (5), 21234, 21319 (2). Tukang Besi Is.: 20104. Komodo: RMNH 20811 (9), 21415 (6), 21471, 21584 (3). N Sumbawa: RMNH 20812 (2), 21336, 21348, 21626 (2), 21646 (2), 21680 (5). Banda: RMNH 8333-8339 (15), 8341-8343 (4), UZMK (27). PAPUA NEW GUINEA. Bismarck Sea: ULB. Gulf of Papua: WAM 819.84 (3). AUSTRALIA. Kimberley: WAM 387.83, 403.83, 178.85, 221.85, 222.85, 1011.85, 536.86, 757.86, 762.86. C Great Barrier Reef: QMB GL3610. S Great Barrier Reef: QMT. NEW CALEDONIA: USNM 78282, ZMA 6271, 6290. MARIANA IS. Guam: USNM 79993, 80442, 80445, 80449. MARSHALL IS.: USNM 44831 (3), 44833-44834. GILBERT IS.: MCZ 5412, USNM 77896-77898 (13). SAMOA IS.: QMT. COOK IS.: GPC. SOCIETY IS.: MNHN. MARQUESAS IS.: BMNH 1973.4.17.24.

Characters. — Adult animals are unattached and monostomatous. Juvenile specimens vary from round to slightly hexagonal, while full-grown corals vary from discoidal to slightly oval. Wedge-shaped, regenerating fragments are very rare. The corals are thick and vary from slightly concave to arched. The diameter of the examined coralla varies between 1.0 and 12.0 cm.

The length of the fossa, measured at its bottom, is 1/12 to 1/6 of the corallum length. The septal edges at both ends of the fossa diverge slightly, the other ones stand upright. The columella is formed by a mingled mass of loosely

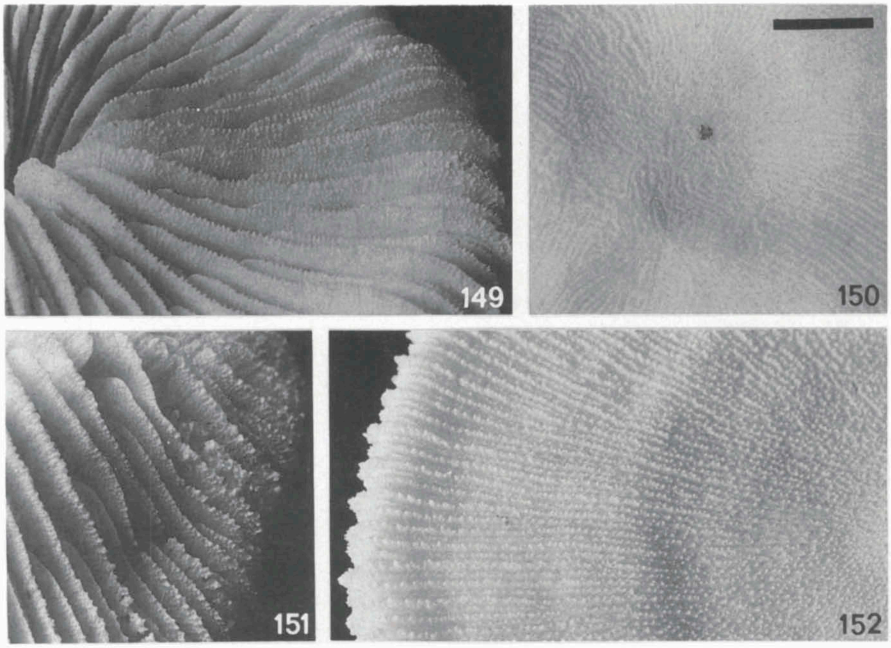


Figs. 143-148. Large corals (anthocyathi) of *Fungia (Cycloseris) costulata* with anomalously coarse septo-costal ornamentations (SW Sulawesi, Indon.). Figs. 143-145. Upper surface of three corals (RMNH 21083 [1], 21447 [2]). Figs. 146-148. Aboral surface of the same corals.

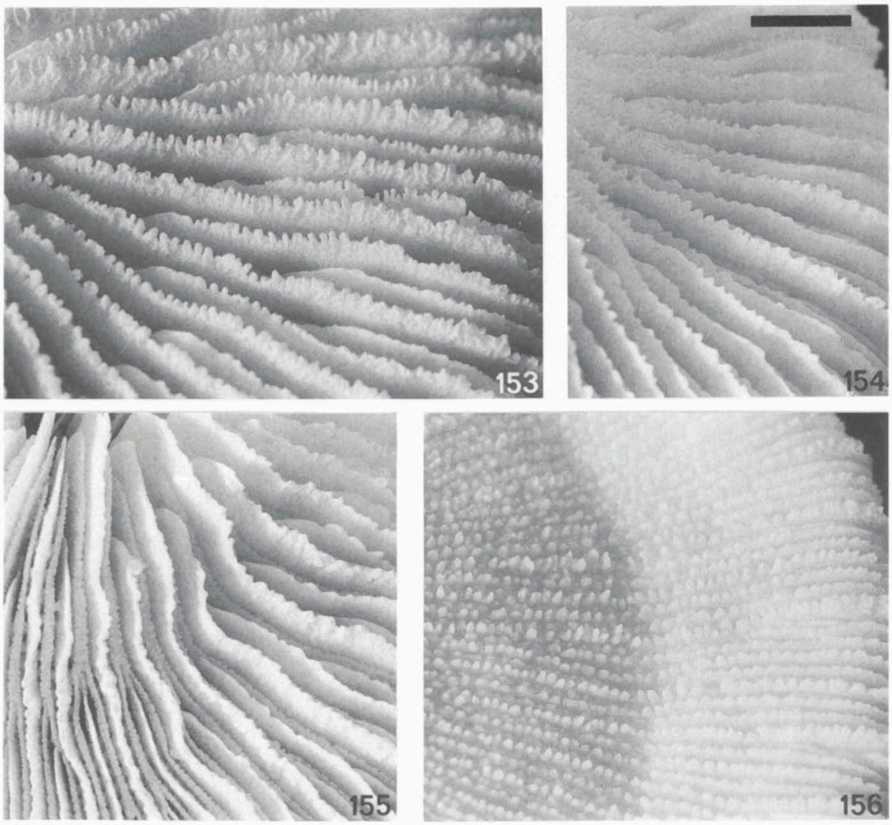
packed trabeculae and paliform lobes with the tips either pointing upwards or in various directions.

The septa are densely packed and straight. They are unequal in thickness and in height. The septa of lower orders, which are the thickest and highest, are solid; they are flanked by perforated septa of higher orders. Tentacular lobes are rare. The septal margins are usually finely ornamented with sharp and granular dentations (figs. 149, 151). The septal margins may also be irregularly ornamented, which gives them a frayed appearance (figs. 153-155). Their number varies from 10 to 70 per cm. The septal sides are densely covered by fine granulations which are irregularly dispersed or arranged in rows perpendicular to the septal margin. The compound synapticulae connecting the septa laterally can be distinguished in spite of the tight septal arrangement.

The solid corallum wall is ungranulated and may show a detachment scar at the aboral side of small specimens in anthocyathus-stage. The costae are almost equal in size; they are straight and prominent near the corallum margin (figs. 152, 156), but less distinct and sometimes intermingled near the centre (fig. 150). The costae are ornamented with fine or coarse, granular and acute



Figs. 149-152. Close-ups of *Fungia (Cycloseris) costulata* corals. Scale bar: 0.5 cm. Fig. 149. Septa of the coral in fig. 137a. Fig. 150. Centre of the aboral surface of the coral in fig. 141 showing intermingled costae. Fig. 151. Septa of the coral in fig. 139b. Fig. 152. Costae of the coral in fig. 142.



Figs. 153-156. Close-ups of large *Fungia (Cycloseris) costulata* corals. Scale bars: 0.5 cm. Fig. 153. Septa of the coral in fig. 143 showing frayed margins. Fig. 154. Septa of the coral in fig. 144 with the original dentation lost. Fig. 155. Septa of the coral in fig. 145. Fig. 156. Costae of the coral in fig. 146 with thickened, but still simple, costal spines.

spines. Their number varies from 15 to 80 per cm.

The living animal is usually brown with white (fig. 5), sometimes ochre. It rarely shows a violet margin. The small tentacles are transparent, green or brown.

Geographical distribution (fig. 157). — The range extends from the Red Sea and Madagascar towards the Society and the Marquesas Islands. In the NW Pacific it reaches the Ryukyu Islands (S Japan).

Remarks. — The loss of the holotype of *F. costulata* (loc. south coast of Sri Lanka) was already mentioned by Döderlein (1902: 81). Therefore the specimen described by Gardiner (1909) from the Pearl Banks near Ceylon is presently designated neotype. Two specimens in the USNM-collection are from the same locality.

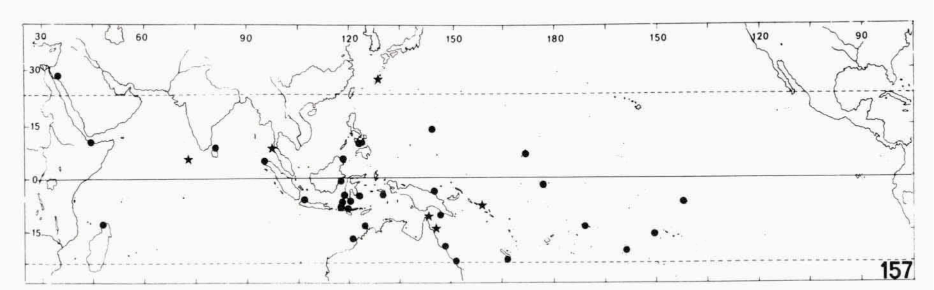


Fig. 157. The range of *Fungia (Cycloseris) costulata*. Records are from examined material (●) and published illustrations (★).

According to Boschma (1923c) *F. costulata* has costae which are more equal than those of *F. marginata*. When large series of *F. costulata* are made, however, it may be observed that in some specimens the costae of the first cycles are relatively thick and prominent, particularly at the corallum margin. This difference in size between low and high order costae, however, is very variable. Therefore it is concluded that the syntypes of *F. marginata*, despite their relative large costae, are relatively small, immature specimens of *F. costulata*.

To indicate another difference between *F. costulata* and *F. marginata*, Boschma (1923c: 141) states that the former species does not have an altogether solid wall. According to Ortmann (1889: 519) the corallum wall of *F. costulata* is solid, almost completely without perforations ("Wand dicht, fast ganz ohne Poren"). Ortmann's (1889: pl. 14 fig. 8) picture of the holotype of *F. costulata* clearly shows that the wall is abraded at one side, making it appear perforated.

The holotypes of *F. halophila* and *F. wanneri* fit in the large polymorphic range of *F. costulata*. Where they are kept is not known, but they are well enough illustrated to recognize them as corals belonging to *F. costulata*.

The holotype of *F. doederleini*, which actually is the specimen of *F. costulata* from the Solomon Islands (ZMB 4063a) figured by Döderlein (1902), is lost. The paratype, which was illustrated by Yabe & Sugiyama (1941), belongs to *F. granulosa*. They considered Döderlein's specimen not as belonging to *F. costulata* and therefore gave it a new name. Like Boschma (1923c) they were misguided by the abraded appearance of the holotype of *F. costulata*. Because Döderlein's specimen, i.e. the holotype of *F. doederleini*, definitely belongs to *F. costulata*, the two species are synonyms.

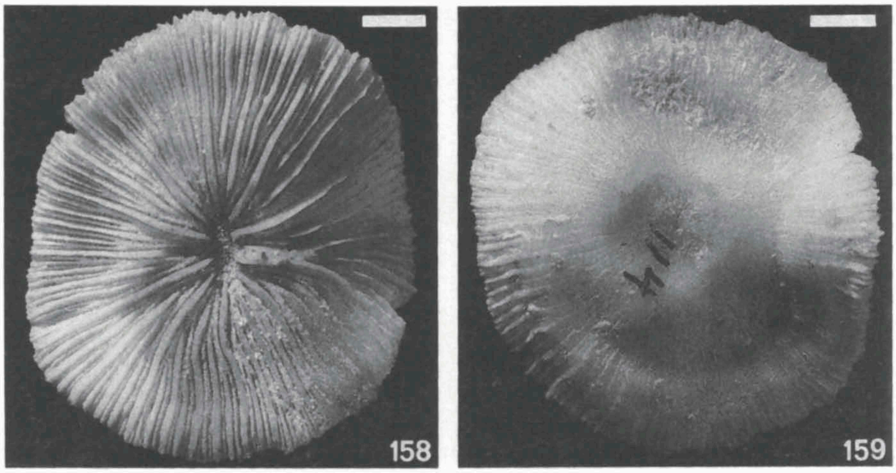
Specimens of *F. costulata* may be confused with those of *F. cyclolites*. They have a rounder outline, a shorter fossal opening and less distinct costae. *F. costulata* is more similar to *F. tenuis* and *F. vaughani*, but it has more equal costae.

Fungia (Cycloseris) tenuis Dana, 1846
(figs. 6, 158-175)

Fungia tenuis Dana, 1846: 290, pl. 18 fig. 1 ("Pacific Ocean, and probably the Paumoto Archipelago"); Döderlein, 1902: 61; Boschma, 1925: pl. 11 figs. 136-137. Not: Boschma, 1923c.
Cycloseris tenuis — not: Moseley, 1881; Cairns, 1984a.
Fungia erosa Döderlein, 1901: 357 (no locality given); Döderlein, 1902: 73-74, pl. 4 figs. 1, 1b, pl. 5 figs. 4-4a; Van der Horst, 1921: 6; Yabe & Sugiyama, 1941: 76 pl. 65 figs. 4-4d. Boshoff, 1981: 21. (New synonymy).
Fungia distorta — Döderlein, 1902: 74-77 (partim), pl. 3 figs. ee-ff, pl. 5 figs. 3-3a.
Cycloseris cyclolites — Gardiner, 1905: 944-945 (partim), pl. 91 figs. 17-19; Veron & Marsh, 1988: 81 (partim).
Fungia cooperi Gardiner, 1909: 275, pl. 35 fig. 10 ("Hulule, Male Atoll" and "Turadu, Mahlosmadulu Atoll, both Maldive Archipelago"); Boschma, 1929: 45. (New synonymy).
Fungia marginata Boschma, 1925: 199-202 (partim).
Fungia cyclolites — Boschma, 1925: 205-210 (partim).
Fungia moluccensis — Boschma, 1925: 210-214 (partim), pl. 6 fig. 49.
Cycloseris döderleini — Nemenzo, 1971: 154-155, pl. 5 fig. 2; 1981: 183, fig. 200; 1986: 141.
Cycloseris cooperi — Pillai, 1972: 202.
Cycloseris costulata — Veron & Marsh, 1988: 81 (partim).

Type material examined. — USNM 114 (holotype of *Fungia tenuis*; type loc. PAUMOTO ARCHIPELAGO?); UMZC (6 syntypes of *Fungia cooperi*; type loc. MALDIVES).

Other material. — DJIBOUTI: MNHN 1364. SEYCHELLES: BMNH 1981.3.5.462-463. MALDIVES: RMNH 14247, 15794, 22155, YPM 7837, 7844-7845. PHILIPPINES. SW Luzon: BMNH 1878.6.6.22. Mindoro: MCZ 3974 (3). Cebu: UPZD 1274-1275. S CHINA SEA. Macclesfield Bank: BMNH 1892.10.17.132. INDONESIA. SW Sulawesi: RMNH 15674, 15727, 20837 (2), 20904 (2), 21029 (5), 21607 (2), 21610, 21612 (20), 21632-21633 (177), 21635 (12), 21647 (4), 21662 (4), 21665 (4), 21677, 21679 (7), 21719, 21729 (2), 21731 (3), 21739 (7), 21749 (12), 21754 (19), 21755 (107), 21759 (57), 21769-21770 (5), 21772-21773 (6), 21775 (5), 21780 (4), 21785 (4),



Figs. 158-159. Upper and lower surface of the holotype of *Fungia tenuis* (USNM 114; Paumoto Is.?). Scale bar: 0.5 cm.

21793 (2), 21796, 22050 (4). Tiger Is.: RMNH 21081 (4), 21123 (3), 21175 (5), 21203. Komodo: RMNH 20399, 22051-22052 (8). N Sumbawa: RMNH 20534 (18), 20044 (4), 21623 (12), 21638 (8), 21678 (2). Tukang Besi Is.: RMNH 20047 (4), 20196 (2). S Moluccas: WAM 1378.88. Ambon: RMNH 8346. Banda: RMNH 8340, 8358. Arafura Sea: BMNH 1892.4.5.48/50. Biak: USNM 80021. AUSTRALIA. Kimberley: 262.83, 571.86. PAPUA NEW GUINEA. Bismarck Sea: ULB. MARIANA IS. Guam: USNM 79986-79987, 79997 (2), 80089 (2), 80092 (6), 80437-80438, 80440-80441, 80447. PITCAIRN IS.: USNM: 80080 (2).

Characters. — Adult animals are monostomatous and free-living. Their outline varies from discoidal to slightly oval. Fragmented, wedge-shaped specimens are rarily observed (only one specimen is known: RMNH 15674 from SW Sulawesi). The coralla vary from thin to thick and from flat to arched. The length of the specimens varies between 2.0 and 8.5 cm.

The length of the fossa, measured at its bottom, is 1/10 to 1/5 of the corallum length. The septal edges at both ends of the fossa diverge slightly, those at the sides stand upright. The columella is formed by a mingled mass of tightly packed paliform lobes with the tips pointing upwards or in various directions.

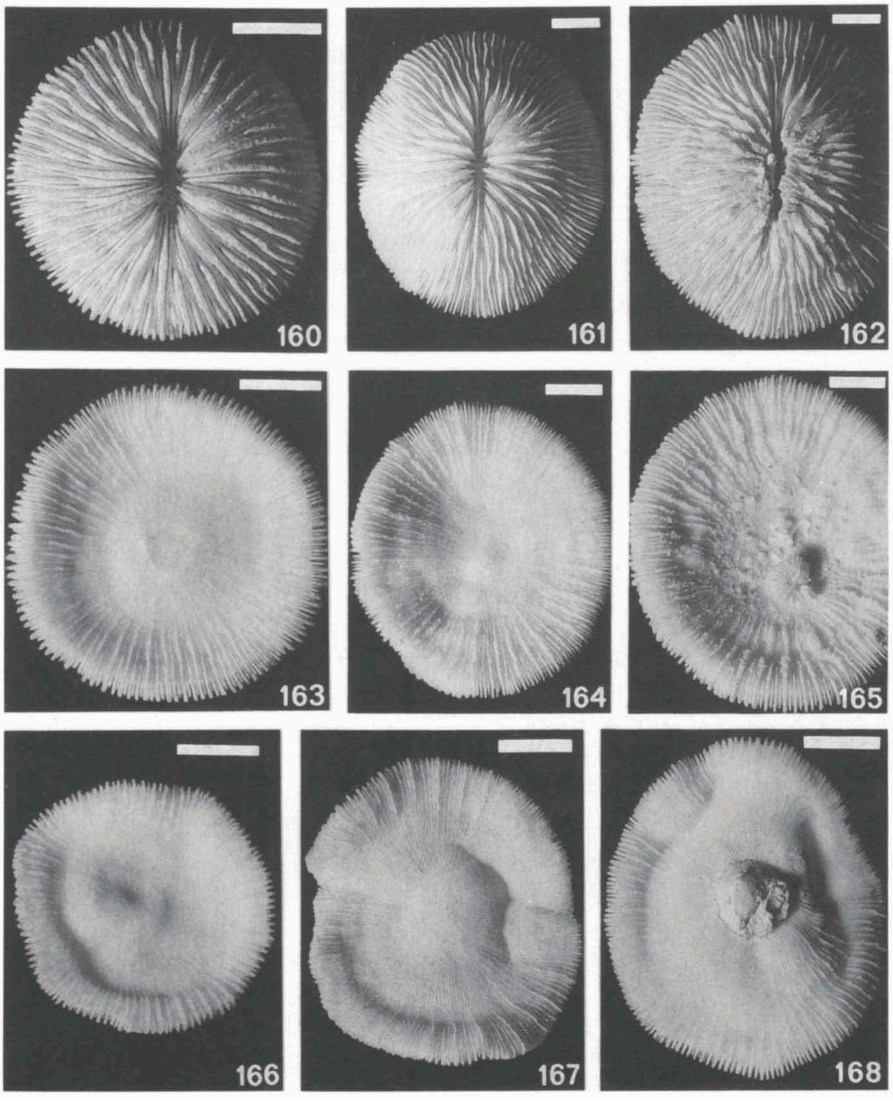
The septa are densely packed; they are either straight or a little wavy. The septa of lower orders are thick, solid and exsert. They are flanked by septa of higher orders which are thinner, lower and often fenestrate. Tentacular lobes are absent. The septal margins are ornamented with fine, sharp and granular dentations. Their number varies from 30 to 60 per cm. The septal sides are densely covered by fine granulations, which are irregularly dispersed or arranged in rows perpendicular to the septal margin. The compound synapticulae which connect the septa laterally cannot always easily be detected, because of the tight septal arrangement.

The solid corallum wall is ungranulated. It may show a detachment scar on small specimens in anthocyathus-stage (fig. 163). The costae are either straight or wavy. At the centre they are relatively unclear, equally sized and wavy, while towards the periphery they become more prominent, straight and less equal in size. The lower order costae are more exsert than the other ones. In small specimens the costae are finely ornamented with acute, granular spines. In large coralla the relatively thick lower order costae are irregularly covered with long spines, which point in various directions. The number of spines varies from 20 to 70 per cm.

The living animal is usually brown with white. Both ends of the mouth are often dark brown (fig. 6). The small tentacles are transparent.

Geographical distribution (fig. 176). — The longitudinal distribution of the species ranges from Djibouti towards the Pitcairn Islands, which in addition to being the most eastern limit are also the most southern. The northernmost location known is the south coast of Honshu, Japan.

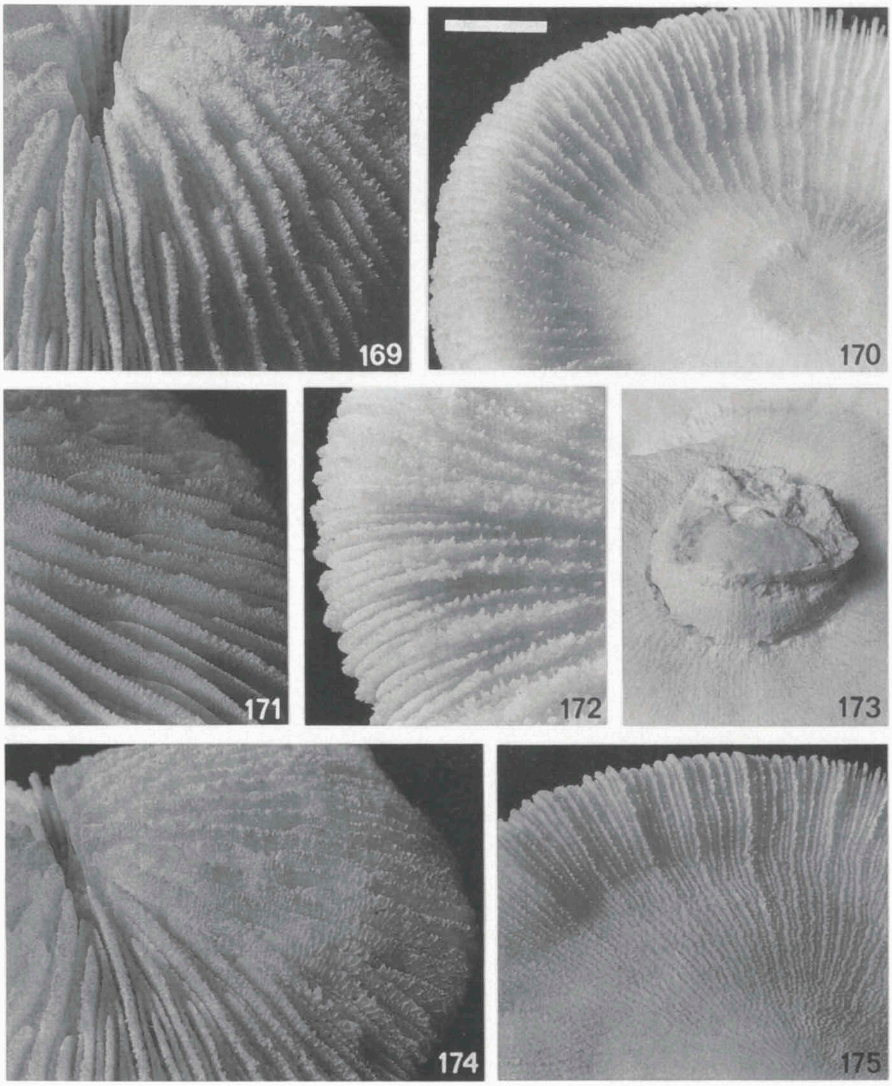
Remarks. — Although the holotype is small, it clearly shows the iregularly arranged unequal costae which make it easy to distinguish specimens of *F. tenuis* from those of other species. Döderlein (1902: 66), in his revision of



Figs. 160-168. Corals of *Fungia (Cycloseris) tenuis*. Scale bars: 1 cm. Figs. 160-162. Upper surface of three corals. Fig. 160. RMNH 8346 (Ambon, Indon). Fig. 161. RMNH 15727 (SW Sulawesi, Indon.). Fig. 162. RMNH 8358 (Banda, Indon.). Figs. 163-165. Aboral surface of the same corals. Note the newly developed anthocaulus at the aboral side of the coral in fig. 165. Figs. 166-168. Aboral surface of three corals. Fig. 166. RMNH 15794 (Maldives). Fig. 167. RMNH 8340 (Banda, Indon.). Fig. 168. RMNH 14247 (Maldives).

Fungia, erroneously synonymized *F. tenuis* with *F. patella* Ellis & Solander (= *F. fungites*). Since this synonymization, *F. tenuis* became more or less overlooked, which caused that its specimens remained unrecognized.

The holotype of *F. erosa* is no longer at the MZS (neither at the ZMB) and



Figs. 169-175. Close-ups of *Fungia (Cycloseris) tenuis* corals. Scale bar: 0.5 cm. Fig. 169. Septa of the coral in fig. 160. Fig. 170. Costae of the same coral. Fig. 171. Septa of the coral in fig. 161. Fig. 172. Costae of the same coral. Fig. 173. Centre of the aboral side of the coral in fig. 168; note the stalk with which it was attached to the substratum. Fig. 174. Septa of the coral in fig. 162. Fig. 175. Costae of the same coral.

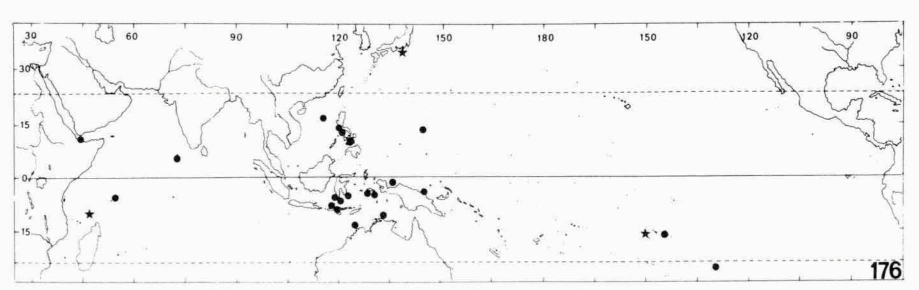


Fig. 176. The range of *Fungia (Cycloseris) tenuis*. Records are from examined material (●) and published illustrations (★).

must therefore be considered lost. Döderlein's (1902) pictures of the holotype are clear enough to show that the species' characters are similar to those of *F. tenuis*. The septal margins of the holotype are frayed, which is not an uncommon anomaly in *Fungia*. In this case it is not a useful diagnostic character and therefore *F. erosa* can be regarded as a junior synonym of *F. tenuis*.

Gardiner (1909) placed *F. cooperi* in Döderlein's (1902) *repanda* -group (currently better known as the subgenus *Verrillofungia*), although it lacks the typical septal and costal ornamentations of that group. The syntypes of *F. cooperi* cannot be distinguished from *F. tenuis* specimens; therefore *F. cooperi* must be considered a junior synonym of *F. tenuis*.

Apart from its costae, *F. tenuis* is very similar to *F. costulata*. *F. vaughani* has also exsert lower order costae, but these are sharper and more regularly arranged. *F. tenuis* is usually thicker than *F. vaughani* and does not show the other species' distinct rows of granulations on the costal sides.

Fungia (Cycloseris) vaughani Boschma, 1923
(figs. 7, 177-184, 615, 618)

Fungia patella — Vaughan, 1907a: 128-130 (partim), pl. 27 figs. 2-3a, pl. 28 figs. 2-2a ; Reed, 1971: 38, fig. 3.

? *Fungia (Cycloseris) stammi* Felix, 1921: 38-39, pl. 142 figs. 16-16a (Miocene, "Britisch Ost-Borneo").

Fungia vaughani Boschma, 1923c: 17-18, pl. 10 figs. 27-27b (Honolulu and Hilo, Hawaii); 1925: 205.

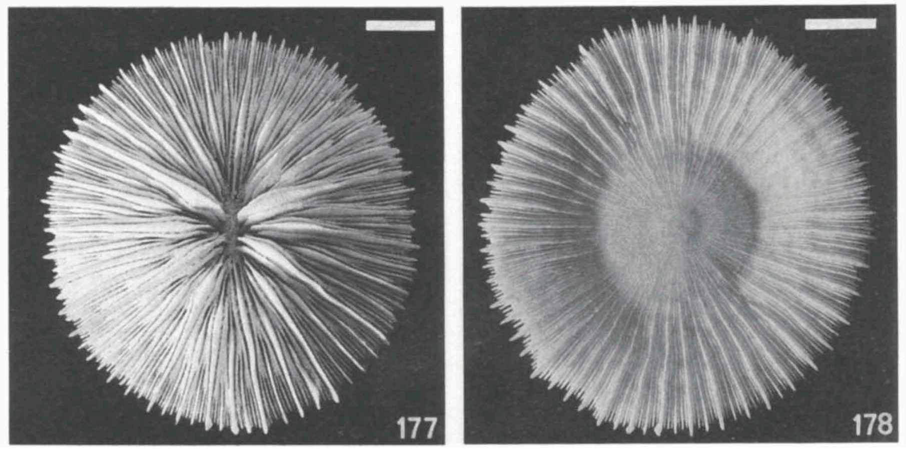
Cycloseris hexagonalis — Wells, 1954: 447; Maragos, 1977: 212, figs. 3, 86-87.

Cycloseris vaughani — Wells, 1954: 447, pl. 157 figs. 4, 6; 1972: 184-186, figs. 1.2-3; Maragos, 1977: 208-209, figs. 2, 82-83; Veron & Pichon, 1979: 116-118, figs. 188-191; Faure, 1982: 97; Randall & Myers, 1983: 17, figs. 335-336; Maragos & Jokiel, 1986: 144; Veron, 1986b: 325; Veron & Kelley, 1988: 28. Not: Veron, 1986a: 31; Veron & Marsh, 1988: 81.

Diaseris distorta — Cairns, 1984a: 8, pl. 1 fig. D.

Cycloseris tenuis — Cairns, 1984a: 8, 10, pl. 1 fig. E.

Cycloseris costulata — Veron & Marsh, 1988: 81 (partim).



Figs. 177-178. Upper surface and lower surface of the lectotype of *Fungia vaughani* (RMNH 8345; Hawaii). Scale bars: 1 cm.

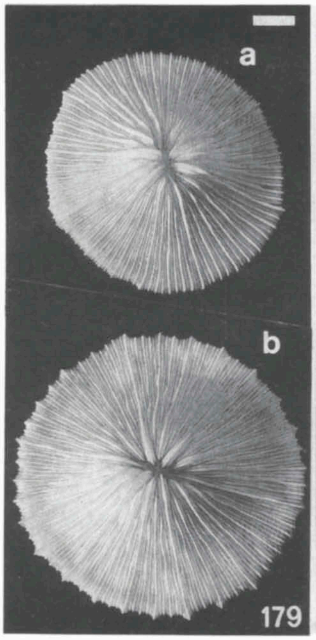
Type material examined. — RMNH 8345 (lectotype [present designation] of *Fungia vaughani*; type loc. Hilo, HAWAII); USNM 20835-20836 (3), UZMK (3) (paralectotypes of *Fungia vaughani*; HAWAII).

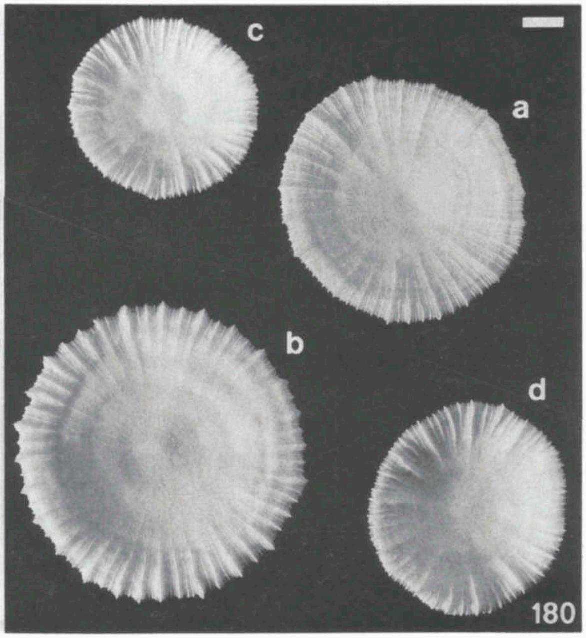
Other material. — N MADAGASCAR: USNM 77733 (3). MALDIVES: MCZ 3579 (11). S CHINA SEA. Tizard Bank: BMNH 1889.9.24.41/58. PHILIPPINES. Romblon: USNM 78091 (many frags.). Cebu: USNM 77939. Leyte: USNM 78093 (2). Sulu Is.: USNM 77777 (3), 77782, 77953 (2), 78087-78088 (many frags.), 78231, 80085. INDONESIA. SW Sulawesi: RMNH 20918, 22071-22079 (132). Tiger Is.: RMNH 22046 (3). Komodo: RMNH 21412 (9), 22047 (2). AUSTRALIA. Kimberley: WAM 485.84. N Great Barrier Reef: AIMS 14994-14995. PAPUA NEW GUINEA. Bismarck Sea: ULB. Gulf of Papua: WAM 826.84. NEW CALEDONIA: ZMA 6258. MARIANA IS. Guam: USNM 79985 (2), 79989, 79991-79992 (3), 79995 (5), 80090, 80093 (3), 80450. MARSHALL IS.: USNM 44824-44830 (12), 44832. HAWAII IS.: RMNH 8319 (6); USNM 60566-60584 (many small specimens), 62463-62467 (6), 77785, 78048-78052 (36), 78161-78217 (many frags.), YPM 6839. PITCAIRN IS.: USNM 80074, 80076-80078 (4), 80082. EASTER I.: USNM 53163 (2).

Characters. — Adult animals are monostomatous and free-living. The outline of complete corals varies from discoidal to slightly oval; they vary from thin to thick and from flat to slightly arched. Juvenile specimens have a hexagonal outline; they are thin and flat. The corals are able to break into wedge-shaped fragments which can regenerate into new individuals. The diameter of the examined specimens varies between 0.5 and 8.0 cm.

The length of the fossa, measured at its bottom, is 1/12 to 1/7 of the corallum length. The septal edges around the fossa stand upright, except at both ends, where they diverge. The columella is formed by a mingled mass of tightly packed trabeculae and paliform lobes with the tips either pointing upwards or in various directions.

The septa are densely packed and straight. The septa of lower orders are



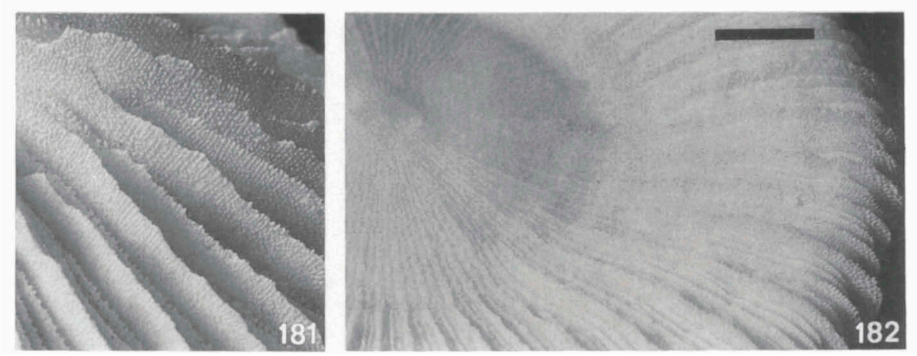


Figs. 179-180. Corals (anthocyathi) of *Fungia (Cycloseris) vaughani* (RMNH 22079; SW Sulawesi, Indon.). Scale bars: 1 cm. Fig. 179. Upper surface of two corals. Fig. 180. Aboral surface of the same corals and of two additional ones.

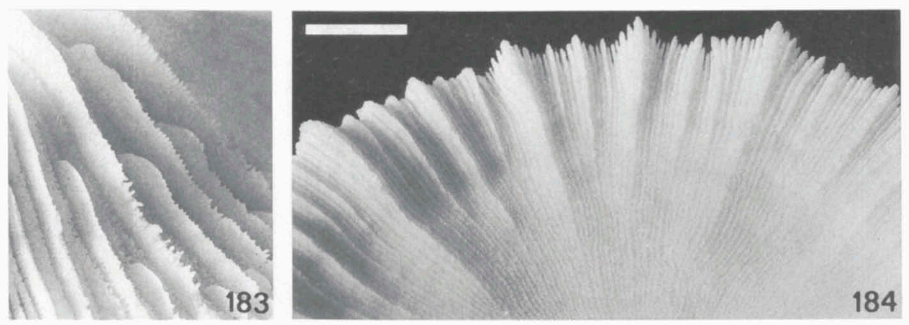
thick, solid and very high; those of higher orders are thinner, much lower and usually perforated. Tentacular lobes are absent. The septal margins are ornamented with small, sharp granular dentations. Their number varies from 40 to 90 per cm. The septal sides are densely covered by fine granulations which are arranged in rows perpendicular to the septal margin (figs. 181, 615). The compound synapticulae which connect the septa laterally can be detected, in spite of the tight septal arrangement.

The corallum wall is solid and, apart from the costae, it is not granulated. The wall may show an attachment scar on individuals in anthocyathus-stage. The costae are straight and distinct near the corallum margin, but become vague towards the centre. The lower order costae are more protruding than the other ones and have their sides covered by rows of granulations, like those on the septa (fig. 182). All costal margins are finely ornamented with granular and acute costal spines (fig. 618). Their number varies from 40 to 80 per cm.

The living animal is light to dark brown with white patches (fig. 7). The small tentacles are white or transparent. The mouth may be white, red or brown. The soft tissue at the aboral side of the animal is more tightly attached to the skeleton than it is in any other species.



Figs. 181-182. Close-ups of the lectotype of *Fungia vaughani* (RMNH 8345). Scale bar: 0.5 cm. Fig. 181. Septa. Fig. 182. Costae and the detachment scar. The granulation pattern on the septal sides continues on the costal flanks.



Figs. 183-184. Close-ups of *Fungia (Cycloseris) vaughani* corals. Scale bar: 0.5 cm. Fig. 183. Septa of the coral in fig. 179b. Fig. 184. Costae of same coral.

Geographical distribution (fig. 185). — The range extends from N Madagascar towards Hawaii and Easter Island.

Remarks. — In the description of *Fungia vaughani*, Boschma (1923) refers to corals studied by himself and to specimens described as *F. patella* by Vaughan (1907). A lectotype had to be designated because not all corals which Vaughan identified as *F. patella* actually belong to *F. vaughani*.

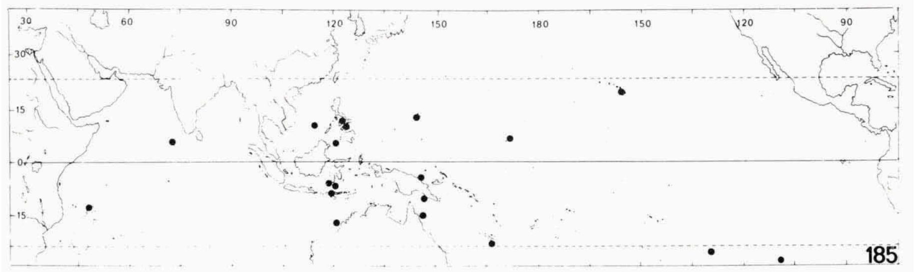


Fig. 185. The range of *Fungia (Cycloseris) vaughani*. Records are from examined material (●).

It is not clear whether *Fungia stammi* is synonymous with *F. vaughani* or not. The description and pictures given by Felix (1921) are not clear enough to compare the two species with each other. The underside of the figured holotype looks very much like that of *F. vaughani*, more than that of any other species.

A diagnostic character of *F. vaughani* is determined by its very sharp and protruding, regularly shaped lower order costae which resemble the septa very closely in their ornamentation. *F. tenuis* and *F. spinifer* are also species with relatively large lower order costae, but these are more irregularly ornamented. The costal spines of these species are irregularly shaped and point in various directions.

In the literature, juvenile specimens of the species have been misidentified as *F. hexagonalis*, a species of which small individuals also have a hexagonal outline. Even in juvenile stage, corals of the two species can easily be distinguished because those of *F. vaughani* have prominent low order costae and those of *F. hexagonalis* have a relatively smooth under-surface.

Subgenus **Verrillofungia** Wells, 1966

Type species: *Fungia repanda* Dana, 1846. By original designation.

Fungia (Verrillofungia) (partim) Wells, 1966: 238-239; Veron & Pichon, 1979: 146; Ditlev, 1980: 56; Chevalier & Beauvais, 1987: 706; Veron & Kelley, 1988: 31.

Characters. — The outline of the monostomatous animals is circular or slightly oval. All species are free-living. The corals remain complete, they do not break into wedge-shaped fragments. Adults of only one species have a perforated corallum wall. In no species the wall is granulated. The septal dentations vary from small to large. The granulations on the septal fringe are fused in ridges parallel to the septal margin. On large dentations they show zigzag patterns. In one species the costae are almost of equal size; in the other ones they are unequal. The costal spines are usually short, blunt and club-shaped; they are rarely long and sharp. The spines are covered by granulations which may give them an echinose appearance.

Remarks. — Before Wells (1966) described *Verrillofungia*, the group was known as the *repanda* -group, which for the first time was recognized as such by Döderlein (1901: 356; 1902: 105). Besides the well known species *F. repanda* and *F. concinna*, the subgenus also contains the less commonly known species *F. scabra*, and *F. spinifer*. *F. granulosa*, originally placed in the *repanda*-group by Döderlein (1901) and consequently classified with *F. (Verrillofungia)* by Veron & Pichon (1979), is now transferred to a new subgenus, *Wellsofungia*.

At first sight, some species of *Verrillofungia* showing an imperforate corallum wall may appear to be similar to species of *Cycloseris*. In the former subgenus the septal and costal ornamentations are more complex than those in the latter.

Fungia (Verrillofungia) spinifer Claereboudt & Hoeksema, 1987
(figs. 190-201)

Cycloseris hexagonalis — Nemenzo, 1980: 290-291.
Cycloseris marginata — Nemenzo, 1980: 291-292, fig. 1.
Cycloseris patelliformis — Nemenzo, 1980: 292-293, fig. 2.
Fungia (Verrillofungia) spinifer Claereboudt & Hoeksema, 1987: 304-308, figs. 2-8 (Laing Island, Bismarck Sea).

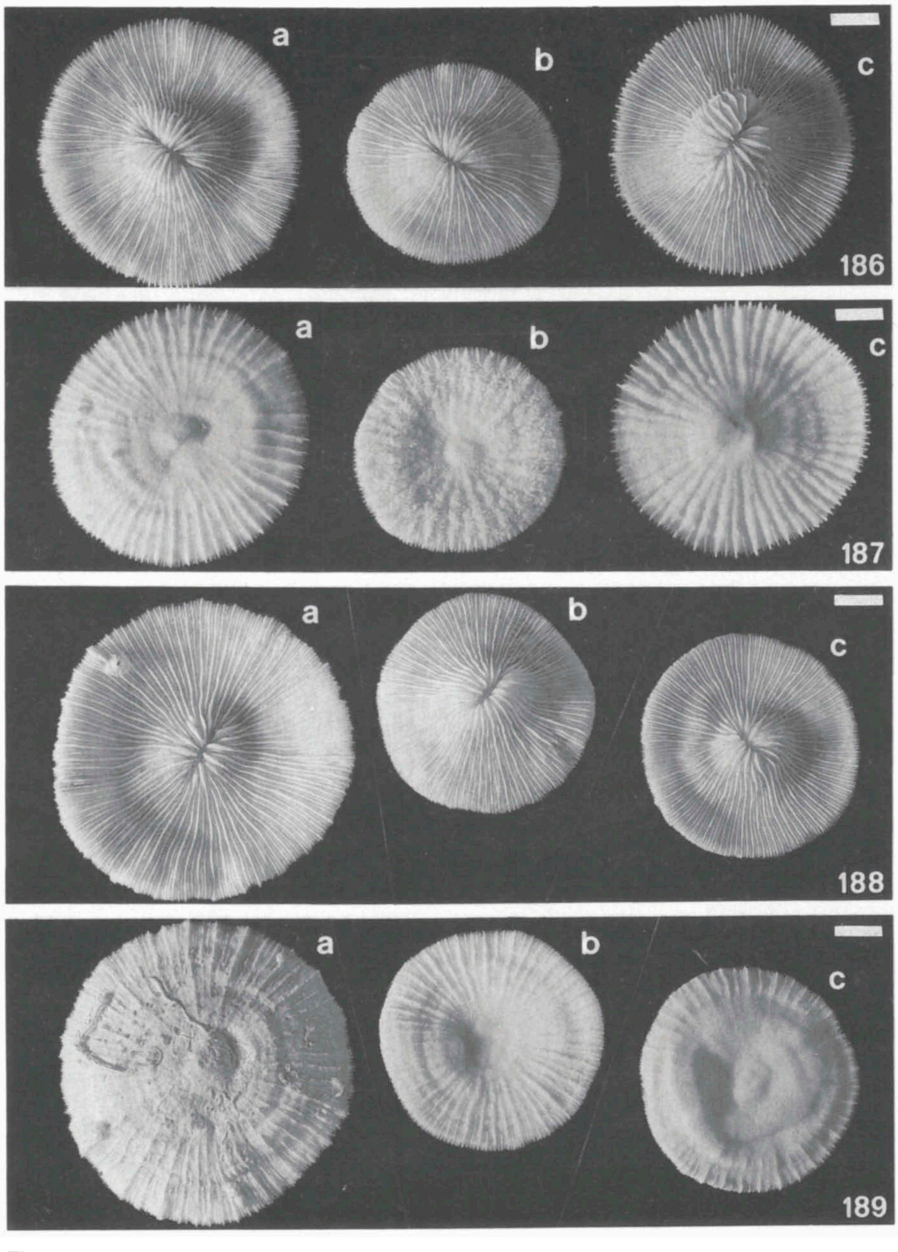
Type material examined. — RMNH 17620 (holotype) and RMNH 16621-17623, IRSNB/KBIN 27009-401 (4 paratypes of *Fungia spinifer*; type loc. Laing Island, Bismarck Sea, PAPUA NEW GUINEA; RMNH 17624, IRSNB/KBIN 27009-402 (2 paratypes of *F. spinifer*; Madang, PAPUA NEW GUINEA).

Other material. — S CHINA SEA. Macclesfield Bank: BMNH 1893.9.1.180/226. PHILIPPINES. Cebu: UPMSI 331-333. INDONESIA. E Kalimantan: RMNH 22175 (2). SW Sulawesi: RMNH 22057, 22096-22097. N Sumbawa: RMNH 21645. Komodo: RMNH 22174. PAPUA NEW GUINEA. Bismarck Sea: ULB. Solomon Sea: WAM 419.81. MARIANA IS. Guam: USNM 79996.

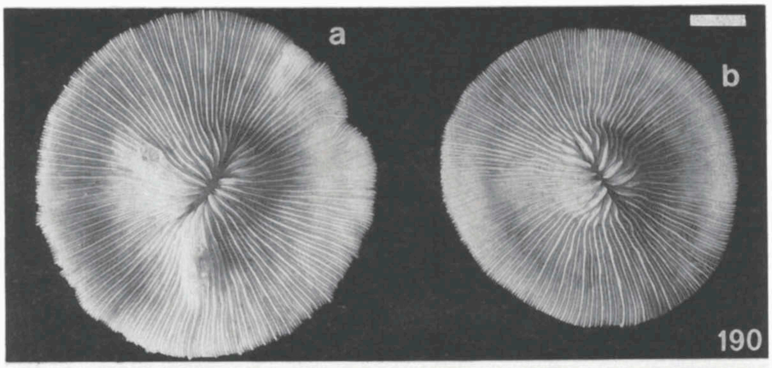
Characters. — Adult animals are monostomatous and unattached. They are discoidal, thin and usually flat but sometimes slightly arched or concave. They do no form fragmentation slits. The diameter of the specimens varies between 1.5 and 12.5 cm.

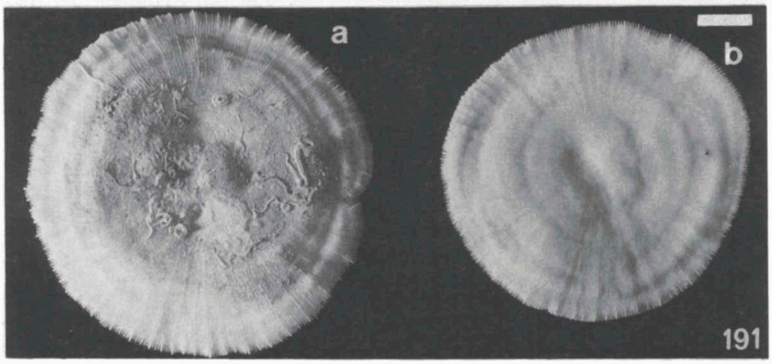
The length of the central fossa, measured at its bottom, is 1/13 to 1/6 of the coral length. The septal edges at both sides of the fossa stand perpendicular to the bottom of the fossa, whereas those at both of its ends diverge away from it. The columella is formed by a mingled mass of tightly packed, partly fused trabeculae and paliform lobes, which have their tips pointing in various directions.

The septa are densely packed and straight. The solid septa of lower orders are thicker and more protruding than the partly perforated septa of higher orders. Tentacular lobes are absent. The septal margins are ornamented with fine, angular dentations (figs. 192-194). Their number varies from 30 to 60 per cm. The septal sides are densely covered by fine granulations which are partly



Figs. 186-189. Corals (anthocyathi) of *Fungia (Verrillofungia) spinifer*. Scale bars: 2 cm. Figs. 186-187. Upper and lower surface of type specimens from Papua New Guinea showing strongly developed costae: (a) the holotype (RMNH 17620), (b-c) two paratypes (RMNH 17623, 17622). Figs. 188-189. Upper and lower surface of corals from Indonesia with slightly exsert costae from: (a) Komodo (RMNH 22174), (b) SW Sulawesi (RMNH 22096), (c) N Sumbawa (RMNH 21645).



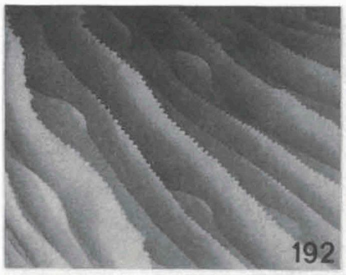


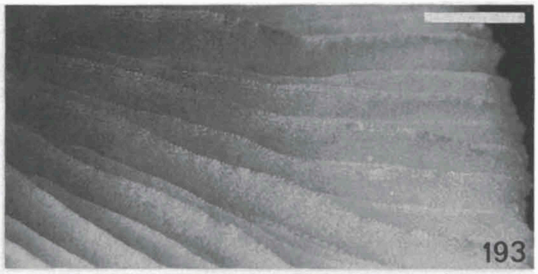
Figs. 190-191. Upper and lower surface of two corals (anthocyathi) of *Fungia (Verrillofungia) spinifer* from SW Sulawesi (Indonesia) showing slightly developed costae: (a) RMNH 22097 and (b) RMNH 22057. Scale bars: 2 cm.

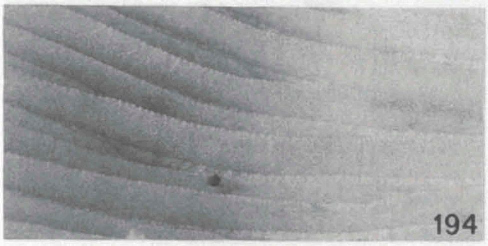
fused in ridges parallel to the septal margin (figs. 193-194). The compound synapticulae which connect the septa laterally can easily be detected.

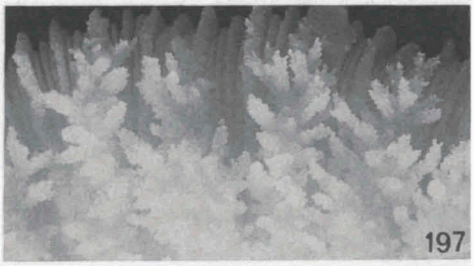
The corallum wall is solid and not granulated; it may show a detachment scar at the aboral side of small specimens in anthocyathus-stage. The underside may be partly overgrown by epibionts (figs. 189a, 191). The costae are unequal in size; those of lower orders usually grow relatively thick and exsert, those of higher order cycles remain smaller. The costae are usually straight and distinct near the corallum margin, whereas they are less distinct and sometimes undeveloped at the centre (figs. 187, 189). The costae are ornamented with spines which vary from extremely echinose, long and directing in various directions (figs. 196-197) to small and granular (figs. 198-199), or to smooth, blunt, and laterally flattened (figs. 200-201). The number of the spines varies from 12 to 40 per cm.

The colour of the living animal varies from brown to greyish violet. The small tentacles are transparent. The margin of the mouth is radially striped in violet and white.









Figs. 192-201. Close-ups of *Fungia (Verrillofungia) spinifer* corals. Scale bar: 0.5 cm. Fig. 192. Septa of the paratype in fig. 186c showing distinct tentacular lobes and fine dentations. Fig. 193. Septa of the coral in fig. 188b showing the granulation pattern on its sides. Fig. 194. Septa of the coral in fig. 190a showing the granulation pattern. Fig. 195. Costae of the holotype (see fig. 187a). Fig. 196. Costae of the coral in fig. 187c. Fig. 197. Costae of the coral in fig. 187b. Fig. 198. Costae of the coral in fig. 189b. Fig. 199. Low costae with short, almost granular spines of the coral in fig. 189c. Fig. 200. Slightly exsert costae with short, blunt spines of the coral in fig. 191a. Fig. 201. Slightly exsert costae with short, blunt spines of the coral in fig. 189a.

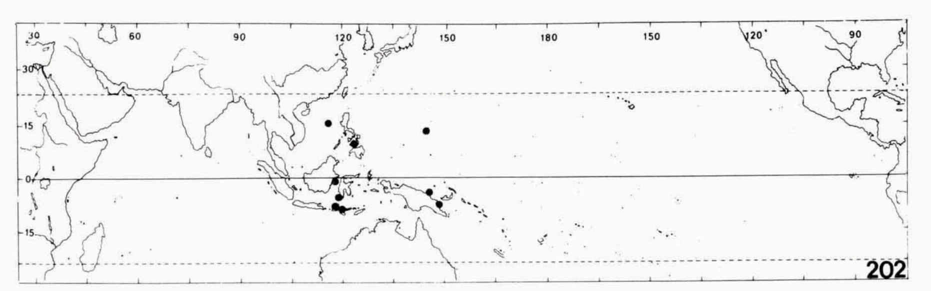


Fig. 202. The range of *Fungia (Verrillofungia) spinifer*. Records are from examined material (●).

Geographical distribution (fig. 202). — The species has been recorded in the Central Indo Pacific, from the South China Sea to the Marianas (Guam).

Remarks. — Because of its most commonly observed thin and flat shape, *F. spinifer* may be confused with *F. fragilis*, *F. vaughani* or some other species belonging to *Fungia (Cycloseris)*. It differs from these species by having coarser septal and costal ornamentations and by having the granulations on the septal fringe mainly arranged parallel to the septal margin instead of perpendicular.

The septal and costal ornamentations of *F. spinifer* resemble most closely those of *F. scabra*, which does not have the thin appearance of *F. spinifer*, and which has septa that are more exsert and costae that are more equal.

Fungia (Verrillofungia) scabra Döderlein, 1901
(figs. 8, 203-218, 619-620, 622)

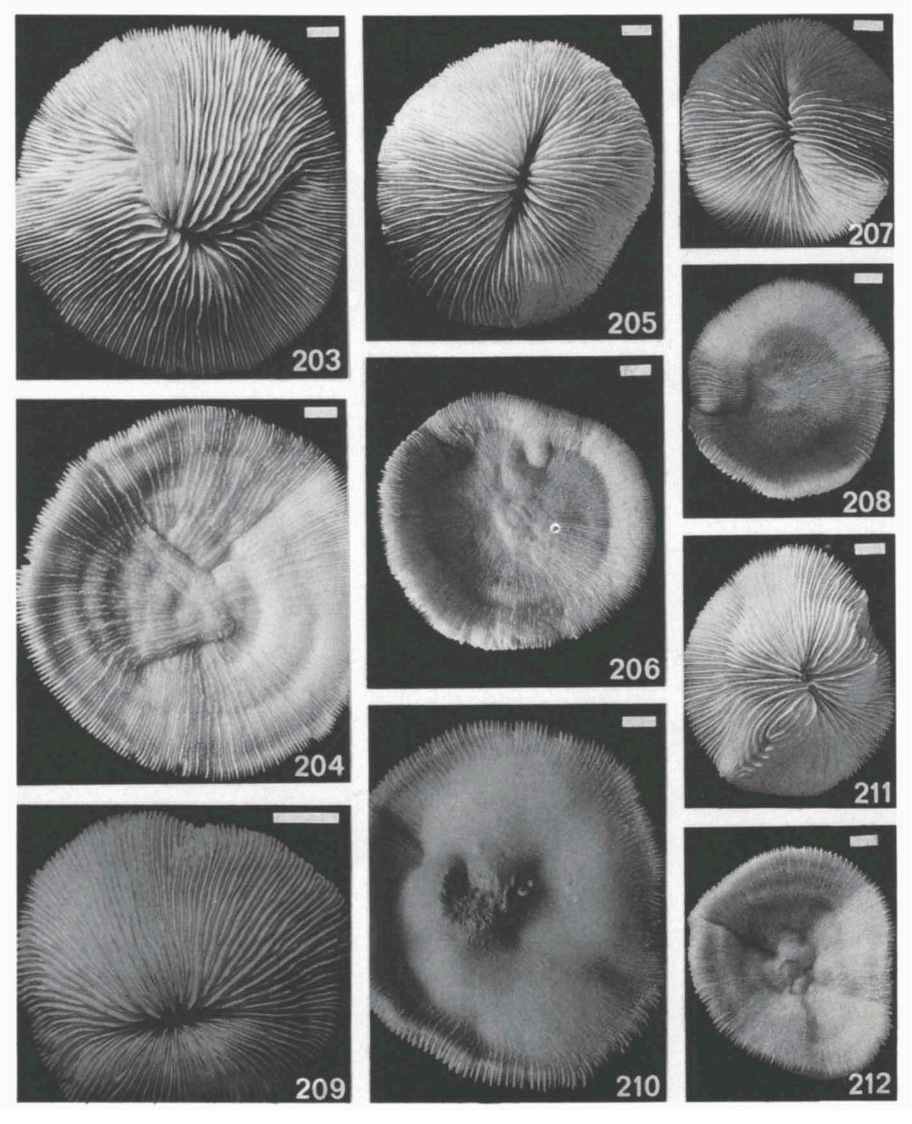
Fungia scabra Döderlein, 1901: 358 ("Singapur und Celebes"); 1902: 110-111, pl. 9 figs. 1-2; Van der Horst, 1921: 63; Gerth, 1925: 41-42; Faustino, 1927: 176-177, pl. 53 figs. 1-2; Nemenzo, 1955: 72, pl. 12 figs. 2-3; 1981: 198, fig. 222; 1986: 152, fig. 176.

? *Fungia zuffiardiae* Montanaro, 1932: 182-183, pl. 21 fig. 6, pl. 22 fig. 1 (Plio-Pleistocene, Sudan).

Fungia (Verrillofungia) scabra — Veron & Pichon, 1979: 154-156, figs. 251-256; Ditlev, 1980: 56; Veron, 1986b: 342; Wood & Tan, 1987: 197; Veron & Kelley, 1988: 28, 32, fig. 10a. Not: Randall & Myers, 1983.

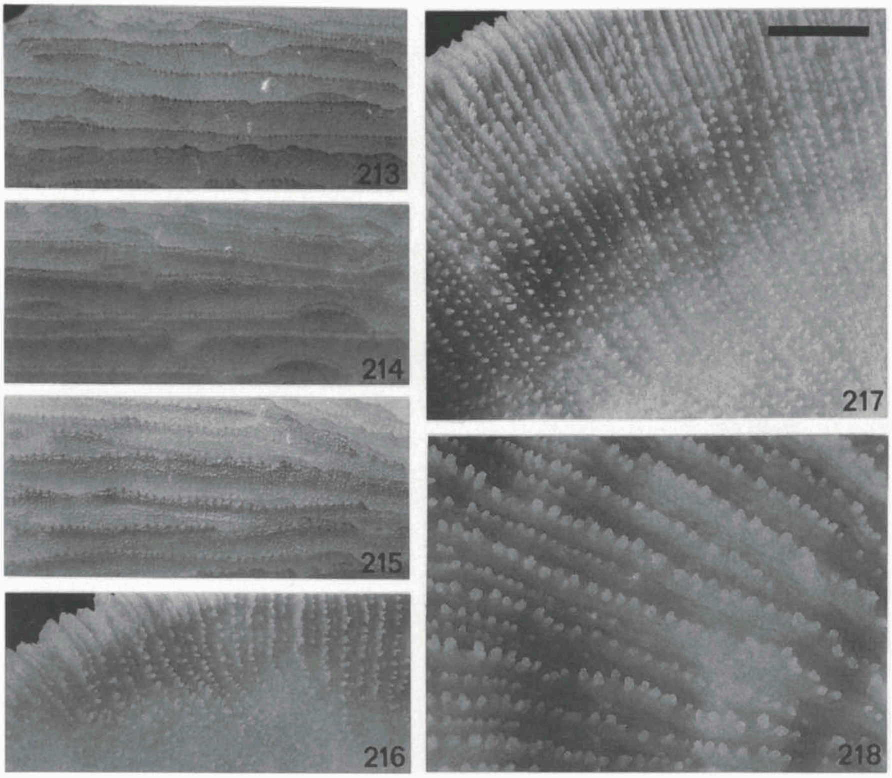
Type material examined. — MZS (lectotype [present designation] of *Fungia scabra*; type loc. Sulawesi, INDONESIA; the only specimen still available; for illustration, see Döderlein, 1902: pl. 9 fig. 1).

Other material. — INDIAN OCEAN: RMNH 9530 (2). SEYCHELLES: BMNH 1981.3.5.412-413/469-471/475. SINGAPORE: BMNH 1891.8.9.7, MCZ 34, RMNH 16027. HONG KONG: BMNH 1935.9.21.4. PHILIPPINES: BMNH 1923.12.7.2, USNM 45407, 77961. SW Luzon: BMNH 1878.6.6.22. Bohol: UPZD 566. Sulu Is.: USNM 77979, 77993. INDONESIA. Sumatra: RMNH 9531, ZMB 3097. Belitung (Billiton): ZMA 476. Java: RGM 77660 (fossil). NW Java: RMNH 16101. SW Sulawesi: RMNH 10773, 20814 (27), 20817 (35), 20820 (17), 20951, 20972 (4), 20982 (4), 20991 (2), 20996, 21692. N Sulawesi: ZMA 607. Rotti: ZMA 450. AUSTRALIA. Great Barrier Reef: AIMS 204, 791, 12984. SOCIETY IS.: BMNH 1892.10.16.6/9, 1959.8.6.18-20.



Figs. 203-212. Corals (anthocyathi) of *Fungia (Verrillofungia) scabra*. Scale bars: 1 cm. Figs. 203-204. Upper and lower surface of a large, regenerated broken coral (RMNH 9531; Sumatra, Indon.). Figs. 204-208. Upper and lower surface of two corals (RMNH 20184; SW Sulawesi, Indon.). Figs. 209-210. A coral from SW Sulawesi (RMNH 10773). Figs. 211-212. Another specimen from the same area (RMNH 20814).

Characters. — Adult animals are monostomatous and free-living. They are irregularly circular and usually thick. The corals vary from flat to highly arched. They do not form fragmentation slits, but they may break by severe



Figs. 213-218. Close-ups of *Fungia (Verrillofungia) scabra* corals. Scale bar: 0.5 cm. Fig. 213. Septa of a coral from the Indian Ocean (RMNH 9530). Fig. 214. Septa of a coral from the same sample showing clear tentacular lobes. Fig. 215. Septa of the coral in fig. 203. Fig. 216. Costae of the coral in fig. 210. Fig. 217. Costae of a coral from the Indian Ocean (RMNH 9530). Fig. 218. Costae of the coral in fig. 204.

environmental conditions (figs. 203-204). The diameter of the specimens varies between 1.0 and 14.0 cm.

The length of the central fossa, measured at its bottom, is 1/9 to 1/4 of the coral length. The septal edges at both sides of the fossa stand upright, whereas those at both ends diverge away from it. The columella is formed by a mingled mass of tightly packed, partly fused trabeculae and paliform lobes which have their tips pointing either upwards or in various directions.

The septa are densely packed and almost of equal thickness and height; they are either straight or slightly bending. The solid septa of lower orders are slightly thicker and more protruding than those of higher orders which are usually perforated. Tentacular lobes are scarcely present. The septal margins are finely ornamented with sharp, irregularly angular dentations (figs. 213-215). Their number varies from 20 to 75 per cm. The septal sides are densely granulated. The granulations are usually arranged in irregular rows or fused in ridges parallel to the septal margin (figs. 213-215, 620); they appear less frequently to be distributed in rows perpendicular to the septal margin. The compound synapticulae can be easily detected because of the thin appearance of the septa (fig. 209).

The corallum wall is solid and not granulated. A detachment scar is distinct at the aboral side of small specimens in anthocyathus-stage (fig. 210). The costae are equal to subequal in size; they are straight and distinct from the centre to the corallum margin. The costal spines are small, club-shaped and granulated or elongate and echinose (figs. 217-218, 622). Their number varies from 15 to 40 per cm.

The colour of the living animal is usually a greyish brown (fig. 8). The outer margin of the polyp is sometimes pink or violet. The tentacles are small and transparent.

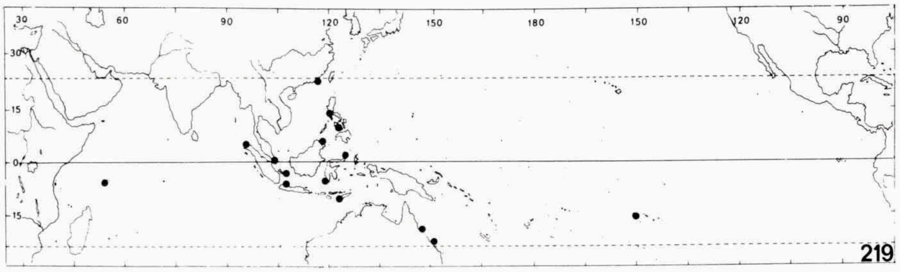


Fig. 219. The range of *Fungia (Verrillofungia) scabra*. Records are from examined material (●).

Geographical distribution (fig. 219). — The species has been collected from the Seychelles (West Indian Ocean) towards the Society Islands (Central Pacific). Its most northerly known locality is Hong Kong.

Remarks. — The only syntype known to be left has been designated lectotype. The syntypes of *Fungia zuffardiae* from the Plio-Pleistocene of Sudan resemble very much specimens of *F. scabra*; most probably they are conspecific.

F. scabra can easily be distinguished from other *F. (Verrillofungia)* species. In general, its corals are rounder, thicker and more arched than those of *F. concinna*. Its septal and costal ornamentations are finer, its septa thinner and its costae more equal in size. Compared to *F. spinifer* the septa are more protruding and more equal. The costal spines of the two species are very similar in form. Some specimens from the Great Barrier Reef very much resemble *F. (Wellsofungia) granulosa*, a species with a perforated corallum wall.

Fungia (Verrillofungia) concinna Verrill, 1864
(figs. 9, 220-233)

Fungia tenuifolia — Milne Edwards & Haime, 1851: 78 (partim); 1860: 9 (partim).

Fungia repanda Dana, 1846: 295-296 (partim), pl. 19 figs. 1-2; Veron & Marsh, 1988: 83-84 (partim).

Fungia concinna Verrill, 1864: 50-51 (partim; Zanzibar); Quelch, 1886: 133-134; Ortmann, 1888: 178; Döderlein, 1902: 113-114, pl. 12 figs. 1-3, pl. 13 fig. 4; Gravier, 1907: 342; Vaughan, 1907b: 261; Gardiner, 1909: 276-277; Gravier, 1911: 61; Vaughan, 1918: 127; Van der Horst, 1921: 63-64; Matthai, 1924: 44; Umbgrove, 1924: 12; Boschma, 1925: 217-219; Faustino, 1927: 177-178, pl. 54 figs. 1-2; Boschma, 1929: 45; Hoffmeister, 1929: 361; Thiel, 1932: 75-78, pl. 8 figs. 1-2; Ma, 1937: 133-134 (partim), pl. 66 fig. 2; Umbgrove, 1938: 272; 1939: 43-44; 1940: 292-293; Yabe & Sugiyama, 1941: 79, pl. 73 figs. 1-1c, pl. 74 fig. 3, pl. 75 figs. 1-2d; Wells, 1954: 449, pl. 161 figs. 1-3; Nemenzo, 1955: 68-69, pl. 13 fig. 1b; Stephenson & Wells, 1955: 25; Pillai, 1972: 203; Chevalier, 1979: 132; Boshoff, 1981: 21; Nemenzo, 1981: 195, fig. 216; Lamberts, 1983: 8; Scheer & Pillai, 1983: 81-82, pl. 18 figs. 6-8; Wood, 1983: 115; Wallace, 1984: 38, fig. 22.5; Johnston, 1986: 159; Nemenzo, 1986: 149-150, fig. 174a; Veron, 1986a: 32; Veron & Marsh, 1988: (partim). Not: Umbgrove, 1946a; 1946b; Shirai, 1980.

Fungia patella — Verrill, 1864: 50.

Fungia serrulata Verrill, 1864: 51 ("Kingsmills Islands").

Fungia plana Studer, 1877: 650-651 (partim), pl. 4 fig. 15 ("Blanche Bai, Neu-Pommern"); Quelch, 1886: 136; Döderlein, 1902: 111-112, pl. 11 figs. 2-5; Gravier, 1907: 342; Von Marenzeller, 1907: 89; Vaughan 1907b: 260-261; Gravier, 1911: 61; Yabe & Sugiyama, 1935: 396; Ma, 1937: 143-144, pl. 60 fig. 1, pl. 66 fig. 4; Talbot, 1965: 463; Hamilton & Brakel, 1984: 252.

Fungia danai — Gardiner, 1898: 527.

Cycloseris hexagonalis — Gardiner, 1899a: 169; 1899b: 171-175, pl. 19 figs. 10-14, pl. 20 figs. 15-24.

Fungia granulosa — Vaughan, 1906: 830-831, pls. 70-71, pl. 74 fig. 2.

Fungia laciniosa Boschma, 1925: 198-199 (partim).

? *Fungia pleistocenica* Montanaro, 1932: 183, pl. 22 fig. 3 (Plio-Pleistocene, Sudan).

Fungia sibogae — Umbgrove, 1946a: 90, pl. 1 figs. 1-2.

Fungia (Verrillofungia) concinna — Rosen, 1971a: 75; Pillai & Scheer, 1973: 470; Maragos, 1974: 248; Scheer & Pillai, 1974: 38; Maragos & Jokiel, 1978: 61; Veron & Pichon, 1979: 150-153, figs. 245-250; Ditlev, 1980: 56; Faure, 1982: 99; Randall & Myers, 1983: 17, figs. 97, 339-340; Veron, 1986b: 341; Sakai & Yamazato, 1987: 46; Wood & Tan, 1987: 197; Veron & Kelley, 1988: 28, 32, figs. 9h-i.

Fungia (Verrillofungia) plana — Ditlev, 1980: 56.

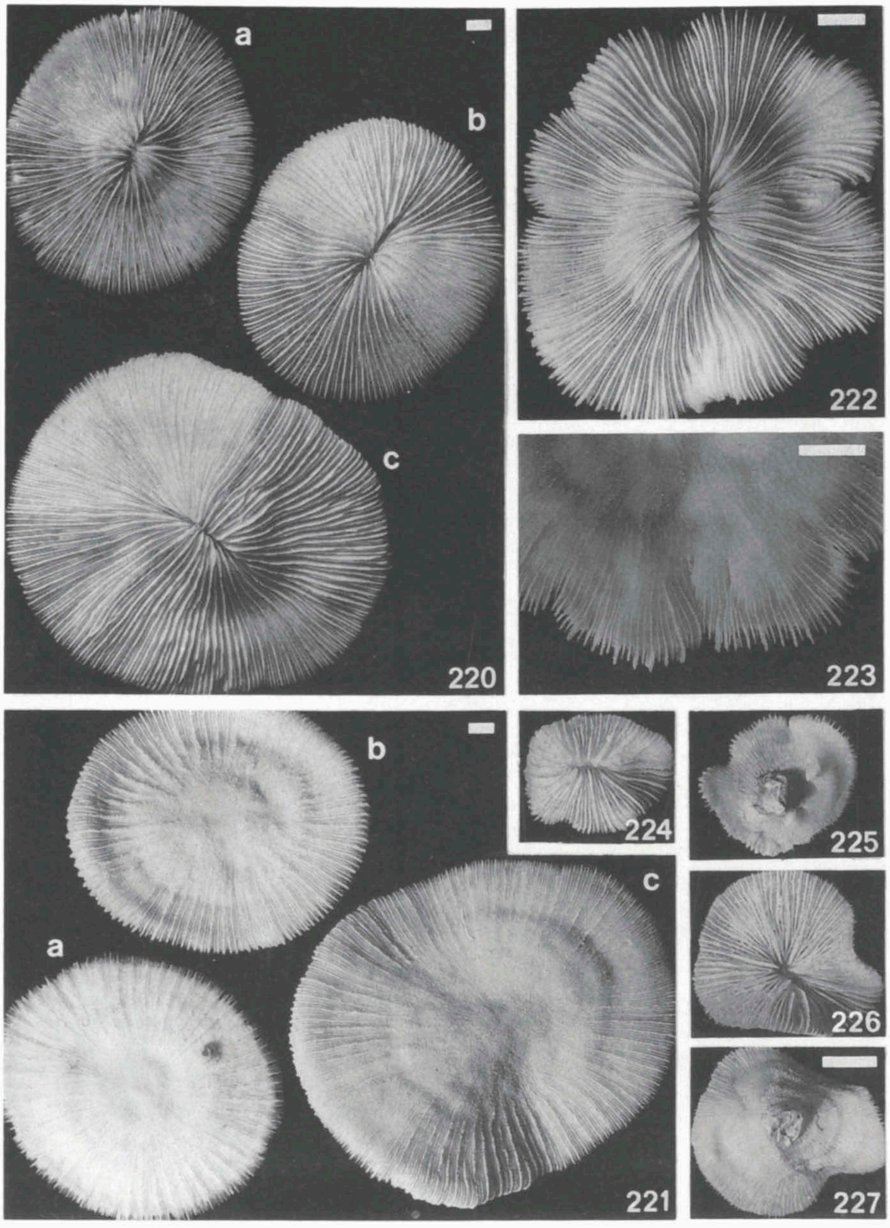
Cycloseris sinuousa Nemenzo, 1983: 273, fig. 3. (Mactan Island, Cebu). (New synonymy).

Cycloseris vaughani — Veron, 1986a: 31 (partim); Veron & Marsh, 1988: 81 (partim).

Fungia klunzingeri — Veron, 1986a: 32; Veron & Marsh, 1988: 83.

Type material examined. — USNM 123 (paralectotype of *Fungia repanda*; FIJI); USNM 112 (paralectotype of *Fungia repanda*; Sulu Sea, PHILIPPINES); MCZ 5377 (60), YPM 55-56 (lectotype [present designation] and 61 paralectotypes of *Fungia concinna*; type loc. ZANZIBAR); MCZ 5412 (lectotype [present designation] and 16 paralectotypes of *Fungia serrulata*; type loc. KINGSMILL IS.); YPM 1801 (paralectotype of *Fungia serrulata*; KINGSMILL IS.); ZMB 1795 (lectotype [present designation] of *Fungia plana*; type loc. SOLOMON IS.; for illustrations, see Döderlein, 1902: pl. 11 figs. 3-3a); UPMSI 501 (holotype of *Cycloseris sinuousa*; type loc. Mactan Island, Cebu, PHILIPPINES).

Other material. — RED SEA: BMNH 1898.8.1.38. DJIBOUTI: MNHN 1361-1362, 3519-3521, USNM 21981, 21983 (2). TANZANIA: USNM 78234. ZANZIBAR: MCZ 392, 5164 (11), 5397,

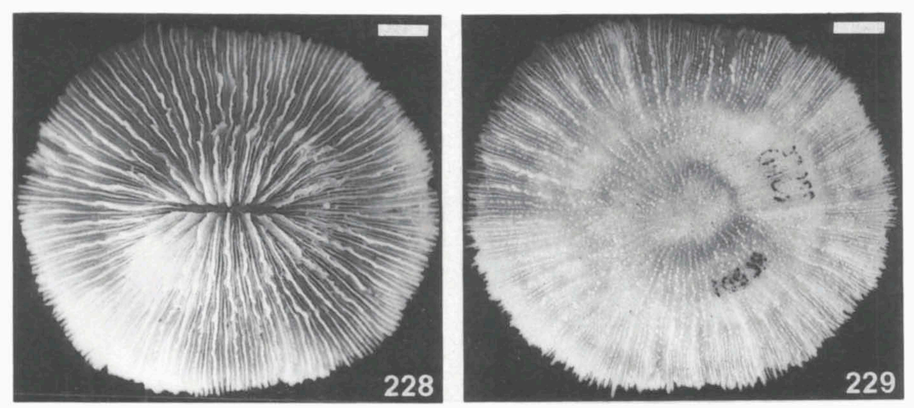


Figs. 220-227. Corals of *Fungia (Verrillofungia) concinna* from NW Java, Indonesia. Scale bars: 1 cm. Figs. 220-221. Upper and lower surface of three corals: (a) ZMA 338, (b) RMNH 16194, (c) RMNH 16198. Figs. 222-223. Upper and lower surface of a coral with a lobate margin and distinct clefts (RMNH 16192). Figs. 224-227. Upper and lower surface of two broken-off anthocauli (RMNH 16198).

USNM 78235. N MADAGASCAR: ZMA 1715. SEYCHELLES: USNM 78292 (2), YPM 7876. CHAGOS IS.: YPM 7863. SINGAPORE: AMNH 1877, BMNH 1891.8.9.4, 1898.12.1.8, MCZ 5395 (59), YPM 50, 1433, 8231. PHILIPPINES: USNM 45448. E Mindoro: UPZD 27. Cebu: UPZD 519. Mindanao: USNM 77971 (2). Sulu Is.: USNM 78001. INDONESIA. E Bangka: RMNH 9506. Belitung (Billiton): BMNH 1883.7.24.82, ZMA 347-350. Java: RGM 77770 (fossil), 77990 (fossil). NW Java: RMNH 16192-16206 (38). Paternoster Is.: ZMA 341, 346, 5096. SW Sulawesi: RMNH 15681-15682, 15685, 20723, 20726 (31), 20735, 20740 (2), 20828 (2), 20876-20877 (13), 21019. Tiger Is.: RMNH 20595 (2), 21294 (3). Tukang Besi Is.: RMNH 20100 (2). Komodo: RMNH 20392, 21384, 21410, 21462. N Sumbawa: RMNH 20510 (2), 21691 (2). NE Sumba: RMNH 20245, 20281. Moluccas: RMNH 9505. Ambon: RMNH 9398, 9497 (3). Banda: BMNH 1886.12.9.186. RMNH 8306 (5), 8367 (2), 16028 (4), USNM 78339 (9). Togian Is.: RMNH 9403, 9414. Talaud Is.: RMNH 15758 (2). Kei Is.: RMNH 8375. PALAU IS.: USNM 78014 (3), 78020-78021 (3). PAPUA NEW GUINEA. Bismarck Sea: ULB. AUSTRALIA. Kimberley: WAM 227.83, 229.83, 211.85, 220.85, 570.86, 578.86, 586.86, 697.86. C Great Barrier Reef: QMB G2875, G8071, GL3198, GL3606. S Great Barrier Reef: QMT. MARSHALL IS.: USNM 44858-44859 (3), 44861, 78304-78308 (12). NEW CALEDONIA: RMNH 16026. FIJI IS.: MCZ. TONGA IS.: BMNH 1891.3.6.112/114-115, USNM 77845 (3). PHOENIX IS.: USNM 78262. SAMOA IS.: AMNH. LINE IS.: USNM 78325 (2). HAWAII IS.: MCZ 5410 (2). SOCIETY IS.: MCZ (11), MNHN, RMNH 8976-8978 (6), 16029-16030 (3), USNM 77805, 77856. TUAMOTU IS.: USNM 77799 (3).

Characters. — Adult corals are free-living and monostomatous. Their outline varies from circular to slightly oval. Some corals form slits in the corallum wall (figs. 222-223), but no specimen has been observed to fragment because of these fissures. The corals vary in thickness; in cross-section they range from slightly arched to slightly concave. The length of the specimens varies from 3.0 to 17.0 cm.

The length of the central fossa, measured at its bottom, is 1/10 to 1/5 of the coral length. The septal edges at both sides of the fossa stand upright, whereas those at both ends of the mouth diverge away from it. The columella is formed by a mingled mass of tightly packed trabeculae and paliform lobes with the tips



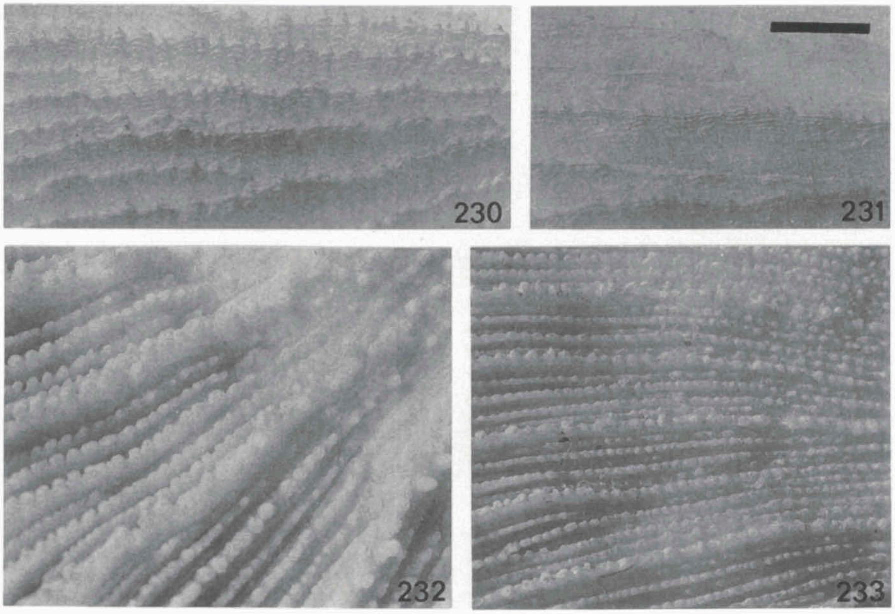
Figs. 228-229. Upper and lower surface of the holotype of *Cycloseris sinuousa* (= *Fungia (Verrillofungia) concinna*, UPMSI 501; Mactan I., Cebu, Philipp.). Scale bars: 1 cm.

pointing either upwards or in various directions.

The septa are densely packed and straight. The septa of lower order cycles are solid, thicker and higher than those of higher orders, which are usually perforated. Distinct tentacular lobes are not present. The septal margins are ornamented with irregularly angular dentations which vary from fine to coarse. Their number varies from 6 to 33 per cm. The septal sides are densely granulated. The granulations are fine and evenly dispersed at the base of the septa whereas at the fringe they are fused in wavy ridges parallel to the septal margin (figs. 230-231). The compound synapticulae connecting the septa laterally are discernible, in spite of the tight septal arrangement.

The corallum wall is solid and not granulated. A detachment scar is distinct at the aboral side of young specimens in anthocyathus-stage (figs. 225, 227). The costae are more or less equal in small specimens, but those of lower orders are more prominent in larger specimens. The costae are straight and distinct near the corallum margin, but less distinct and sometimes wavy near the centre. The costae are coarsely ornamented. The costal projections are club-shaped, blunt and granular at the tips (figs. 232-233). Their number varies from 12 to 40 per cm.

The living polyp is usually brown, but can also be an ochre colour or brown



Figs. 230-233. Close-ups of *Fungia (Verrillofungia) concinna* corals. Scale bar: 0.5 cm. Fig. 230. Septa of the coral in fig. 220b. Fig. 231. Septa of the coral in fig. 220c. Fig. 232. Costae of the coral in fig. 221b. Fig. 233. Costae of the coral in fig. 221c.

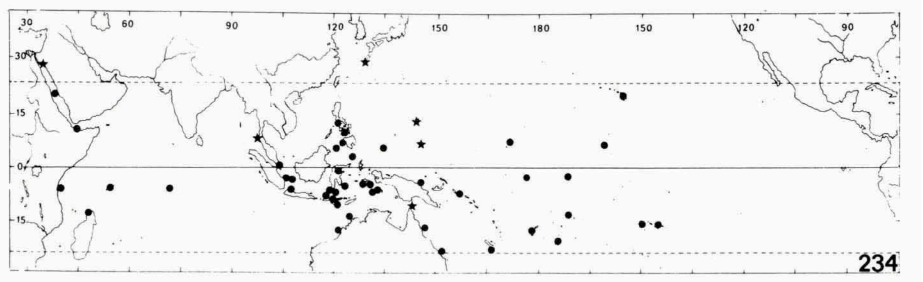


Fig. 234. The range of *Fungia (Verrillofungia) concinna*. Records are from examined material (●) and published illustrations (★).

combined with pink, grey or violet (fig. 9). The small tentacles are usually colourless.

Geographical distribution (fig. 234). — In the West Indian Ocean, the species occurs from the Red Sea to Tanzania and Madagascar. In the Pacific, the distribution extends eastward towards the Hawaiian Islands and the Tuamotu Archipelago. The southernmost location is Nouméa, the northernmost one is the Ryukyu Islands, southern Japan.

Remarks. — The specimen designated lectotype of *Fungia plana* cannot be seperated from *F. concinna*. According to Döderlein (1902) the two species differ in the fineness of their septal dentations, but using this character, specimens can be put in a continuous series including both "species". The other type specimen of *F. plana*, the one designated paralectotype, belongs to *F. paumotensis*. The holotype of *Fungia pleistocenica* is an abraded specimen with a shape similar to that of *F. concinna*; therefore the two are probably synonymous.

It is not clear why the holotype of *Cycloseris sinuousa* (figs. 228-229) originally was identified as a *Cycloseris*. In its original description, its crinkled septa, irregularly distributed septal dentations and unequal costae are supposed to be distinctive characters. A crinkled margin is an irregularity or deformation which can be observed in several species of *Fungia* (see for example fig. 155), which makes it useless as a diagnostic character.

F. concinna is often confused with *Fungia repanda*. The two species can be distinguished by the latter's perforate corallum wall, while the wall of *F. concinna* is solid. This difference is not always clear in juvenile specimens, which often causes identification problems. Usually *F. concinna* is flatter and more oval than the other species. In cross-section it is often concave whereas *F. repanda* is more frequently convex. Compared to *Fungia scabra*, *F. concinna* is flatter and has coarser septal and costal ornamentations.

Fungia (Verrillofungia) repanda Dana, 1846 (figs. 10, 235-242, 621, 623-624)

Fungia repanda Dana, 1846: 295-296 (partim), pl. 19 fig. 3 ("Feejee Islands and the East Indies"); Milne Edwards & Haime, 1851: 81; 1860: 12; Verrill, 1864: 50; Studer, 1880: 45; Ridley, 1883: 257; Quelch, 1886: 134; Ortmann, 1889: 519-520; Döderlein, 1902: 115-117, pl. 12 figs. 4-5, pl. 13 figs. 1-3, 5-7; Bedot, 1907: 218; Gardiner, 1909: 277; Van der Horst, 1921: 64-65; Boschma, 1925: 219-220, pl. 7 fig. 74; Faustino, 1927: 178-179, pl. 55 figs. 1-2; Boschma, 1929: 45; Thiel, 1932: 73-74; Yabe & Sugiyama, 1935: 396; Abe, 1938: 479-481, figs. 1b, 5; Eguchi, 1938: 361; Ma, 1937: 135-136 (partim), pl. 50 figs. 1-2, pl. 66 fig. 1; Umbgrove, 1939: 44, pl. 12 fig. 2; 1940: 293-294, pl. 27 figs. 4-5; Yabe & Sugiyama, 1941: 78-79, pl. 73 figs. 2-3d, pl. 74 figs. 2-2e, pl. 75 figs. 3-3b; Umbgrove, 1946a: 91-92; Nemenzo, 1955: 66-67, pl. 13 fig. 1a; Purchon, 1956: 157; Wells & Davies, 1966: 48; Pillai, 1972: 203; Pichon, 1974: 176; Utinomi, 1975: 71; Zou, 1978: 100-101; Green, Harris, Robertson & Santavy, 1979: 298; Chevalier, 1979: 132; 1980: 66; Wijsman-Best, Faure & Pichon, 1980: 612; Betterton, 1981: 205, pls. 86-87; Nemenzo, 1981: 195, fig. 217; Lamberts, 1983: 9; Pillai, 1983: 86; Scheer & Pillai, 1983: 81, pl. 18 figs. 3-5; Zou & Chen, 1983: 91; Hamilton & Brakel, 1984: 252; Werner, 1984: pl. 3; Johnston, 1986: 159; Nemenzo, 1986: 150, fig. 174b; Veron, 1986a: 32; Loo & Chou, 1988: 29; Veron & Marsh, 1988: 83-84 (partim). Not: Searle, 1956; Baguis & Christian, 1977; Shirai, 1980.

Fungia discus Dana, 1846: 291 (partim), pl. 18 figs. 3-3a ("Tahiti, Society Islands"). (New synonymy). Not: Milne Edwards & Haime, 1851; 1860; Studer, 1877, 1880; Ortmann, 1888; 1889; Gardiner, 1898; Whiteledge, 1898.

Not *Cycloseris discus* Quelch, 1886.

Fungia integra Dana, 1846: 296-297, pl. 19 fig. 4 ("East Indies"). (New synonymy).

Fungia linnaei Milne Edwards & Haime, 1851: 82-83 ("les mers de la Chine"); 1860: 13.

Fungia concinna Verrill, 1864: 50-51 (partim); Umbgrove, 1946b: 534 (partim), pl. 81, figs. 5-6; Shirai, 1980: 529.

Fungia serrulata Verrill, 1864: 51 (partim).

Fungia samboangensis Vaughan, 1906: 829-830, pl. 68, pl. 69 fig. 1, pl. 74 fig. 1 ("Samboanga, Philippine Islands"); Faustino, 1927: 180-181, pl. 56 figs. 1-3; Nemenzo, 1955: 67-68; 1981: 196, fig. 218; 1986: 150.

? *Fungia laevis* Montonaro, 1932: 179-180, pl 21 fig. 3 (Plio-Pleistocene, Sudan).

Fungia danai — Ma, 1937: 136 (partim), pl. 44 figs. 1-2.

Fungia granulosa — Ma, 1937: 143, pl. 56 fig. 1, pl. 57 fig. 1, pl. 66 fig. 3.

Fungia fieldi — Yabe & Sugiyama, 1941: 79, pl. 77 figs. 1-1e; Zou & Chen, 1983: 91.

Fungia (Verrillofungia) repanda — Rosen, 1971a: 76; Ditlev, 1976: 6; Pillai & Scheer, 1976: 44; Faulkner & Chesher, 1979: 287 (partim); Veron & Pichon, 1979: 146, 148-150, figs. 239-244; Ditlev, 1980: 56, fig. 234; Faure, 1985: 271; Veron, 1986b: 340; Sakai & Yamazato, 1987: 46; Wood & Tan, 1987: 197; Veron & Kelley, 1988: 28, 31-32..

Fungia (Danafungia) subrepanda — Scheer & Pillai, 1974: 38, pl. 17 figs. 5-6.

Fungia subrepanda — Shirai, 1980: 528.

Fungia fungites — Veron & Marsh, 1988: 83 (partim).

Type material examined. — USNM 122 (lectotype [present designation] of *Fungia repanda*; type loc. FIJI); MCZ 530-531 (2 paralectotypes of *Fungia repanda*; FIJI); USNM 144 (lectotype [present designation] of *Fungia discus*; type loc. Tahiti, SOCIETY IS.); MCZ 425B (holotype of *Fungia integra*; type loc. EAST INDIES); MCZ 5377 (10), YPM 1438 (11 paralectotypes of *Fungia concinna*; ZANZIBAR); MCZ 5412 (paralectotype of *Fungia serrulata*; KINGSMILL IS.); USNM 21139 (holotype of *Fungia samboangensis*; type loc. Zamboanga, SW Mindanao, PHILIPPINES).

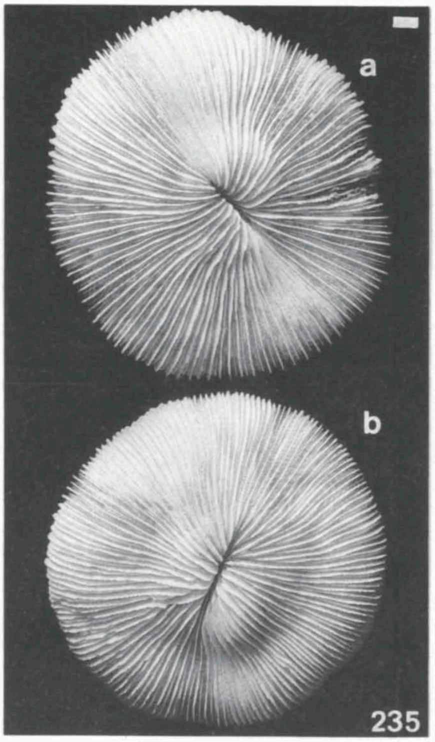
Other material. — RED SEA: RMNH 9499 (3), 9504, 9507 (2), ZMA 351. ZANZIBAR: MCZ 5164. N MADAGASCAR: USNM 77720 (2), 77736 (2), WAM 271.81, ZMA 6520. MAS-

CERENE IS. Mauritius: ZMA 6524. SEYCHELLES: BMNH 1981.3.5.474, MNHN Fun56-58, RMNH 12099. MALDIVES: USNM 78286, YPM 7855, 7862. CHAGOS IS.: USNM 77745 (4). N SRI LANKA: YPM 1508 (2). JAPAN: ZMA 369. Kanagawa: MCZ 1071. SINGAPORE: AMNH 1767, BMNH 1891.2.3.31, 1892.9.25.4, MCZ 5289 (3), 5302, 5379 (120), MNHN Fun87, YPM 54, 1429 (2), 1802, 1950, ZMA 463. MALAYSIA. Malacca Str.: BMNH 1883.11.8.13. Sabah: USNM 47954. PHILIPPINES. SW Luzon: USNM 77933 (3), E Mindoro: MCZ 3970, UPZD 28, 30. Burias: USNM 78005. Cebu: BMNH 1886.12.9.369, UPZD 522. Bohol: UPZD 542. Mindanao: USNM 77973 (3). Sulu Is.: RMNH 9501, USNM 22019, 77992 (2), 78002. INDONESIA. N Sumatra: RMNH 9508. Belitung (Billiton): BMNH 1883.7.24.81, ZMA 375, 454-462, 488, 491-493. Java: RGM 77648 (fossil), 77775 (fossil). NW Java: RMNH 16177-16185 (18), USNM 21953. SW Sulawesi: RMNH 15686-15690 (9), 20705 (4), 20743 (2), 20746 (5), 20751 (11), 20829 (2), 20903, 20955 (2), 21020 (3), ZMA 478, 5518 (2). Tiger Is.: RMNH 21118, 21165, 21299. Paternoster Is.: RMNH 9400 (2), ZMA 342, 345. Tukang Besi Is.: RMNH 15763, 20117. Togian Is.: RMNH 8510, 9402, 9404, 9406, 9409-9411, 9413, 9415, 9513 (3). Talaud Is.: RMNH 15762. Komodo: RMNH 20393 (5), 21478. N Sumbawa: RMNH 20503 (3), 21693. NE Sumba: RMNH 20244 (2), 20280. Flores: RMNH 9493 (3), ZMA 453, 486. Kera: RMNH 14373, 16225. Rotti: ZMA 452. Tanimber Is.: RMNH 15760. Moluccas: WAM 1378.88 (3), ZMA 466, 6458. Ambon: BMNH 1886.12.9.202, RMNH 8369, 8382. Banda: BMNH 1886.12.9.204/370, RMNH 8370-8371 (10), 8384, 8386, 16223, USNM (3). Obi Latu: RMNH 15761 (2). N Halmahera: USNM 78052 (5). Kei Is.: RMNH 8388 (5). Biak: RMNH 15767 (4). Palau Is.: USNM 47086, 78015 (2), 78025-78026, 78039 (3), 78042. PAPUA NEW GUINEA. Bismarck Sea: ULB. SOLOMON IS.: BMNH 1884.12.11.4, USNM 78076. CAROLINE IS.: USNM 15745, 77795 (2), 77844 (2), 78057-78058. AUSTRALIA. Christmas I.: WAM: 265.87, 267.87. Kimberley: WAM 1013.85, 533.86. Pilbara: WAM 202.77. Houtman Abrolhos Is.: WAM 30.88. Northern Territory: RMNH 20871. Torres Str.: MCZ (2). C Great Barrier Reef: BMNH 1891.3.9.153, 1892.12.1.436, QMB G2876, G6777, G8070, GBR285, GL3607, GL3613, GL3617, GL3621, USNM 78345. S Great Barrier Reef: QMB G6600, QMT. NEW CALEDONIA: MNHN, USNM 78283 (2), ZMA 6280, 6285, 6287. MARSHALL IS.: AMNH, USNM 44860 (2), 77860-77861, 78314. GILBERT IS.: USNM 77906-77913 (31), 78351. FIJI IS.: BMNH 1956.9.24.4, USNM 78347. TONGA IS.: USNM 77847 (3). SAMOA IS.: AMNH, USNM 46828, 77828 (4), YPM 6099. SOCIETY IS.: BMNH 1886.12.9.206-207/366-368, 1892.10.16.6-8, 1959.8.6.14-17/21/29, 1973.4.17.15, MNHN, RMNH 8979, 8984, 16031-16032 (3), USNM 21140, 77804 (3), 77806-77807 (27), 77857 (2), 77959, 78333. Tuamotu Is.: USNM 77798, 77808 (3).

Characters. — Adult animals are monostomatous and unattached. They vary in thickness, from discoidal to slightly oval and from flat to slightly arched. No fragmented corals have been observed. The length of the specimens varies between 3.0 and 23.5 cm.

The length of the central fossa, measured at its bottom, is 1/10 to 1/5 of the corallum length. The septal edges at both of its sides stand upright, whereas those at both ends diverge away from it. The columella is formed by a mingled mass of tightly packed trabeculae and paliform lobes with the tips either pointing upwards or in various directions.

The septa are densely packed and straight. The septa of lower orders are thick and solid, whereas those of higher orders are thin and often perforated. The lower order septa are more exsert than those of higher orders. Tentacular lobes are absent. The septal margins are coarsely ornamented with angular dentations. Their number varies from 5 to 23 per cm. The septal sides are densely granulated. Near the septal margins the granulae are fused in ridges parallel to the septal margin, in zigzag patterns (figs. 239-240, 621). They are more evenly dispersed further down. The compound synapticulae connecting the septa laterally can be detected, in spite of the tight septal arrangement.



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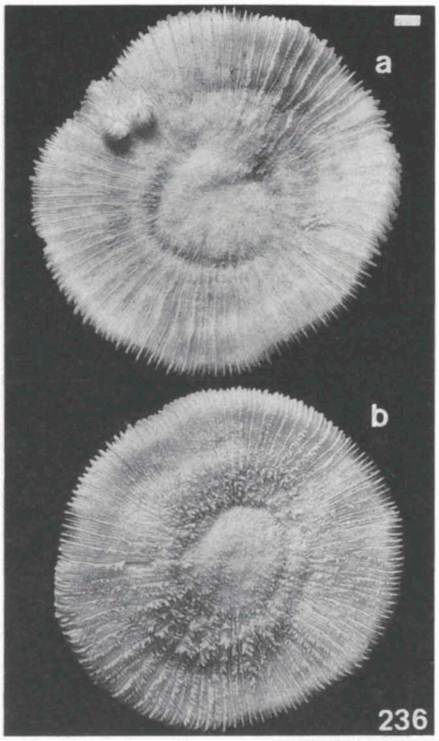

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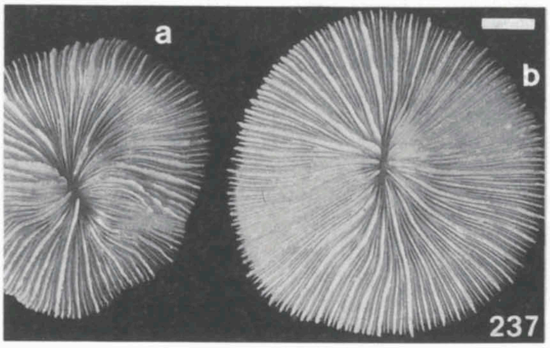

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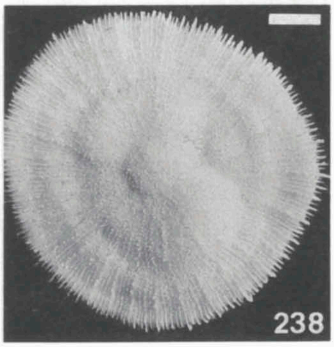
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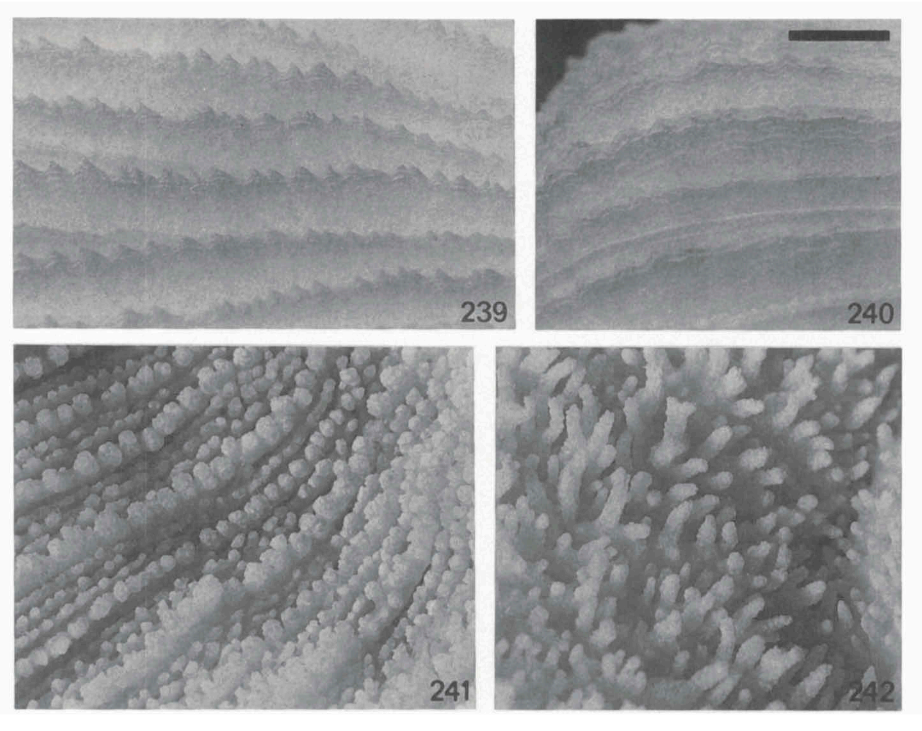
Figs. 235-238. Corals (anthocyathi) of *Fungia (Verrillofungia) repanda* from NW Java, Indonesia. Scale bars: 1 cm. Figs. 235-236. Upper and lower surface of two corals: (a) RMNH 16178, (b) RMNH 16179. Fig. 237. Upper surface of two small corals (RMNH 16184). Fig. 238. Aboral surface of the coral in fig. 237b.

The corallum wall is not granulated; it is perforated in adult specimens, but can still be solid in juvenile specimens. A detachment scar is distinct at the aboral side of small specimens in anthocyathus-stage. The costae are unequal, straight and distinct near the corallum margin, while they are less distinct and sometimes wavy near the centre. All costae are coarsely ornamented. The costal spines are usually club-shaped, blunt and granular at the tips, but sometimes elongate and branched with sharp points in various directions (figs. 241-242, 623-624). Their number varies from 12 to 18 per cm.

The living animal is usually brown (fig. 10), sometimes combined with pink patches. The tentacles are small and transparent.

Geographical distribution (fig. 243). — The species is known to occur from the Red Sea and East Africa eastwards to Japan and the Tuamotu Archipelago.

Remarks. — A lectotype of *F. repanda* has been designated, because some of the syntypes are specimens of *F. concinna*. Many nominal taxa prove to be synonyms of *F. repanda* Dana. Two synonymous species have been described



Figs. 239-242. Close-ups of *Fungia (Verrillofungia) repanda* corals. Scale bars: 0.5 cm. Fig. 239. Septa of the coral in fig. 235a. Fig. 240. Septa of the coral in fig. 235b. Fig. 241. Costae of the coral in fig. 236a. Fig. 242. Costae of the coral in fig. 236b.

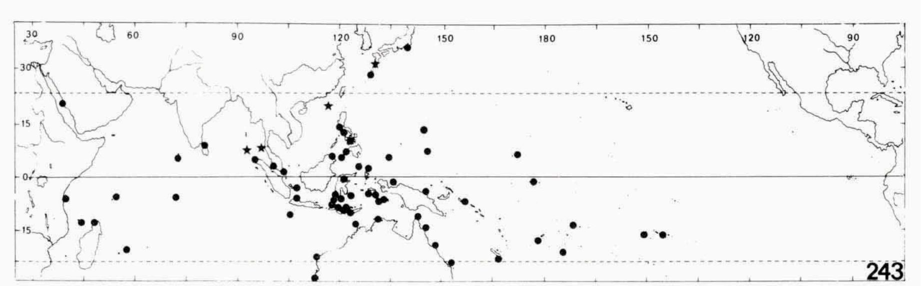


Fig. 243. The range of *Fungia (Verrillofungia) repanda*. Records are from examined material (●) and published illustrations (★).

by Dana (1846) himself; their types come from different localities. Among the syntypes of several other species, such as *F. concinna*, specimens of *F. repanda* have been found. The fossil syntypes of *F. linnaei* are probably lost. (There are several specimens in the MNHN with that name, but these are not from the type locality). The fossil syntypes of *F. laevis* from Sudan are very likely juvenile specimens of *F. repanda*, because of their relatively round shape and unequal costae. The specimens are very much abraded so that it is not certain to which species they actually belong.

F. repanda differs from *F. concinna*, mainly by its perforate corallum wall. At some locations, like the Togian Islands (E Sulawesi), the species is superficially difficult to distinguish from *F. fungites*, another species with a perforated corallum wall but with more smooth and elongate septo-costal ornamentations.

Subgenus **Danafungia** Wells, 1966

Type species: ***Fungia danai*** Milne Edwards & Haime, 1851, sensu Wells, 1966 [= ***Fungia scruposa*** Klunzinger, 1879]. By original designation.

Fungia (Danafungia) Wells, 1966: 239; Ditlev, 1980: 56; Veron & Pichon, 1979: 132, 134; Chevalier & Beauvais, 1987: 706; Veron & Kelley, 1988: 31.

Characters. — The animals are discoidal. The corallum wall is granulated; it is either solid or perforated. The septa and costae are strongly alternating in height. The septal dentations are irregularly angular and are either fine or very coarse. The costae of lower order cycles are more heavily ornamented than those of higher cycles. The costal spines are usually long and coarsely granulated.

Remarks. — The subgenus was originally described by Döderlein (1901: 356; 1902: 117) as the "*Danai* -Gruppe". He described the type species, *F.*

danai, as a coral with a perforated wall (1902: 129), whereas the lectotype of that species has a distinct solid wall. In the literature, ever since Döderlein's (1902) revision, the perforated wall has been used to characterize the species, while this character actually belongs to its ally *F. scruposa*.

The most characteristic feature of the subgenus is the difference in size between the lower and the higher order costae. The lower order costae are covered with large spines (some of which are the largest found in the Fungiidae), whereas those of the higher order costae remain almost bare apart from some granulations. The spines of the higher order costae are either undeveloped or rudimentary. At present three distinct species are recognized, of which *F. (D.) fralinae* is the least well known.

Fungia (Danafungia) fralinae Nemenzo, 1955
(figs. 11-12, 244-253, 625-626, 629-630)

Fungia fralinae Nemenzo, 1955: 65-66, pl. 11 figs. 1-2 (Pinamungajan); 1981: 192, fig. 212; 1986: 147, fig. 170.

Cycloseris similis Nemenzo, 1976: 242-243, pl. 6 fig. 1 (loc. unknown, Philippines); 1981: 185, fig. 203; 1986: 142, fig. 163. (New synonymy).

Type material examined. — UPZD 569 (holotype of *Fungia fralinae*; type loc. Pinamungajan, Cebu, PHILIPPINES); UPZD 1386 (holotype of *Cycloseris similis*; type loc. PHILIPPINES).

Other material. — PHILIPPINES. Cebu: UPMSI 198, 247. INDONESIA. SW Sulawesi: RMNH 15699, 20609 (14), 20760-20761 (4), 20795 (19). Komodo: RMNH 21513 (24). N Sumbawa: RMNH 20806 (2), 21314 (13), 21617 (2), 21670 (4). PAPUA NEW GUINEA. Bismarck Sea: ULB. AUSTRALIA. Great Barrier Reef: BMNH 1892.12.1.432. GILBERT IS.: MCZ 5412.

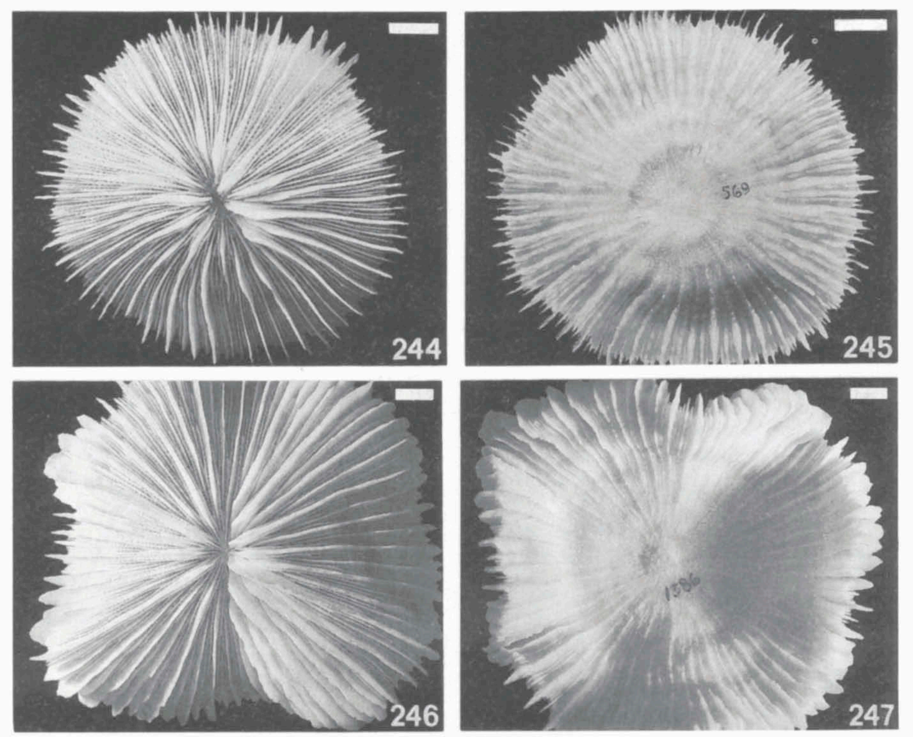
Characters. — Adult animals are unattached, monostomatous and discoidal. Fragmentation slits have not been observed. The septa are exsert, which gives the animals a thick appearance. The coralla are not heavily built. They vary from flat to slightly arched. The diameter of the specimens varies between 1.5 and 15.0 cm.

The length of the central fossa, measured at its bottom, is 1/14 to 1/8 of the corallum length. The septal edges at its sides stand upright, whereas those at both ends diverge away from it. The columella is formed by a mingled mass of loosely packed trabeculae and paliform lobes with their tips either pointing upwards or in various directions.

The septa are thin, exsert, loosely packed and straight. The septa of lower order cycles are solid and more protruding than the perforated septa of higher orders. Tentacular lobes are absent. The septal margins are ornamented with fine angular dentations (figs. 250-251). Their number varies from 15 to 25 per cm. The granulations are fine and regularly dispersed at the base of the septa, whereas on the septal fringe the septal margins they are thinly distributed in faint rows perpendicular to the septal margin (figs. 625-626). The compound synapticulae connecting the septa laterally can be easily distinguished, because of the loose septal arrangement.

The corallum wall is solid. It is distinctly granulated (figs. 629-630) and it shows a detachment scar at the aboral side of all anthocyathi. The costae are very unequal in size; they are straight and distinct near the corallum margin, whereas near the centre they are less clear. The lower order costae are covered by sharp, erect costal spines (figs. 252-253). Their number varies from 8 to 22 per cm. The spines on the higher order costae remain absent or are only rudimentary in appearance.

The colour of the living animal is predominantly transparent olive-green (fig. 11). The tentacles are of the same colour; their tips, however, are strikingly violet (fig. 12). The length of extended tentacles may be up to 2 cm.

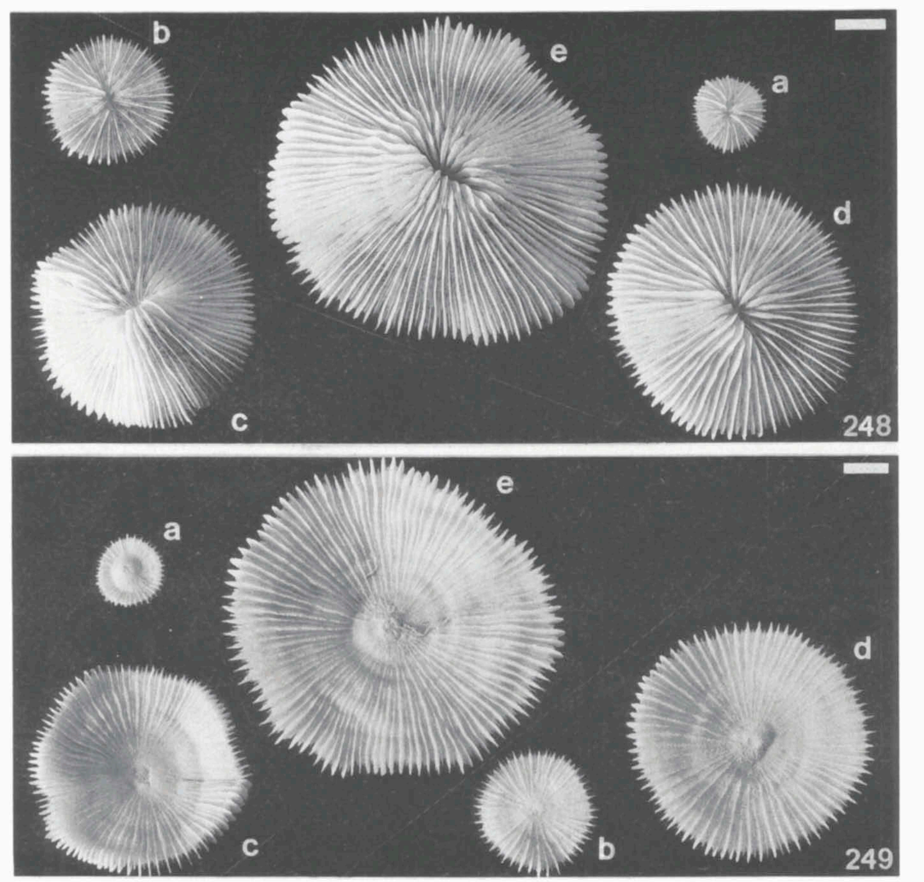


Figs. 244-247. Two holotypes from the Philippines. Scale bars: 1 cm. Figs. 244-245. Upper and lower surface of the holotype of *Fungia (Danafungia) fralinae* (UPZD 569; Cebu). Figs. 246-247. Upper and lower surface of the holotype of *Cycloseris similis* (= *F. (D.) fralinae*, UPZD 1386; loc. unknown).

Some of the tentacles are bifurcated (fig. 12). The soft parts of the polyp are usually found expanded.

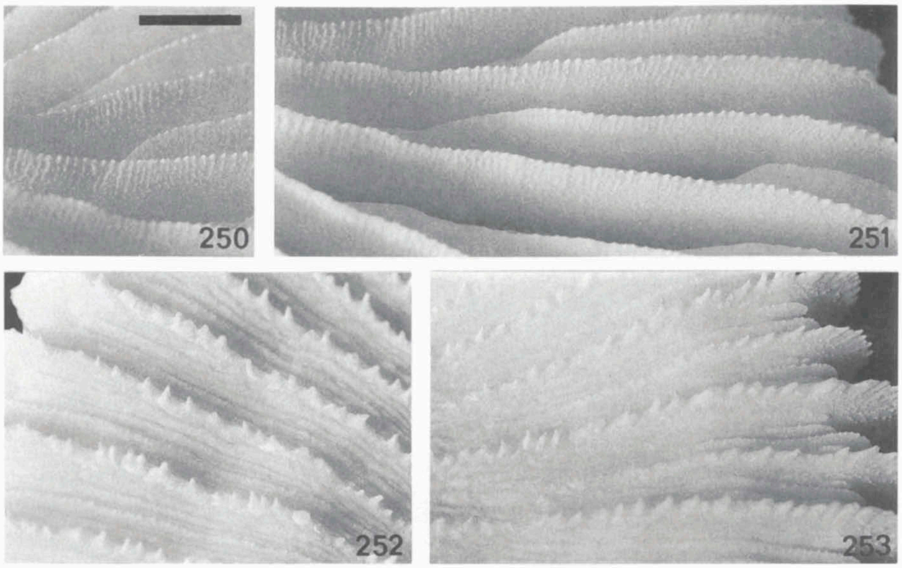
Geographical distribution (fig. 254). — The species is known to occur in the Central Indo-Pacific. Its easternmost location is the Kingsmill Group of the Gilbert Islands.

Remarks. — The species has been described twice by the same author under different names, which may be due to the different growth forms of the two holotypes (figs. 244-247). Live specimens have not been studied before. The olive-green colour of the polyp and the unique violet tentacle tips, make it easily recognizable in the field. The thin and high septa and the fine septal dentations are diagnostic characters of the skeleton within the subgenus *Danafungia*.



Figs. 248-249. Upper and lower surface of five corals (anthocyathi) of *Fungia (Danafungia) fralinae* from SW Sulawesi, Indonesia (RMNH 20795). Scale bars: 2 cm.

A remaining detachment scar is also mentioned in the original description of *F. klunzingeri* Döderlein, 1901, a synonym of *F. horrida*. Specimens of the latter species keep a detachment scar for instance when they occur in silty environments; the scar usually regenerates quickly in individuals that live in clear water.



Figs. 250-253. Close-ups of *Fungia (Danafungia) fralinae* corals from SW Sulawesi, Indonesia (RMNH 20795). Scale bar: 0.5 cm. Figs. 250-251. Septa with fine dentations; granulations arranged in rows perpendicular to the septal margin. Figs. 252-253. Costae strongly differing in size, bearing cone-shaped spines and granulations.

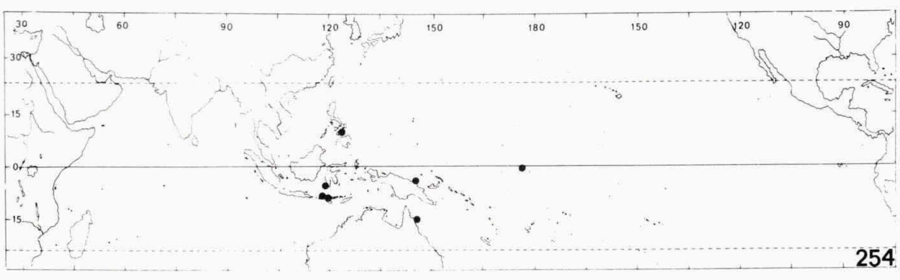


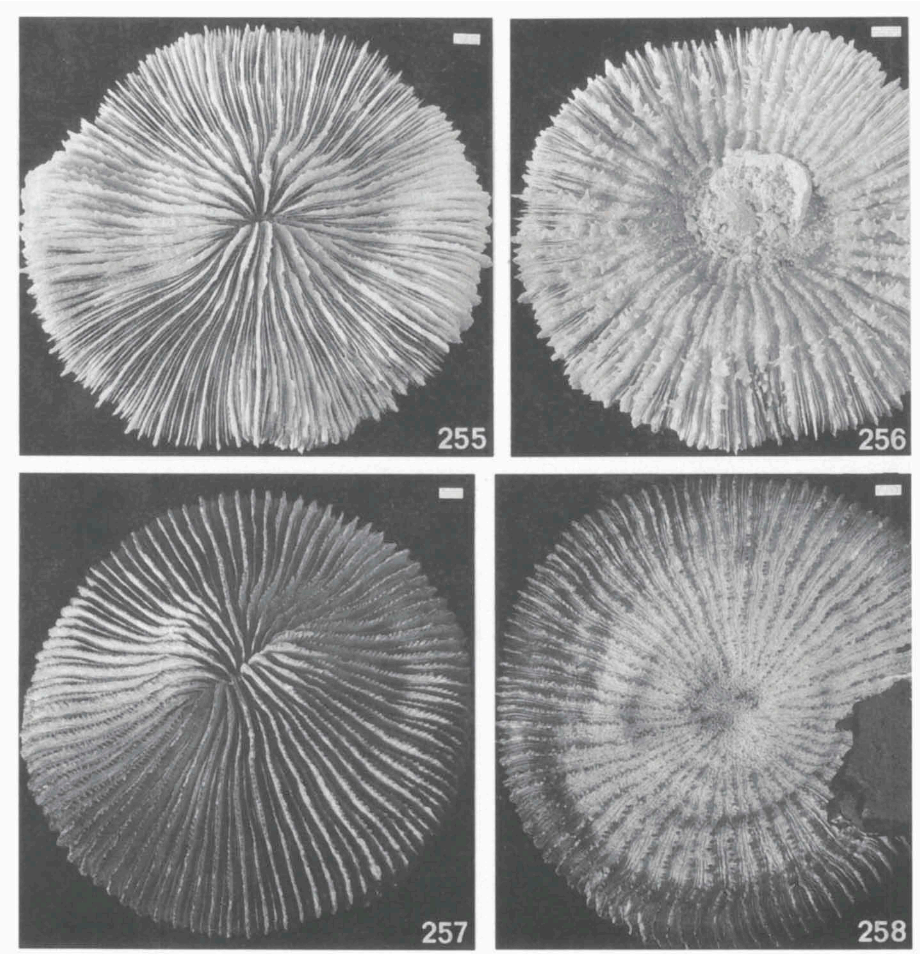
Fig. 254. The range of *Fungia (Danafungia) fralinae*. Records are from examined material (●).

Fungia (Danafungia) horrida Dana, 1846

(Figs. 13, 255-280)

Fungia horrida Dana, 1846: 298-299, pl. 19 fig. 7 ("Feejee Islands"); Milne Edwards & Haime, 1860: 15; Studer, 1877: 648; Quelch, 1886: 134-135; Döderlein, 1902: 122-124, pl. 14 figs. 1-1a; Von Marenzeller, 1907: 89; Matthai, 1924: 44-45, pl. 9 fig. 2, pl. 10 fig. 1; Boschma, 1925: 220 (partim); Nemenzo, 1955: 66, pl. 12 figs. 4-5; Stephenson & Wells, 1955: 26; Pillai, 1972: 203; Pichon, 1974: 176; Boshoff, 1981: 22; Nemenzo, 1981: 193, fig. 213; Pillai, 1983: 86; Scheer & Pillai, 1983: 83, pl. 19 figs. 5-6; Johnston, 1986: 159; Nakamori, 1986: pl. 14, fig. 2; Nemenzo, 1986: 147-148, fig. 171; Veron, 1986a: 32; Veron & Marsh, 1988: 83.

Fungia danae Milne Edwards & Haime, 1851: 80 ("Habite Manille"; partim); 1860: 11, pl. D10 fig. 1; Verrill, 1864: 50. (New synonymy).



Figs. 255-258. Type specimens. Scale bars: 1 cm. Figs. 255-256. Upper and lower surface of a syntype of *Fungia (Danafungia) horrida* (USNM 120; Fiji). Figs. 257-258. Upper and lower surface of the lectotype of *Fungia danai* (= *F. (D.) horrida*, MNHN 484; Manila, Philipp.).

Fungia danai — Semper, 1872: 274, pl. 21 fig. 4; Studer, 1877: 647; Studer, 1880: 45; Ortmann, 1888: 177; 1889: 520-521; Faustino, 1927: 181-182 (partim), pl. 58 fig. 3. (Valid emendation).

Fungia valida Verrill, 1864: 51 (partim; Zanzibar); Klunzinger, 1879: 62-63, pl. 8 figs. 7-8; Quelch, 1886: 135; Ortmann, 1888: 177-178; Döderlein, 1902: 125-126, pl. 16 figs. 1-1a, 2; Umbgrove, 1940: 294; Stephenson & Wells, 1955: 26-27; Boshoff, 1981: 22; Veron & Kelley, 1988: 28; Veron & Marsh, 1988: 83. (New synonymy).

Fungia acutidens Studer, 1877: 649, pl. 4 fig. 13 ("Carteret Harbour, Neu-Irland"); Quelch, 1886: 135; Döderlein, 1902: 121-122, pl. 14 fig. 2-2a; Gardiner, 1909: 278; Van der Horst, 1921: 13. (New synonymy).

Fungia klunzingeri Döderlein, 1901: 358 ("Rothes Meer"); 1902: 124-125, pl. 15 figs. 1-1a; Gardiner, 1909: 267; Van der Horst, 1921: 13; Fricke & Schuhmacher, 1983: 172; Scheer & Pillai, 1983: 84, pl. 19 figs. 7-8; Schuhmacher & Mergner, 1985: 428. (New synonymy). Not: Veron, 1986a; Veron & Marsh, 1988.

Fungia (Cycloseris) inaequicostata Gerth, 1925: 41, pl. 6 figs. 1-1a (Miocene, "Goenoeng Linggapadang bei Margasari", Java). (New synonymy).

Fungia inaequicostata — Umbgrove, 1946a: 91.

Fungia c.f. *concinna* — Umbgrove, 1946a: 92.

Fungia (Danafungia) danai — not: Ditlev, 1976; Pillai & Scheer, 1976; Faure, 1977; Veron & Pichon, 1979; Ditlev, 1980; Faure, 1982; Randall & Myers, 1983; Veron, 1986b.

Fungia (Danafungia) valida — Maragos & Jokiel, 1978: 61; Veron & Pichon, 1979: 143-144, figs. 232-233; Veron, 1986b: 338.

Fungia (Verrillofungia) repanda — Faulkner & Chesher, 1979: 287 (partim), pl. 102.

Fungia (Danafungia) horrida — Veron & Pichon, 1979: 139, 141-143, figs. 226-231; Randall & Myers, 1983: 17, figs. 348-349; Veron, 1986b: 337 (partim).

Fungia (Danafungia) klunzingeri — Veron & Pichon, 1979: 144-146, figs. 234-238; Veron, 1986b: 339; Veron & Kelley, 1988: 28.

Fungia repanda — Shirai, 1980: 528.

Cycloseris sinensis — Nemenzo, 1971: 156; 1981: 185, fig. 202; 1986: 141.

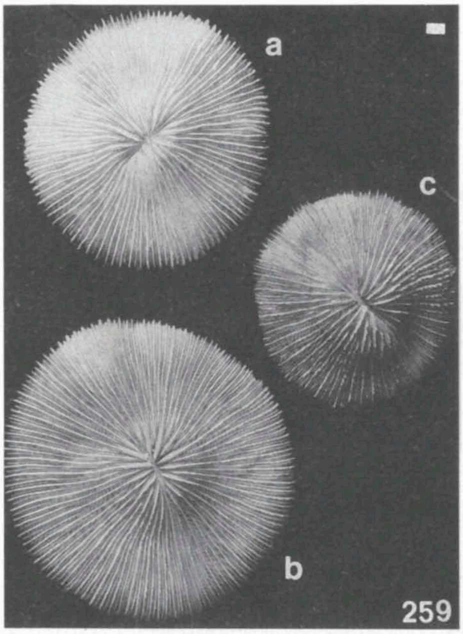
Cycloseris costulata — Veron & Marsh, 1988: 81 (partim).

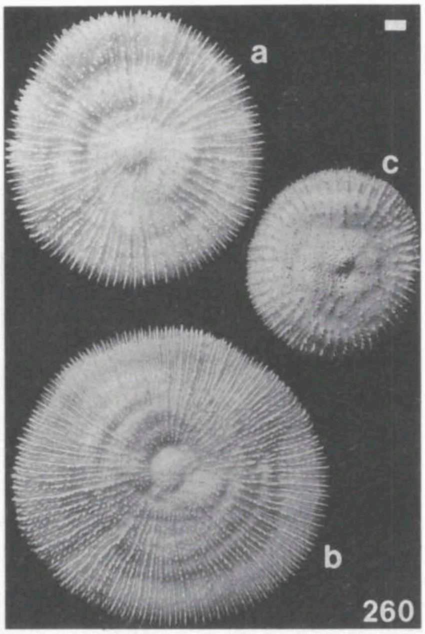
Type material examined. — USNM 120, YPM 1948 (2 syntypes of *Fungia horrida*; type loc. FIJI); MNHN 484 (lectotype [present designation] of *Fungia danai*; type loc. Manila, PHILIPPINES); MCZ 126 (lectotype [present designation] of *Fungia valida*; type loc. ZANZIBAR); MCZ 393 (2), 5400-5401 (8), MNHN Fun92, YPM 63 (12 paralectotypes of *Fungia valida*; ZANZIBAR); RGM 3890-3891, 167556 (syntypes of *Fungia inaequicostata*; type loc. Gunung Linggapadang, Java, INDONESIA).

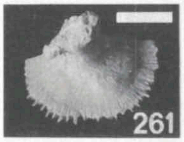
Other material. — RED SEA: HLM RM74, USNM 48095, 77746, 78250, ZMA 440. Gulf of Aqaba: NS 9295, 3069, RMNH 18064 (4). Gulf of Suez: HLM X2:3-29, SLR 841-2. DJIBOUTI: MNHN 3515-3516, USNM 21984. PHILIPPINES. Santa Cruz Is.: AMNH 1968. E Mindoro: UPZD 120. Negros: USNM 77967. Cebu: UPZD 529. INDONESIA. Java: RGM 77655 (fossil), 77658 (fossil), 77776-77777 (fossil). NW Java: RMNH 16171 (6), 16173-16176 (23), 16210-16212 (9), 16214 (3), 16216 (5). SW Sulawesi: RMNH 15698, 15700-15703 (5), 20523 (8), 20544 (12), 20560 (2), 20635 (2), 20644, 20659, 20661-20662, 20667 (15), 20675 (4), 20677 (11), 20686 (13), 20830 (2), 20881 (5), 20956 (2), 21039 (5). Tiger Is.: RMNH 20627 (3), 21071 (7), 21216. Togian Is.: RMNH 9538-9539. Komodo: RMNH 20409, 20235, 21463 (4), 21514. N Sumbawa: RMNH 21640 (3), 21669, 21696. NE Sumba: RMNH 20236 (2). Kera: RMNH 16224. Tukang Besi Is.: RMNH 20102 (2). N Halmahera: USNM 78066. S Moluccas: WAM 1378.88. Banda: UZMK. Kei Is.: RMNH 8375. Biak: RMNH 15768. PALAU IS.: USNM 47048-47085. AUSTRALIA. Kimberley: WAM 262.83, 391.83, 1010.85, 1012.85, 522.86, 655.86. Torres Str.: MCZ 5491. C Great Barrier Reef: QMB GL3201. PAPUA NEW GUINEA. Bismarck Sea: ULB. SOLOMON IS.: BMNH 1938.3.17.1. NEW CALEDONIA: USNM 78073, ZMA 6289. VANUATU (NEW HEBRIDES): AIMS. MARSHALL IS.: USNM 44856. GILBERT IS.: USNM 77893-77895, 78349. PHOENIX IS.: USNM 78260. FIJI IS.: BMNH 1886.12.9.195. TONGA IS.: BMNH

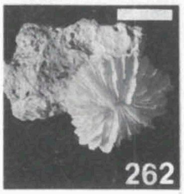
1891.3.6.113. SAMOA IS.: AMNH. COOK IS.: GPC. SOCIETY IS.: BMNH 1886.12.9.205, 1973.4.17.14, MNHN, USNM 77812.

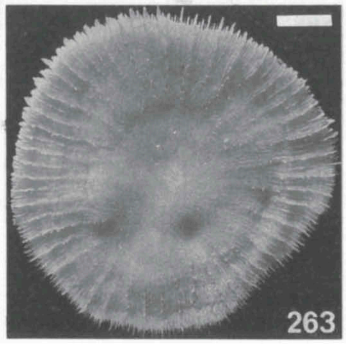
Characters. — Adult animals are unattached, monostomatous and discoidal. Fragmentation slits are absent. The coralla are relatively thick and they vary from flat to slightly arched. The diameter of the specimens varies between 3.5 and 21.5 cm.

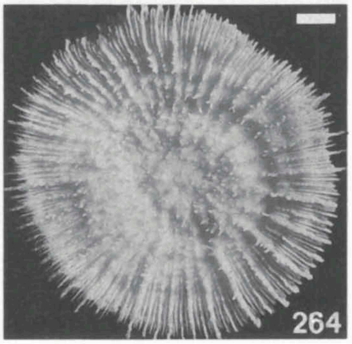






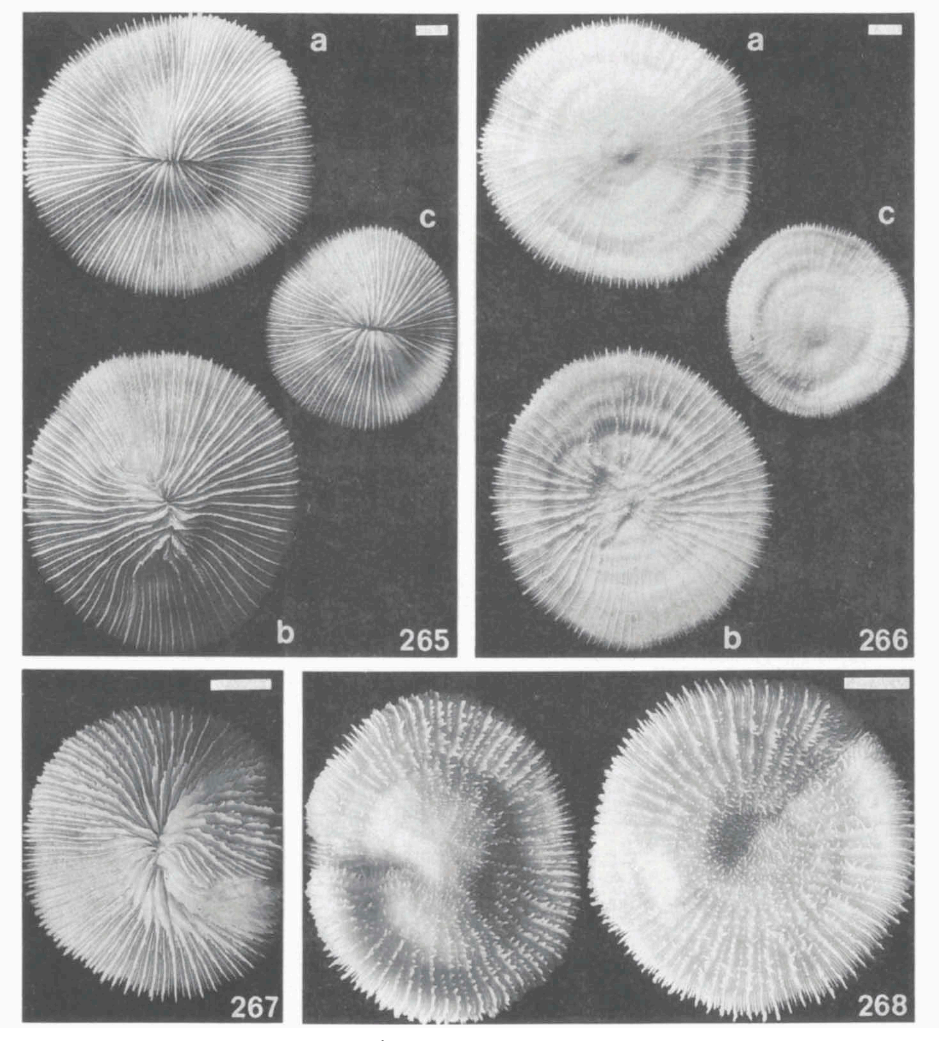






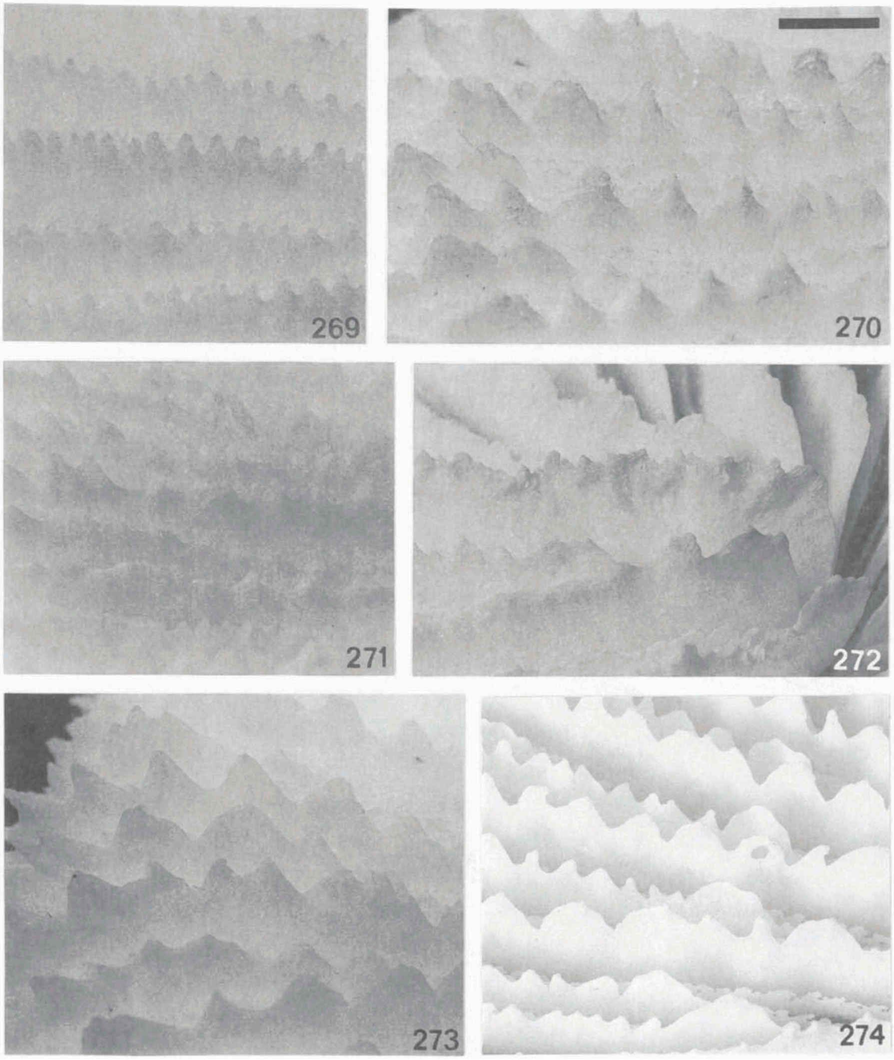
Figs. 259-264. Corals of *Fungia (Danafungia) horrida* from Indonesia. Scale bars: 1 cm. Figs. 259-260. Upper and lower surface of three specimens (anthocyathi) with large septal dentations: (a-b) RMNH 16173, 16171 (NW Java) and (c) RMNH 9538 (E Sulawesi). Fig. 261. Aboral surface of a broken-off anthocaulus (RMNH 16175; NW Java). Fig. 262. Upper surface of an anthocaulus (RMNH 16175; NW Java). Fig. 263. Aboral surface of an anthocyathus with conspicuously short spines (RMNH 16214; NW Java). Fig. 264. Aboral surface of a coral with long spines (RMNH 15698; SW Sulawesi).

The length of the central fossa, measured at its bottom, is 1/10 to 1/5 of the corallum diameter. The septal edges at both of its sides stand upright, whereas at both ends of the fossa they diverge away from it. The columella is formed by a mingled mass of loosely packed trabeculae and paliform lobes with their tips either pointing upwards or in various directions.



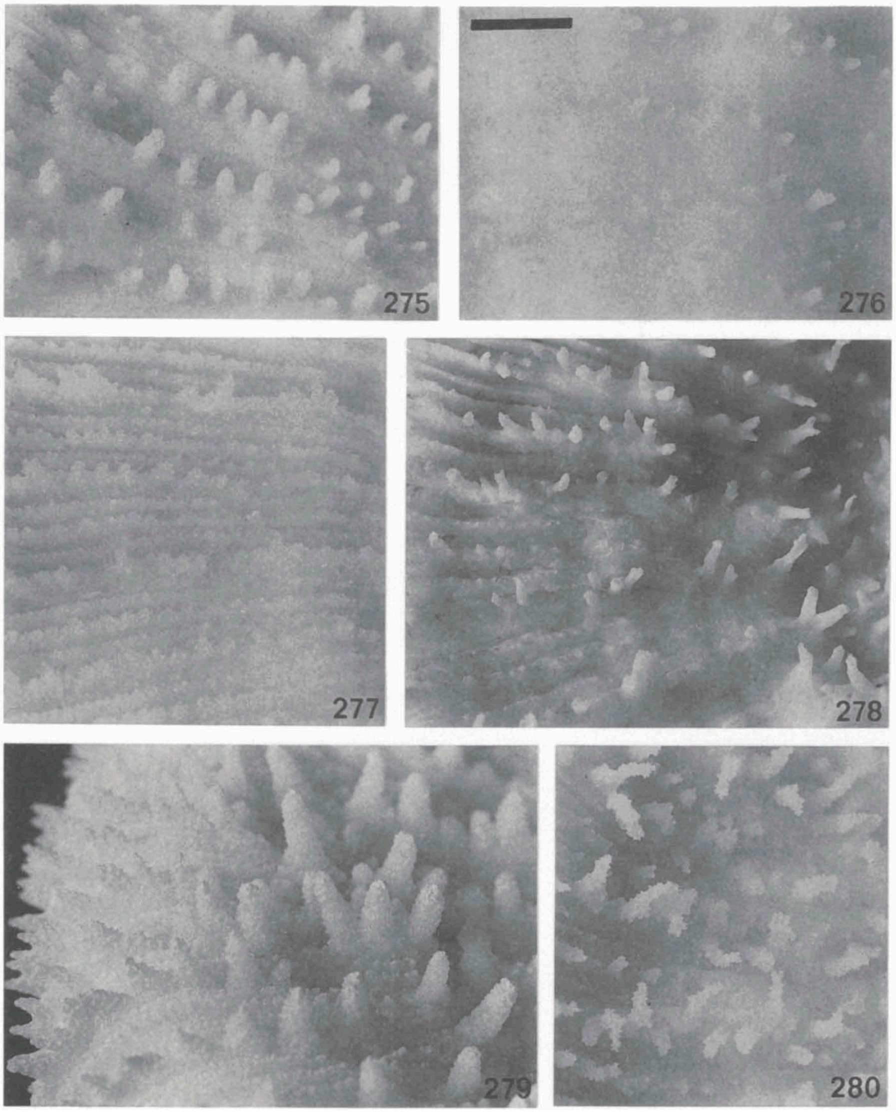
Figs. 265-268. Corals (anthocyathi) of *Fungia (Danafungia) horrida* from NW Java, Indonesia. Scale bars: 2 cm. Figs. 265-266. Upper and lower surface of three corals with relatively fine septo-costal ornamentations: (a) RMNH 16171, (b) RMNH 16174, (c) RMNH 16214. Fig. 267. Upper surface of a coral with large septal dentations (RMNH 16175). Fig. 268. Aboral surface of two corals with long costal spines: (a) the coral in fig. 267 and (b) RMNH 16176.

The septa are relatively thick, loosely packed and straight. The solid septa of lower order cycles are thicker and more protruding than the perforated ones of higher orders. Tentacular lobes are absent. The septal margins are coarsely ornamented with regularly or irregularly angular dentations (figs. 269-274). Their number varies from 2 to 10 per cm; they are sometimes observed in fused



Figs. 269-274. Septa of *Fungia (Danafungia) horrida* corals. Scale bar: 0.5 cm. Fig. 269. The coral in fig. 265b. Fig. 270. The coral in fig. 259c. Fig. 271. The coral in fig. 259b. Fig. 272. The coral in fig. 264. Fig. 273. The coral in fig. 267. Fig. 274. A coral from NW Java, Indonesia (RMNH 16172).

pairs (fig. 274). The septal sides are thinly to densely granulated. The granulations are fine and irregularly dispersed. In some specimens they are fused in faint ridges parallel to the septal margin. The compound synapticulae connecting the septa laterally can be easily distinguished, because of the loose septal arrangement.



Figs. 275-280. Costae of *Fungia (Danafungia) horrida* corals. Scale bar: 0.5 cm. Fig. 275. The coral in fig. 260c. Fig. 276. The coral in fig. 266c. Fig. 277. The coral in fig. 266a. Fig. 278. The coral in fig. 264. Fig. 279. The coral in fig. 260a. Fig. 280. The coral in fig. 268b.

The corallum wall is solid and granulated. A detachment scar is distinct at the aboral side of small specimens in anthocyathus-stage. The costae are very unequal in size; they are straight and distinct near the corallum margin, but less distinct and wavy near the centre. The lower order costae are coarsely ornamented with blunt or elongate spines covered by coarse granulations which may give the spines a branched appearance (figs. 275-280). The number of the spines varies from 4 to 16 per cm. The projections on the costae of higher orders are rudimentary or absent.

The living animal is variable in colour. It is usually irregularly brown with light and dark patches (fig. 13). Some animals are greyish brown with irregularly white patterns or with a violet mouth and corallum margin. The transparent or white tentacles are small and inconspicuous.

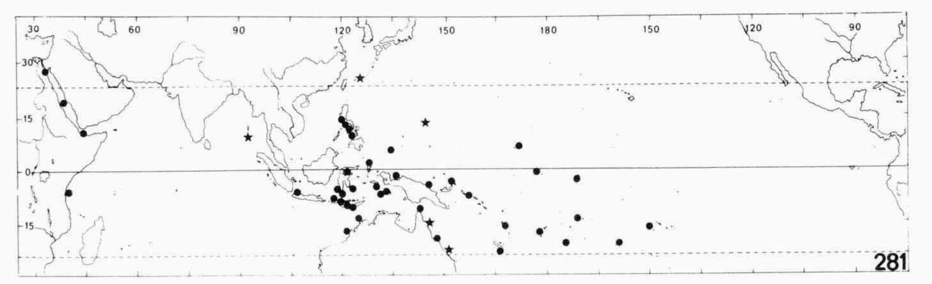


Fig. 281. The range of *Fungia (Danafungia) horrida*. Records are from examined material (●) and published illustrations (★).

Geographical distribution (fig. 281). — The species has been found in the western Indian Ocean and in the Pacific, from Indonesia to the Society Islands.

Remarks. — The syntypes of *Fungia acutidens* and *F. klunzingeri* are no longer present in the collections of ZMB and SMNS (see Döderlein, 1902) and can therefore be considered lost. The clear photographs of these syntypes, published by Döderlein (1902), are very useful for studying the characters of these so-called species. Together with *F. valida* and *F. danai*, they are synonymized with *F.horrida*. The type material of all these nominal taxa can be placed in a continuous series of one highly polymorphic species. The only differences between the type specimens are found in the size of the septal and costal ornamentations. When many specimens are collected at a single location, such as SW Sulawesi, the whole morphological range can be observed with the intermediate forms most abundant. Specimens from the Red Sea may show a detachment scar (as described for *F. klunzingeri*) due tot particular environmental conditions there; it is for example a character commonly shown in silty water. *F. inaequicostata* is a fossil variety of the species. Although its type specimens are severely abraded, they can still be recognized by the solid corallum wall and the relatively large lower order costae.

In the literature, there is a lot of confusion about *F. danai*. The lectotype of *F. danai*, a coral from the Milne Edwards & Haime collection at the MNHN, distinctly shows a solid corallum wall (figs. 257-258). The paralectotypes of *F. danai* are two specimens of *F. scruposa* described by Dana (1846) as *Fungia echinata* and as such referred to in the synonymy by Milne Edwards & Haime (1851: 80). Since Döderlein's (1902) revision the name *F. danai* has been used for *F. scruposa*, a species with a perforated corallum wall.

The corallum of *F. horrida* has a solid wall (figs. 255-256), a character it has in common with *F. fralinae*. The former species is more heavily built and its septa and costae have much coarser ornamentations. The living animals can easily be separated in the field because of their different coloration. *F. horrida* lacks the violet tentacle tips of *F. fralinae*.

Fungia (Danafungia) scruposa Klunzinger, 1879
(figs. 16-17, 282-305, 627-628, 631-632)

Fungia echinata — Dana, 1846: 294-295, pl. 18 figs. 8-9b.

Fungia repanda Dana, 1846: 295-296 (partim).

Fungia dentata — Milne Edwards & Haime, 1851: 80; 1860: 10-11.

Fungia danae Milne Edwards & Haime, 1851: 80-81 (partim); 1860: 11 (partim).

Fungia valida Verrill, 1864: 51 (partim).

Fungia scruposa Klunzinger, 1879: 63, pl. 7 fig. 2, pl. 8 fig. 1 (Koseir, Red Sea); Döderlein, 1902: 133-136, pl. 19 figs. 1-3 (including var. *ternatensis* Döderlein, 1902 [Ternate]); Von Marenzeller, 1907: 89; Van der Horst, 1921: 65; Matthai, 1924: 46; Yabe & Sugiyama, 1935: 396; Ma, 1937: 142, pl. 36 figs. 2-3; Yabe & Sugiyama, 1941: 79-80, pl. 75 figs. 4-4a, pl. 76 figs. 1-1b; Nemenzo, 1976: 243-244, pl. 6 figs. 2-3; Nemenzo, 1981: 193, fig. 214; Scheer & Pillai, 1983: 82-83, pl. 19 figs. 2-3; Johnston, 1986: 159; Nemenzo, 1986: 149, fig. 172; Hoeksema & Moka, 1989: figs. 7a-b. Not: Veron, 1986a; Veron & Marsh, 1988.

Fungia rugosa Quelch, 1886: 135-136, pl. 6 figs. 2-2a (Tahiti, Society Islands). (New synonymy).

Fungia lobulata Ortmann, 1889: 520, pl. 15 fig. 3 ("von der Südküste Ceylons"). (New synonymy).

Fungia corona Döderlein, 1901: 358 ("Singapur"); 1902: 132-133, pl. 15 figs. 2-2a; Gardiner, 1909: 278-279, pl. 35 figs. 11-12; Matthai, 1924: 46; Pillai, 1972: 203. (New synonymy).

Fungia subrepanda Döderlein, 1901: 358 ("Singapur und Celebes"); 1902: 126-129, pl. 17 figs. 1-7; Matthai, 1924: 45; Yabe & Sugiyama, 1935: 396; Yabe & Sugiyama, 1941: 79, pl. 76 figs. 2-2d; Pillai, 1972: 203. (New synonymy). Not: Umbgrove, 1939; Shirai, 1980.

Fungia danai — Döderlein, 1902: 129-132, pl. 14 figs. 3-3a, pl. 15 figs. 3, 4a, pl. 16 figs. 5-5a, pl. 18 figs. 1-4a (including var. *vitiensis* Döderlein, 1902 ["Viti-Inseln"]); Gardiner, 1905: 941; Bedot, 1907: 218; Gardiner, 1909: 278; Van der Horst, 1921: 65; Matthai, 1924: 45-46, pl. 10 fig. 5; Boschma, 1925: 220; Faustino, 1927: 181-182 (partim), pl. 57 figs. 1-2, pl. 58 fig. 2.; Boschma, 1929: 46; Yonge, 1930: 35-36, figs. 20-21a; Thiel, 1932: 78-80, pl. 9 figs. 2-3; Ma, 1937: 136-137, pl. 62 fig. 1, pl. 63 fig. 1, pl. 64 fig. 1; Umbgrove, 1939: 44; 1940: 294; Yabe & Sugiyama, 1941: 79, pl. 74 figs. 1-1d; Nemenzo, 1955: 64-65, pl. 13 figs. 2-3; Ma, 1958: pl. 15; Pillai, 1971a: 324; 1971b: 8; 1972: 203; Pichon, 1974: 176; Zou, 1978: 100; Chevalier, 1979: 132; Nemenzo, 1981: 191, fig. 211; Pillai, 1983: 86; Scheer & Pillai, 1983: 82, pl. 19 figs. 1-2; Zou &

Chen, 1983: 91; Johnston, 1986: 159; Nemenzo, 1986: 147, fig. 169; Veron & Kelley, 1988: 31.

Fungia madagascarensis Vaughan, 1906: 831-832, pls. 72, 73, 74 fig. 3 (Madagascar). (New synonymy).

Fungia fieldi Gardiner, 1909: 277-278, pl. 33 figs. 3-4, pl. 34 fig. 7 (Salomon Atoll, Chagos Is.). (New synonymy). Not: Yabe & Sugiyama, 1941; Zou, 1978; Zou & Chen, 1983.

Fungia repanda — Ma, 1937: 135-136 (partim), pl. 67 fig. 2; Baguis & Christian, 1977: 96.

Fungia samboangensis — Ma, 1937: 136 (partim), pl. 49 figs. 1-2.

Fungia concinna — Umbgrove, 1946b: 534 (partim), pl. 81 figs. 5-6.

Fungia (Danafungia) corona — Rosen, 1971a: 76; Veron & Pichon, 1979: 136-137, figs. 218-221; Veron, 1986b: 336.

Fungia (Danafungia) danai — Pillai, Vine & Scheer, 1973: 459; Ditlev, 1976: 6; Pillai & Scheer, 1976: 43-44; Faure, 1977: 9; Veron & Pichon, 1979: 134-136, figs. 214-217; Ditlev, 1980: 56, figs. 43, 237; Faure, 1982: 103-104; Randall & Myers, 1983: 18, figs. 341-342; Veron, 1986b: 336 (partim); Sakai & Yamazato, 1987: 46.

Fungia (Danafungia) subrepanda — Ditlev, 1976: 6. Not: Scheer & Pillai, 1974.

Fungia fungites — Schuhmacher, 1979: figs. 26-27.

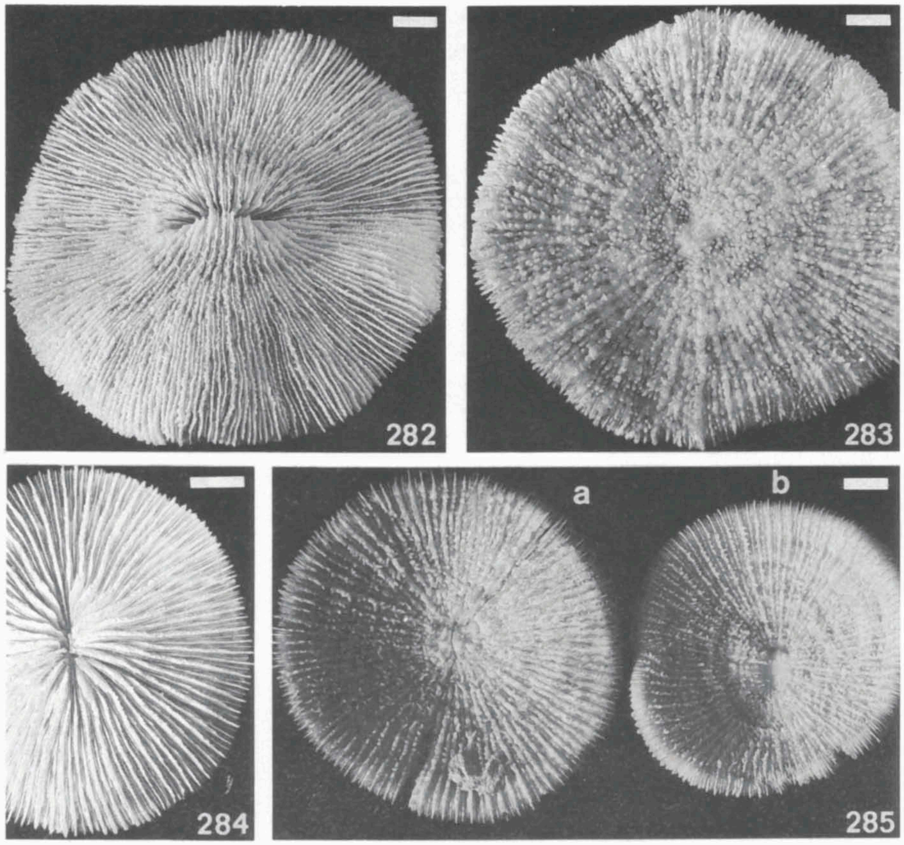
Fungia (Danafungia) scruposa — Veron & Pichon, 1979: 137, 139 (partim), figs. 223, 225; Faure, 1982: 104; Veron, 1986b: 337.

Fungia (Verrillofungia) subrepanda — Sakai & Yamazato, 1987: 46.

Type material examined. — USNM 124 (paralectotype of *Fungia danai*; Fiji); USNM 125 (paralectotype of *Fungia danai*; East Indies); USNM 111 (paralectotype of *Fungia repanda*; Sulu Sea, PHILIPPINES); MCZ 5400 (paralectotype of *Fungia valida*; ZANZIBAR); MNHN 4135 (lectotype [present designation] of *Fungia scruposa*; type loc. Koseir, RED SEA); BMNH 1886.12.9.196/375 (syntypes of *Fungia rugosa*; type loc. Tahiti, SOCIETY IS.); ZMB 4106 (lectotype [present designation] of *Fungia subrepanda*; for illustrations, see Döderlein, 1902: pl. 17 figs. 6-6a); type loc. SINGAPORE; USNM 21141 (holotype of *Fungia madagascarensis*; type loc. MADAGASCAR); UMZC (3 syntypes of *Fungia fieldi*; type loc. Salomon Atoll, CHAGOS IS.).

Other material. — RED SEA: USNM 77740. Gulf of Aqaba: RMNH 15791, 18067, USNM 78265. KENYA: RMNH 17089. ZANZIBAR: MCZ 664. SEYCHELLES. St.-Pierre I.: RMNH 9424. N MADAGASCAR: USNM 77728-77729. MASCARENE IS. Mauritius: ZMA 5590, 5601. CHAGOS IS.: BMNH 1891.4.9.16. MALDIVES: RMNH 22156-22157 (3), YPM 7827, 7831-7832, 7834. SINGAPORE: AMNH 1759, BMNH 1891.8.9.1/6, 1893.7.22.1-2/5-6, MCZ 330, 5394 (44), USNM 77751, YPM 51, 53, 1428 (2), 4012, ZMA 465. MALAYSIA. Sabah: USNM 47949, 47956. HONG KONG: BMNH 1935.9.21.3/5/11. PHILIPPINES: USNM 45404, 77960. SW Luzon: USNM 77936 (2). Burias: USNM 78007. Cebu: USNM 77975. Sulu Is.: USNM 111. INDONESIA: RMNH 15788, ZMA 337, 412. Belitung (Billiton): ZMA 407, 456, 461, 488. Java: RGM 3876 (fossil), 77654 (fossil). NW Java: RMNH 15786-15787, 16033 (3), 16141, 16144-16145 (3), 16148-16151 (20). SW Sulawesi: RMNH 15708-15710, 20401 (13), 20422 (21), 20424, 20561, 20568 (3), 20588, 20882 (3), 20984, 21022. Tiger Is.: RMNH 20638 (2), 21073, 21169, 21204 (5). Komodo: RMNH 20407 (2), 20446, 21464. N Sumbawa: RMNH 21642 (4), 21671. Moluccas: RMNH 9505, 9536-9537. Obi Latu: RMNH 15728. Kei Is.: RMNH 8376, USNM 80451. CAROLINE IS.: USNM 77794. PAPUA NEW GUINEA. Bismarck Sea: ULB. MARIANA IS. Guam: USNM 79994. SOLOMON IS.: BMNH 1938.3.1.3, 1938.3.17.4. AUSTRALIA. C Great Barrier Reef: BMNH 1892.12.1.194/441, QMB G8067, GBR340, GL3614-3616, USNM 78343. S Great Barrier Reef: QMB G6158, QMT. NEW CALEDONIA: ZMA 6276. SAMOA IS.: USNM 77851, YPM 6097-6098. PHOENIX IS.: USNM 78261. SOCIETY IS.: BMNH 1886.12.9.182/192/371-372/376, 1973.4.17.16-23, MNHN, RMNH 8980-8981 (8), 15789, USNM 77814, 77855. COOK IS.: GPC. TUAMOTU IS.: BMNH 1939.1.2.32.

Characters. — Adult animals are unattached, monostomatous and discoidal. The corals are thick and vary from flat to highly arched. There may be



Figs. 282-285. Corals (anthocyathi) of *Fungia (Danafungia) scruposa*. Scale bars: 2 cm. Figs. 282-283. Upper and lower surface of the lectotype (MNHN 4135; Koseir, Red Sea). Fig. 284. Upper surface of an arched coral (RMNH 9537; Moluccas, Indon.). Fig. 285. Aboral surface of arched corals: (a) the coral of fig. 284, (b) RMNH 9536 (Moluccas, Indon.).

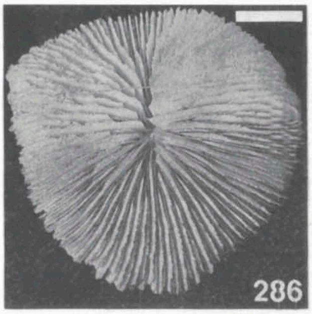
fragmentation slits in the corallum wall, but fragmented forms have not been observed. The diameter of the specimens varies between 3.0 and 38.0 cm.

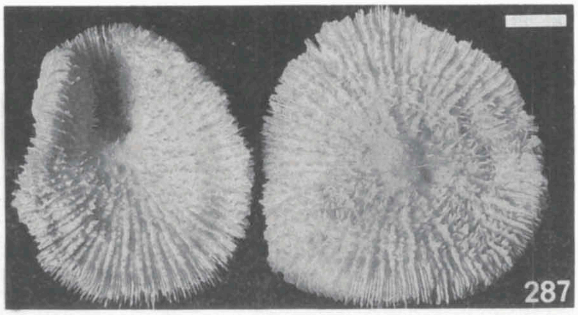
The length of the central fossa, measured at its bottom, is 1/8 to 1/5 of the coral length. The septal edges at both sides of the fossa stand upright, whereas those at both ends diverge away from it. The columella is formed by a mingled mass of loosely packed trabeculae and paliform lobes with their tips pointing in various directions.

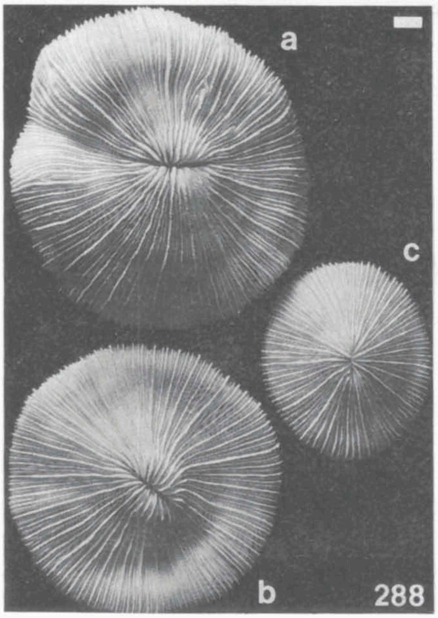
The septa are straight and densely packed. The solid septa of lower order cycles are thicker and more protruding than the perforated ones of higher orders. Tentacular lobes may be present (fig. 298). The septal margins are coarsely ornamented with irregularly angular dentations (figs. 294, 296-299).

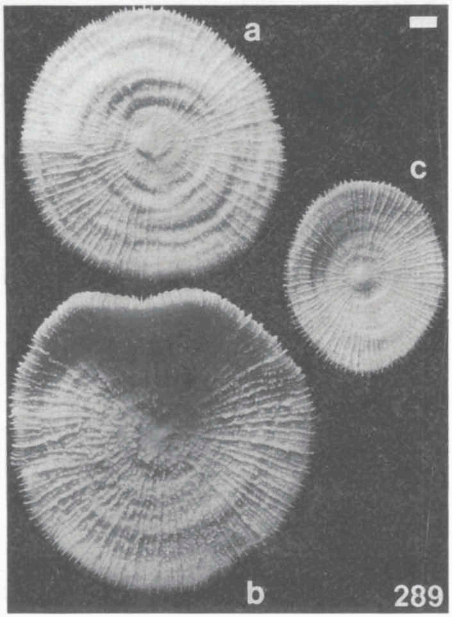
Their number varies from 5 to 16 per cm. The septal sides are thinly to densely granulated. The granulations are fine and either irregularly dispersed or arranged in indistinct rows parallel to the septal margin (figs. 627-628). The compound synapticulae connecting the septa laterally can easily be distinguished in spite of the tight septal arrangement.

In many small specimens the corallum wall is already perforated. The centre usually remains solid and shows a detachment scar at the aboral side of small to medium-sized anthocyathi. The wall is granulated (figs. 631-632). The costae

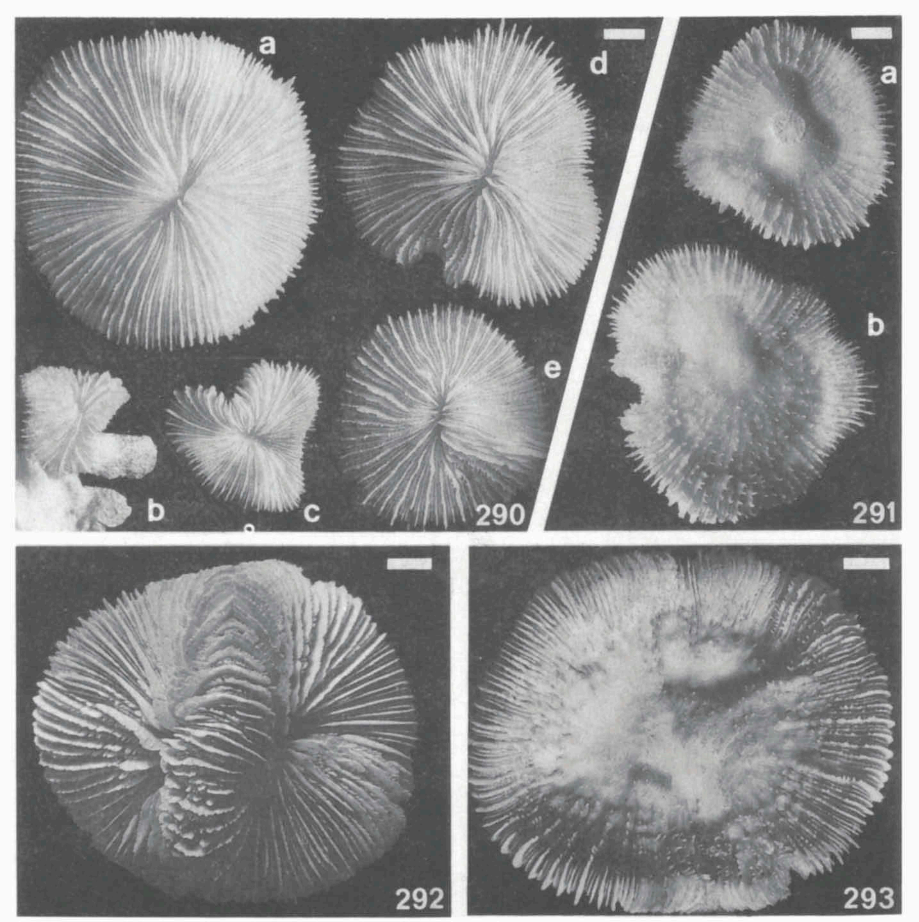








Figs. 286-289. Corals (anthocyathi) of *Fungia (Danafungia) scruposa*. Scale bars: 2 cm. Fig. 286. Upper surface of a syntype of *Fungia rugosa* (BMNH 1886.12.9.196; Tahiti, Society Is.). Fig. 287. Aboral surface of the two syntypes of *Fungia rugosa*: (a) BMNH 1886.12.9.375, (b) the coral in fig. 286. Figs. 288-289. Upper surface of three flat or partly arched corals from NW Java (Indon.): (a) RMNH 16150, (b) RMNH 16149, (c) RMNH 16144.



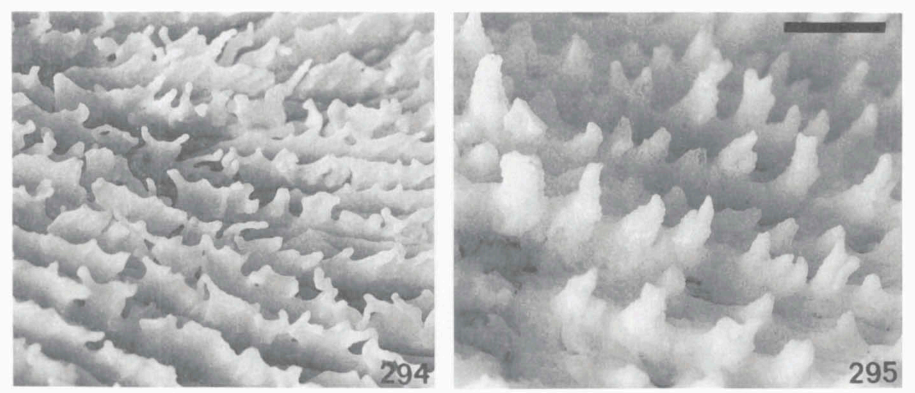
Figs. 290-293. Corals (anthocyathi) of *Fungia (Danafungia) scruposa*. Scale bars: 1 cm. Fig. 290. Upper surface of juveniles from NW Java (Indon.): (a-b, e) RMNH 16149, (c-d) RMNH 16033. Fig. 291. Aboral surface of the corals in figs. 290e (a), 290d (b). Figs. 392-293. Upper and lower surface of two fused individuals with an imperforate centre (RMNH 15786; NW Java, Indon.).

are unequal in size; they are straight and distinct near the corallum margin, but are less distinct and wavy near the centre. The lower order costae are coarsely ornamented with elongate spines which are either blunt or acute. These spines protrude in various directions; because of their coarse granulations they may appear to be branching (figs. 295, 300-305). Their number varies from 4 to 15 per cm. The spines on the costae of higher orders are either rudimentary or absent.

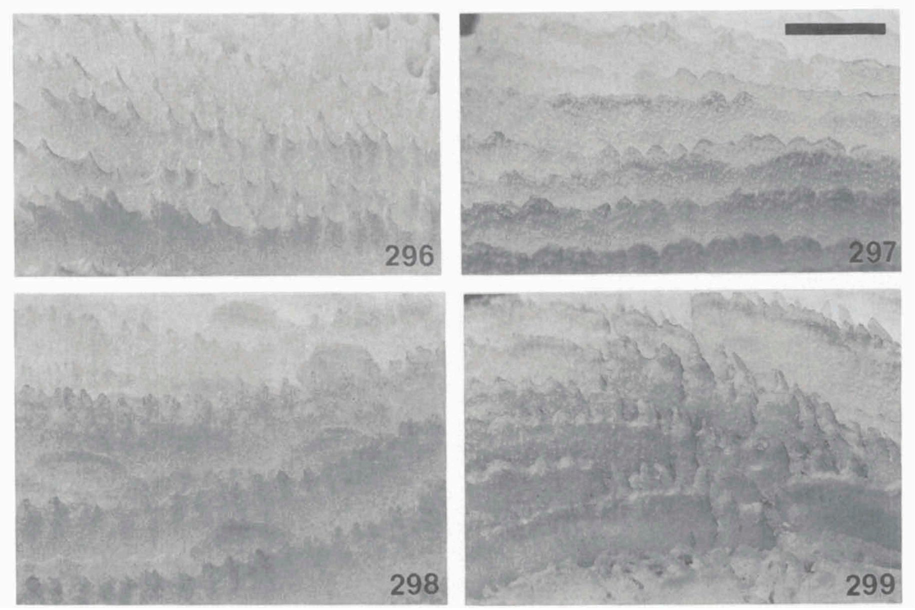
The living animal is usually brown (figs. 16-17). The small tentacles are whitish transparent. The margin of the mouth is radially striped in brown combined with yellow, green or orange.

Geographical distribution (fig. 306). — The range of the species extends from the Red Sea and eastern Africa towards the Tuamotu Archipelago. Its northernmost locality is in the Ryukyu Islands, southern Japan.

Remarks. — The paralectotypes of *F. danai* are two specimens of *F. scruposa* described by Dana (1846) as *Fungia echinata* and as such referred to in the synonymy of *F. danai* by Milne Edwards & Haime (1851: 80). It is unlikely that these authors have observed the specimens described by Dana.

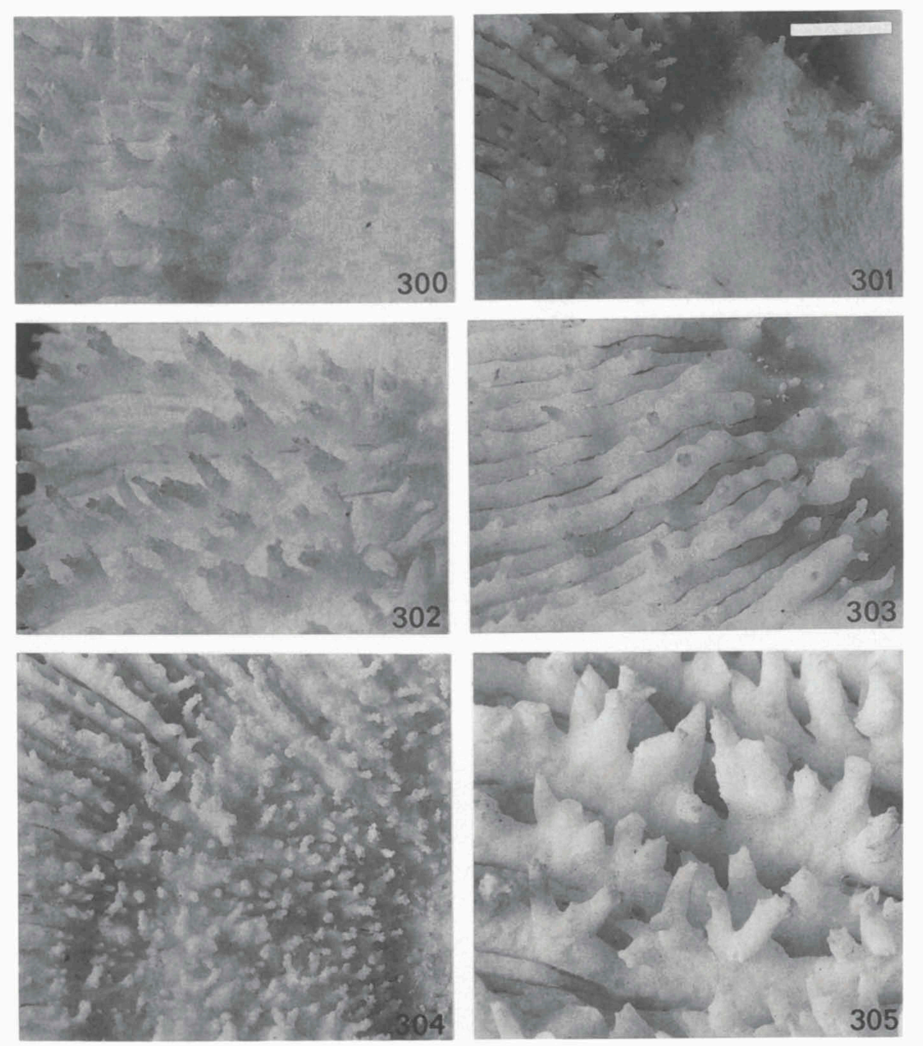


Figs. 294-295. Septa and costae of the lectotype of *Fungia scruposa*. Scale bar: 0.5 cm.



Figs. 296-299. Close-ups of *Fungia (Danafungia) scruposa* corals. Scale bar: 0.5 cm. Fig. 296. Septa of the coral in fig. 288c. Fig. 297. Septa of a coral from Indonesia (ZMA 337). Fig. 298. Septa of the coral in fig. 284. Fig. 299. Septa of the coral in fig. 292.

After Döderlein's (1902) revision of the genus *Fungia*, specimens of *F. scruposa* have often been identified as *Fungia danai* (= *F. horrida*). Döderlein (1902), however, did not refer to the syntype of *F. danai* in the Milne Edwards & Haime collection in Paris. This specimen, which in this revision is designated lectotype of *F. danai*, lacks the perforated corallum wall which serves as a



Figs. 300-305. Close-ups of *Fungia (Danafungia) scruposa* corals. Scale bar: 0.5 cm. Fig. 300. Costae of the coral in fig. 289c. Fig. 301. Costae of the coral in fig. 293. Fig. 302. Costae of the syntype of *Fungia rugosa* in fig. 287b. Fig. 303. Costae of a coral from Indonesia showing an imperforate centre (ZMA 337). Fig. 304. Costae of a coral from unknown locality (ZMA 474). Fig. 305. Costae of the coral in fig. 294a.

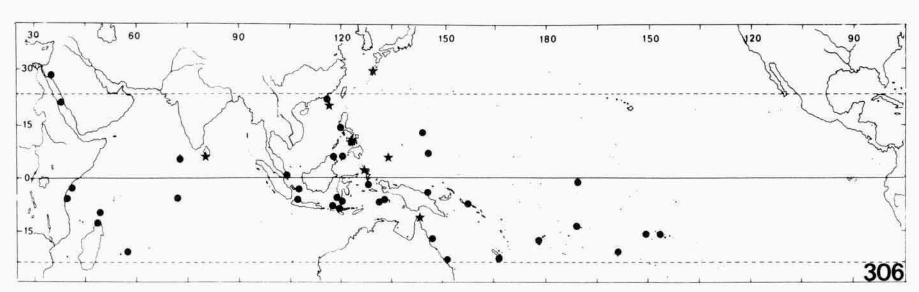


Fig. 306. The range of *Fungia (Danafungia) scruposa*. Records are from examined material (●) and published illustrations (★).

diagnostic character of *F. scruposa*.

Syntypes of *F. scruposa* were donated, exchanged or sold to several museums in the world. After World War II no specimens were left in the original collection at the SMNS (see for example Döderlein, 1902: pl. 19 figs. 1-1a). The specimen which is still present at the MNHN is the only syntype that could be traced and is therefore designated lectotype (figs. 282-283, 294-295). The syntypes of *F. subrepanda* in the SMNS collection are also lost due to the Second World War; the only specimen known to be present in the ZMB collection, is designated lectotype.

The two syntypes of *F. rugosa* represent immature forms of *F. scruposa* (figs. 286-287, 302). The holotypes of *Fungia lobulata* and *F. corona* were no longer present in the ZMB and the MZS collections respectively. They are well enough illustrated to recognize them as specimens belonging to *F. scruposa*. *F. subrepanda* is also a synonym of *F. scruposa*; although the epithet suggests that it resembles *F. repanda*, Döderlein (1902) placed it in his so-called *danai*-group, the present subgenus *F. (Danafungia)*). In the syntypes of *F. subrepanda* the centre of the corallum wall is not perforated. This indicates that the animals did not start making perforations early in the anthocyathus-stage. In large samples of the species, inperforated central zones of various diameters can be observed.

The holotype of *F. madagascarensis* and the syntypes of *F. fieldi* are relatively heavy coralla having long costal spines. They are all very similar as has already been noted by Gardiner (1909). The specimens do not differ essentially from those belonging to *F. scruposa*. Vaughan (1906) placed his *F. madagascarensis* in Döderlein's (1902) *fungites* -group (now subgenus *Fungia*) because of the conical spines. Gardiner (1909) erroneously thought that his *F. fieldi* belonged to the *repanda* -group (now subgenus *Verrillofungia*) because of the granulated surface of the spines. This character is not necessarily typical for *F. repanda* -like corals. The septal dentations of the *F. fieldi* specimens do not bear the typical zigzag patterns of granulations on their sides such as is usually observed in *F. (Verrillofungia)*.

The species is most similar to *F. horrida*, but can easily be distinguished by its perforated corallum wall. Specimens may be confused with those of *F. fungites*, which have septa and costae which are more equal in size and with finer ornamentations.

Subgenus **Fungia** Lamarck, 1801

Type species: *Fungia agariciformis* Lamarck, 1801 [= *Fungia fungites* (Linnaeus, 1758)]. Designated by Leuckart, 1841.

Fungia (Fungia) — Wells, 1966: 239; Veron & Pichon, 1979: 129; Ditlev, 1980: 57; Veron & Kelley, 1988: 31.

Characters. — Adult animals are free-living and have a perforated corallum wall. The septa are ornamented by fine to moderately coarse, usually sharp, dentations. The septal sides are covered by granulations arranged in rows or ridges perpendicular to the septal margin. The costae are either uniform in size or vary only slightly. The costal spines are conical and elongate with sharp granulations at the tip.

Remarks. — After Wells (1966) established several subgenera in *Fungia*, *F. (Fungia)* has only included the type species of the genus, *F. (F.) fungites*; thus Döderlein's (1901) *fungites* -group got a more official taxonomic status. *F. (F.) fungites* cannot be classified with other subgenera because of its almost uniform septa and costae and because of the unique shape of their projections. The coralla are morphologically most similar to those of *F. (Danafungia) scruposa*, which have unequally sized costae. The ornamentations of the septa and the costae are very similar to those of the polystomatous genus *Halomitra*.

Fungia (Fungia) fungites (Linnaeus, 1758)
(figs. 14-15, 307-321, 633-637)

Madrepora fungites Linnaeus, 1758: 793-794 ("Habitat in Mari rubro"; reference to Rumphius, 1750: 247, pl. 88 figs. 1, 4; loc. East Indies); Pallas, 1766: 281-284; Boddaert, 1768: 349-352; Houttuyn, 1772: 112; Forskål, 1775: 134; Müller, 1775: 676-677; Forskål, 1776: pl. 42 figs. 1-3; Ellis & Solander, 1786: 149, pl. 28 figs. 5-6; Wilkens, 1787: 17-24, pl. 13 fig. 47; Esper, 1791: 66-72, 284, pl. 1, pl. 2 fig 2; Gmelin, 1791: 3757.

Fungia patella Ellis & Solander, 1786: 148-149, pl. 28 figs. 1-4 ("Mediterranean Sea"); Esper, 1791: 75-77, pl. 62; Milne Edwards & Haime, 1851: 77-78; 1860: 7-8; Verril, 1864: 50; Klunzinger, 1879: 61-62, pl. 7 fig. 4, pl.8 fig. 2; Studer, 1880: 45; Duncan, 1886: 15; Quelch, 1886: 132-133; Ortmann, 1888: 177; 1889: 519; Gardiner, 1898: 526; Matthai, 1924: 39. (New synonymy).

Madrepora echinata — Esper, 1791: 72-74, 284-285, pl.2 fig. 1.

Fungia agariciformis Lamarck, 1801: 370 ("Aegypt"); 1815, 1816: 236; Oken, 1815: 74; Schweigger, 1820: 414; Lamouroux, 1821: 52, pl. 28 figs. 5-6; Blainville, 1830: 303; Stutchbury, 1833: 495-496, pl. 32 figs. 1-5; Blainville, 1834: 337; Ehrenberg, 1834: 48-50; Leuckart, 1841: 42-46, pl. 4 figs. 1-4; Dana, 1846: 292-293, pl. 18 figs. 5-6 (including var. *tenuifolia* Dana, 1846 [Tahiti]).

Fungia patellaris Lamarck, 1801: 370 (no locality given); 1815, 1816: 236 ("les mers de l'Inde et de la Méditerranée"); Lamouroux, 1821: 52, pl. 28 figs. 1-4; Blainville, 1830: 303, pl. 34 figs. 2-2b; 1834: 337; Lamarck, 1836: 372; Milne Edwards & Haime, 1848: 87-89, pl.6 fig. 1-1f.

Fongia patellaris — Blainville, 1820: 216.

Fongia agariciformis — Blainville, 1820: 216.

Fungia discus Dana, 1846: 291: pl. 18 fig. 3 (partim); Milne Edwards & Haime, 1851: 78-79; 1860: 9; Studer, 1877: 647; 1880: 45; Quelch, 1886: 133; Ortmann, 1888: 177; 1889: 520; Saville-Kent, 1893: 176, pl. 24 fig. 1; Gardiner, 1898: 526; Whitelegge, 1898: 355.
Not *Cycloseris discus* Quelch, 1886.

Fungia dentata Dana, 1846: 293-294, pl. 18 fig. 7 ("East Indies"); Milne Edwards & Haime, 1851: 80; 1860: 10-11.

Fungia confertifolia Dana, 1846: 297-298, pl. 19 fig. 5 ("Feejee Islands"); Milne Edwards & Haime, 1851: 79; 1860: 10; Verrill, 1864: 50; Quelch, 1886: 134; Brüggemann, 1879: 206; Ortmann, 1888: 177.

Fungia tenuifolia — Milne Edwards & Haime, 1851: 78 (partim); 1860: 9 (partim).

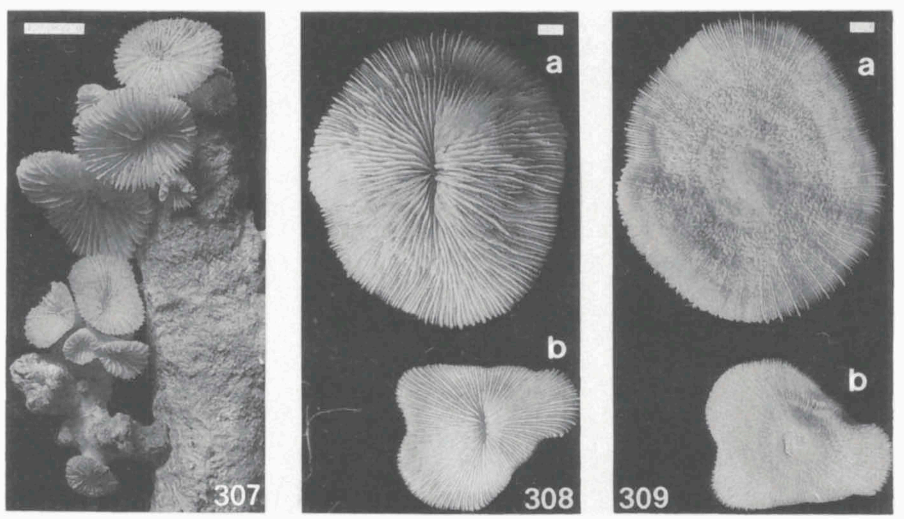
Fungia crassolamellata Milne Edwards & Haime, 1851: 82 ("Patrie inconnue. — Ch. Stokes").

Fungia crassilamellata — Milne Edwards & Haime, 1860: 12. (Changed spelling).

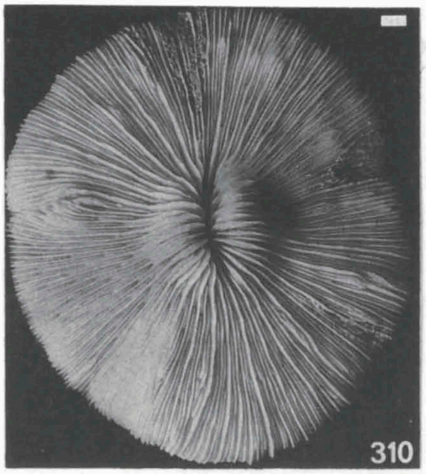
Fungia serrulata Verrill, 1864: 51 (partim).

Fungia haimei Verrill, 1864: 51 (Zanzibar).

Fungia papillosa Verrill, 1866: 42-43 ("Loo Choo Is."); Brüggemann, 1879: 206.



Figs. 307-309. Corals of *Fungia (Fungia) fungites* from NW Java, Indonesia. Scale bars: 1 cm. Fig. 307. Upper surface of anthocauli: (a) RMNH 16169, (b) RMNH 16163. Figs. 308-309. Upper and lower surface of medium-sized anthocyathi: (a) RMNH 16157, (b) RMNH 16166; during the anthocaulus-stage the growth of (b) was obstructed by the substratum.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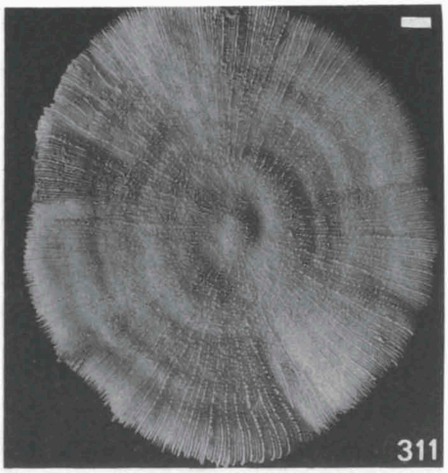
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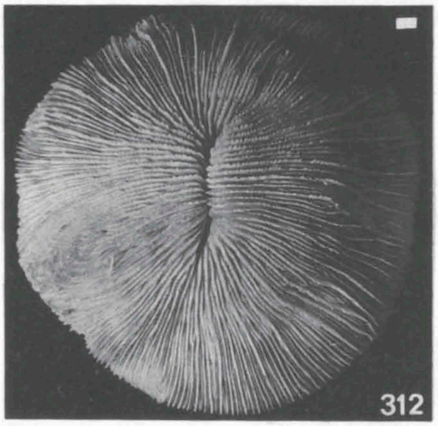
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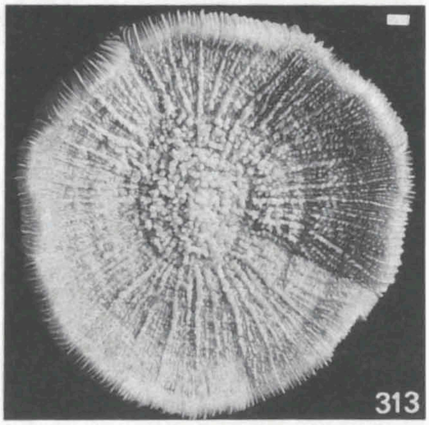
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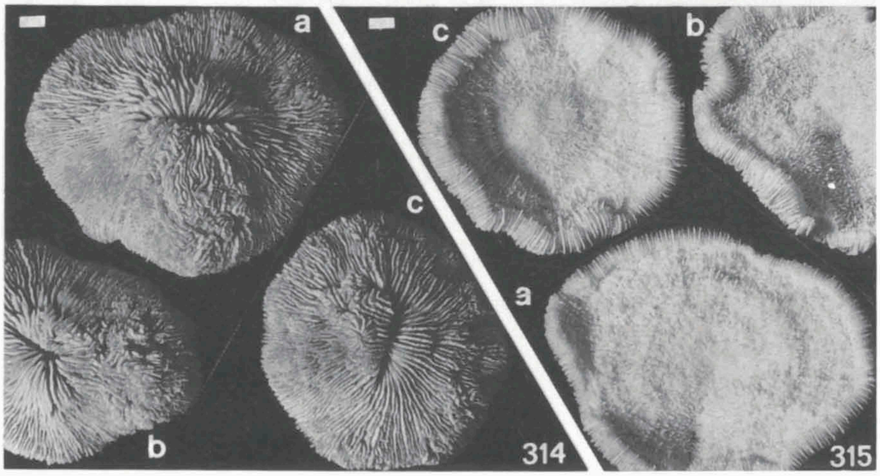

Figs. 310-315. Corals (anthocyathi) of *Fungia (Fungia) fungites* from Indonesia. Scale bars: 1 cm. Figs. 310-311. A flat coral with fine septal dentations (RMNH 16161; NW Java). Figs. 312-313. The neotype, a large, arched coral with coarse septal dentations (RMNH 16235; NW Java). Figs. 314-315. Three corals with supernumerary fossae and irregularly formed septa (Kei Is.): (a) RMNH 8396, (b) RMNH 9394, (c) RMNH 16007.

Fungia lacera Verrill, 1866: 43 (Fiji).

Fungia pliculosa Studer, 1877: 651, pl. 4 fig. 16 ("Bougainville-Insel").

Halomitra fungites — Studer, 1901: 408-409, pl.24 figs; 2-3. Faustino, 1927: 186-188, pl. 60 figs. 4-5.

Fungia fungites — Döderlein, 1902: 136-156, pls. 20-25 (including var. *plicata* Döderlein, 1902 ["Rotes Meer, Koseir"]; var. *incisa* Döderlein, 1902 ["Amboina", "Neu-Pommern, Ralum", "Ternate"]; var. *indica* Döderlein, 1902 ["Singapur", "Java", "Celebes", "Salawatti"]; var. *grandis* Döderlein, 1902 ["Singapur"]; var. *stylifera* Döderlein, 1902 ["Jaluit", "Singapur"]; var. *columnifera* Döderlein, 1902 ["Bougainville-Insel"]); Gardiner, 1905: 940; Bedot, 1907: 218; Gravier, 1907: 342; Von Marenzeller, 1907: 89; Vaughan, 1907b: 261; Gardiner, 1909: 279-280; Harrison & Poole, 1909a: 901; 1909b: 914; Gravier, 1911: 62; Vaughan, 1918: 127-128; Gerth, 1921: 422; Van der Horst, 1921: 66-67; Matthai, 1924: 46-47; Umbgrove, 1924: 12; Boschma, 1925: 220-222, pl. 7 fig. 73; Hoffmeister, 1925: 33-34; Faustino, 1927: 183-184, pl. 58 fig. 1, pl. 59 figs. 1-4; Boschma, 1929: 46; Montanaro, 1932: 184-185, pl. 22 fig. 2; Thiel, 1932: 69-73, pl. 8 fig. 6; Yabe & Sugiyama, 1935: 396; Ma, 1937: 138-142, pl. 51 figs. 1-2, pl. 52 figs. 1-2, pl. 53 figs. 1-3, pl. 54 figs. 1-2, pl. 55 figs. 1-2, pl. 64 figs. 2-3; Eguchi, 1938: 361-362; Umbgrove, 1939: 44-45, pl. 13 figs. 1-2; 1940: 294-295; Crossland, 1941: 40; Yabe & Sugiyama, 1941: 80, pl. 77 figs. 2-3b, pl. 78; Umbgrove, 1950: 646; Wells, 1950: 44; Crossland, 1952: 153; Salter, 1954: 92; Wells, 1954: 448-449, pls. 158-160; Nemenzo, 1955: 62-64, pl. 10 fig. 5, pl. 11 fig. 3; (including var. *insularis* Nemenzo, 1955 [Hundred Islands, Pangasinan]; var. *lucapensis* Nemenzo, 1955 [Hundred Islands, Pangasinan]); Stephenson & Wells, 1955: 26; Purchon, 1956: 157; Searle, 1956: 17, pl. 15; Wells & Davies, 1966: 48; Scheer, 1967: 428; Loya & Slobodkin, 1971: 123; Pillai, 1971a: 324; 1971b: 8; 1972: 203; Pichon, 1974: 176; Maragos, 1974: 248; Sukarno, 1974: 14; Zou, Song & Ma, 1975: 29-30, pl. 3 figs. 6-7; Zou, 1978: 100; Faulkner & Chesher, 1979: 287, pl. 100; Green, Harris, Robertson & Santavy, 1979: 298; Shirai, 1980: 527; Wijsman-Best, Faure & Pichon, 1980: 612; Betterton, 1981: 204, pl. 83; Boshoff, 1981: 22; Nemenzo, 1981: 190-191, figs. 208-210; Lamberts, 1983: 9; Pillai, 1983: 86; Scheer & Pillai, 1983: 84-85, pl. 20 figs. 1-5; Zou & Chen, 1983: 91; Hamilton & Brakel, 1984: 252; Schuhmacher & Mergner, 1985: 428; Johnston, 1986: 159; Nemenzo, 1986: 146, fig. 168; Veron, 1986a: 335; Nishihira, Yanagiya & Sakai, 1987: 56; Loo & Chou, 1988: 26; Veron & Marsh, 1988: 83 (partim); Hoeksema & Moka, 1989: figs. 8a-b. Not: Schuhmacher, 1979.

Fungia actiniformis — Montanaro, 1932: 180-181, pl. 21 fig. 4; Vaughan & Wells, 1943: pl. 18 fig. 4.

Fungia paumotensis — Montanaro, 1932: 181-182, pl. 21 fig. 5; Veron & Marsh, 1988: 84 (partim).

Fungia concinna — Ma, 1937: 133-134 (partim), pls. 58-59, pl.61 fig. 1, pl. 66 fig. 2; Veron & Marsh, 1988: 84 (partim).

Fungia subrepanda — Umbgrove, 1939: 44.

Fungia (Fungia) fungites — Rosen, 1971a: 76; Pillai, Vine & Scheer, 1973: 459; Pillai & Scheer, 1973: 470-471; 1974: 450; Scheer & Pillai, 1974: 38-39; Ditlev, 1976: 6; Pillai & Scheer, 1976: 44; Faure, 1977: 9; Maragos & Jokiel, 1978: 61; Rosen, 1979a: 12; Veron & Pichon, 1979: 129-132, figs. 206-213, 755; Ditlev, 1980: 56, figs. 44, 236; Faure, 1982: 98-99; Randall & Myers, 1983: 17-18, figs. 96, 343-345; Veron, 1986b: 335; Sakai & Yamazato, 1987: 46; Wood & Tan, 1987: 197; Veron & Kelley, 1988: 28, 31, figs. 3-4.

Fungia fieldi — Zou, 1978: 100, pl. 7 figs. 3-4.

Fungia (Danafungia) scruposa — Veron & Pichon, 1979: 137, 139 (partim), figs. 222, 224.

Fungia (Danafungia) danai — Veron, 1986b: 336 (partim).

Fungia (Danafungia) horrida — Veron, 1986b: 337 (partim).

Fungia scruposa — Veron, 1986a: 32; Veron & Marsh, 1988: 83.

Type material examined. — RMNH 16235 (neotype [present designation] of *Madrepora fungites*; type loc. Kepulauan Seribu, NW Java, INDONESIA; see figs. 312-313, 318, 321); MNHN 71 (2 syntypes of *Fungia agariciformis*; type loc. Egypt, RED SEA); MNHN 238 (holotype of *Fungia patellaris*; type loc. INDIAN OCEAN); MCZ 585 (paralectotype of *Fungia discus*; Tahiti,

SOCIETY IS.); USNM 105-108, YPM 1947 (5 syntypes of *Fungia dentata*; type loc. EAST INDIES); USNM 121, ANSP 1495, MCZ 539, 542, 5300-5301, MNHN Fun25-26, 93, YPM 1949 (10 syntypes of *Fungia confertifolia*; type loc. FIJI); USNM (syntypes of *Fungia tenuifolia*; type loc. Tahiti); MCZ 5412, MNHN Fun91 (2 paralectotypes of *Fungia serrulata*; KINGSMILL IS.); MCZ 5389 (4), MNHN Fun53, YPM 60, 1437 (7 syntypes of *Fungia haimei*; type loc. ZANZIBAR); USNM 372 (holotype of *Fungia papillosa*; type loc. Loo Choo Is.); ZMB 1792b (holotype of *Fungia pliculosa*; type loc. Bougainville I., SOLOMON IS.).

Other material. — RED SEA: BMNH 1886.1.5.37, 1898.8.1.35/391, 1937.11.17.212-213/394-395/406/412-413/420/1043, 1950.1.11.188/198/272/600-602/606/608-611, MCZ 5298, 5396 (2), 5406, MNHN 486-487, Fun63-64, RMNH 9456 (14), USNM 77734, 77742 (20), 77748-77750 (3), 78249, YPM 1362. Gulf of Aqaba: BMNH 1965.9.27.1-2, RMNH 16014, 16020, 18066 (2), USNM 78247, 78266 (2). Jeddah: BMNH 1977.8.12.1-2, RMNH 9454 (2), 9466. Gulf of Aden: BMNH 1887.12.11.20-23. DJIBOUTI: MNHN 1365, 1406, 3508-3514, 3523-3524, USNM 21982 (3). KENYA: RMNH 17086-17088. TANZANIA: BMNH 1922.8.16.2, 1946.1.8.85. ZANZIBAR: MCZ 392, 5413 (12). ALDABRA: BMNH 1937.11.17.385-388, 1986.10.6.115-130. N MADAGASCAR: RMNH 9450, USNM 77719 (5), 77721 (2), 77727, 77738 (2). PROVIDENCE IS.: YPM 7877. SEYCHELLES: BMNH 1937.11.17.209, 1950.1.11.604-605/612/624, 1981.3.5.476-478/481/490-502/508-518/520-521, RMNH 12095, USNM 77726, 78290-78291 (11), YPM 7865-7875, 7878-7882. MASCARENE IS. Mauritius: BMNH 1878.6.6.10 (2), MCZ 5381-5382 (104) Rodriguez: BMNH 1876.5.5.38 (3). CHAGOS IS.: BMNH 1891.4.9.12/15, 1937.11.17.217/396, 1950.1.11.1003, 1970.7.30.30 (2), MCZ, USNM 77744 (15). MALDIVES: BMNH 1937.11.17.216, MCZ 5399 (16), 5936, RMNH 16018 (2), 22158-22161 (11), USNM 78289 (3), YPM 7829, 7835, 7839, 7842-7843, 7847-7852, 7859, 7861. LACCADIVE IS.: BMNH 1937.11.17.210-211/392, 1950.1.11.607. N SRI LANKA: BMNH 1882.7.31.9, YPM 1850. SW THAILAND: AMNH. COCOS (KEELING) IS.: USNM 44334-44335 (4), 77929-77930. SINGAPORE: AMNH 1758, 1766, MCZ 5380 (53), USNM 109, 77754-77755, YPM 1431 (2). MALAYSIA. W Malaya: BMNH 1979.9.24.100, RMNH 14456 (10), USNM 77769-77770 (5). Sabah: USNM 47947, 47950. S VIETNAM: USNM 45694. CHINA. Hainan I.: USNM 74930. TAIWAN: BMNH 1870.5.9.2. JAPAN. Ryukyu Is.: USNM 77954 (3), YPM 772. PHILIPPINES: AMNH 1968, USNM 45405, 45411, 45418, 78008. SW Luzon: BMNH 1878.6.6.11 (2), MCZ 962, USNM 77934 (2), 77990, 77996 (13), 78229. E Mindoro: UPZD 79, 590. Cebu: BMNH 1886.12.9.200/380, 1892.10.16.10. SW Mindanao: RMNH 8380, USNM 77172. Sulu Is.: UPZD 125-126, USNM 77994 (3), 78000. INDONESIA. Belitung (Billiton): ZMA 359-364. Bangka: RMNH 9447. N Sumatra: RMNH 9452 (2), 9460, 9558 (2). W Sumatra: ZMA 366, 368. S Sumatra: RMNH 15222. NW Java: RMNH 8377, 9312-9313, 9315-9317, 9319-9321, 9455, 9459, 9472 (11), 16008-16010 (6), 16152-16170 (46), 16226-16234 (91 + many small), ZMA 367, 374, 395 (many small), 5497, 6519 (many small), USNM 77761. Java: RGM 77986 (2 ex., fossil), 77988 (fossil), RMNH 9467, 9471, 9482, 9542, USNM 77760, YPM 6102-6103. Madura: RGM 40935 (2 ex., fossil). N Sulawesi: ZMA 603. SW Sulawesi: RMNH 15691-15697, 15753 (3), 20438 (3), 20448, 20452, 20456-20457 (8), 20461, 20826, 20952 (5), ZMA 478, 490, 1237, 5518 (2). Tanah Jampea: RMNH 15757. Togian Is.: RMNH 9401, 9407-9408, 9410, 9412, 9473-9481, 9511-9512, 9514-9517, 16006. Tiger Is.: RMNH 20545, 20591, 20610, 20649, 21205 (2), 21257 (2), 21313. Tukang Besi Is.: RMNH 15755 (2), 20065 (3), 20103, ZMA 384-385. N Sumbawa: RMNH 21637, 21690. Komodo: RMNH 21382 (3), 21408 (4), 21554 (2). NE Sumba: RMNH 20260, 20339. Sula Besi Is.: ZMA 382. W Flores: ZMA 453. Rotti: RMNH 9464, ZMA 380-381, 383. Samau Is.: ZMA 378. Kera: RMNH 14451 (5). E Timor: ZMA 377, 441. Timor: RMNH 9448. Moluccas: RMNH 9449 (2). Obi Latu: RMNH 15756 (3). Ambon: BMNH 1886.12.9.199, 1946.1.1.8, RMNH 8378-8379, 9463, 16011, USNM 78326 (6). N Halmahera: USNM 78061 (4). Banda: BMNH 1886.12.9.201/203/381, RMNH 8374, 8381, 8385, 16013, 16015-16017 (4), USNM 78328, 78336 (8). Tanimber Is.: RMNH 15754. Kei Is.: RMNH 8383, 8394, 8396, 16007. Biak: RMNH 15766 (3). PALAU IS.: USNM 47081-47802, 47087, 78009, 78022-78023 (3), 77983. MARIANA IS.: USNM 74858, 77766 (13), 77924-77926 (12), 78003. CAROLINE IS.: USNM 15744, 77821 (3), 77823, 78061 (3). PAPUA NEW GUINEA. Bismarck Sea: ULB. SOLOMON IS.: AMNH (9), BMNH 1938.3.17.2, USNM

78075. VANUATU (NEW HEBRIDES): BMNH 1903.1.22.7. AUSTRALIA. Christmas I.: WAM 268.87, 270.87, 272.87, 1379.88. Kimberley: WAM 928.86, 939.86, 587.87, 3.88. Pilbara: BMNH 1953.2.1.2, WAM 380.79, 697.81, 213.85, 855.85. Northern Territory: NTM 1743-1744, 1746, 1748, 1750, 1829-1830, 1832-1833, 6946-6948 (13). N Great Barrier Reef: QMB G2863-2866, G2868-2874 (12), G2877-2880, G7651, G7653, G7660, G8069, G8182-8184, G8186, GBR295-297, GBR320-324, GL3622. C Great Barrier Reef: BMNH 1890.1.8.2-3, 1891.5.9.139, 1892.12.1.147/423/428/433-434/442/444-445/576/581/629, 1897.3.9.125/136-137/140-141/144-145/152/156/159/162, 1934.5.14.160-161/477, QMB G3199, G3200, G6715, G6718-6719, G6775, G6778, GBR298-299, GBR334, GL3605, GL3608, GL3620, GL3968, USNM 53129, 78340-78341 (6). S Great Barrier Reef: NTM 4993, 6243, QMB G6157, G6159-6161 (6), G 6596-6599 (5), G6604-6605, G6607, G6615, G6624, GL3602-3603, GL3624, QMT. NEW CALEDONIA: MNHN 1836, 1842, ZMA 6275 (2), 6278-6279, 6281-6282 (3), 6288, USNM 78071-78072, 78280-78281 (4), 78284 (4). GILBERT IS.: MCZ 5420 (2), USNM 77958. MARSHALL IS.: RMNH 14570-14586, USNM 44850-44855 (14), 44857, 45605, 53128, 77820 (3), 77858-77859 (4), 77870-77889, 78238-78239, 78241, 78295-78297 (25). FIJI IS.: AMNH 337, 3126 (2), BMNH 56.9.24.3, MCZ 5300 (10), 5403 (2), USNM 77852 (12). TONGA IS.: BMNH 1891.3.6.29, USNM 77809 (6), 77846 (2). SAMOA IS.: AMNH 3127, ANSP 4525, BMNH 1877.1.15.55, RMNH 9453, 9469, USNM 17504, 77827 (10), 77838-77843 (8). HAWAII IS.: BMNH 1933.6.2.1. COOK IS.: GPC. SOCIETY IS.: MNHN, USNM 77813 (2), 77816.

Characters. — Adult animals are unattached and usually monostomatous, although they occasionally may produce supernumerary stomata by circumstomadaeal budding (figs. 314-315). Their outline varies from circular to slightly oval. Small anthocyathi may have an irregular outline if their growth had been limited by the substratum (figs. 308a, 309a). The corals are usually thick; they vary from flat to highly arched. The diameter of the specimens varies between 1.0 and 31.0 cm.

The length of the central fossa, measured at its bottom, is 1/12 to 1/6 of the corallum length. The septal edges along its sides stand upward, whereas those at both of its ends diverge from it away. The columella of small specimens is formed by loosely packed trabeculae and paliform lobes with the tips pointing in various directions. In large specimens the columella may be degenerated.

The septa are loosely packed and usually straight. The septa of lower orders are thick and solid, those of higher orders thin and perforated. The septa of lowest orders are more exsert than those of higher orders. Tentacular lobes are present on the septa of some coralla (fig. 635). The septal margins are finely to coarsely ornamented with regularly or irregularly angular dentations which are usually sharp, but sometimes slightly lobate in big specimens (figs. 316, 318, 320). Their number varies from 8 to 25 per cm. The septal sides are thinly granulated. At the septal base, the granulations are fine and irregularly distributed, whereas on the septal fringe they are fused in ridges perpendicular to the septal margin (figs. 633-634). The compound synapticulae connecting the septa laterally can easily be distinguished, because of the loose septal arrangement.

The corallum wall is already perforated in corals in the late anthocaulus stage. A detachment scar is distinct at the aboral side of small anthocyathi. The corallum wall is covered by fine granulations (figs. 636-637). The costae are (almost) equal in size; they are straight and distinct near the corallum margin, less distinct near the centre. The costae are coarsely ornamented by conical spines which are mainly granulated at their tips (figs. 317, 319, 321, 636-637). Their number varies from 6 to 25 per cm.


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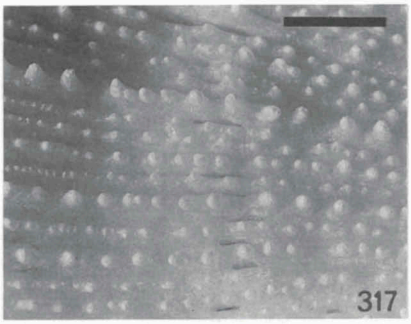
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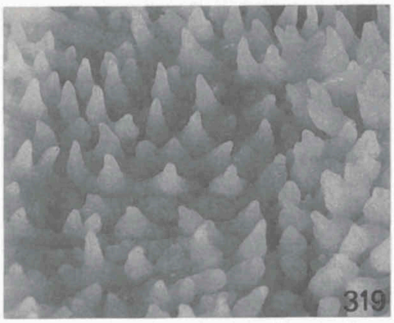
318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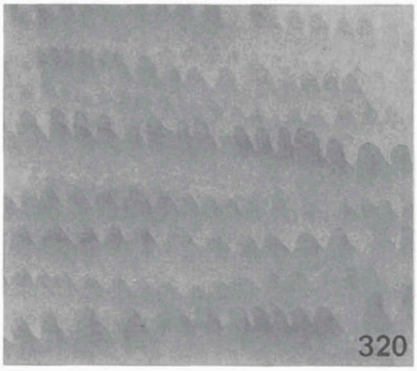
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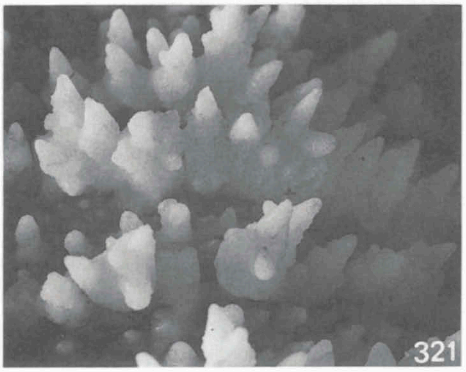

321

Figs. 316-321. Close-ups of *Fungia (Fungia) fungites* corals from NW Java, Indonesia. Scale bar: 0.5 cm. Fig. 316. Septa of the coral in fig. 310. Fig. 317. Costae of the coral in fig. 311. Fig. 318. Septa of the neotype (see fig. 312). Fig. 319. Costae of the coral in fig. 309a. Fig. 320. Septa of a strongly arched coral (RMNH 16153). Fig. 321. Costae of the neotype (see fig. 313).

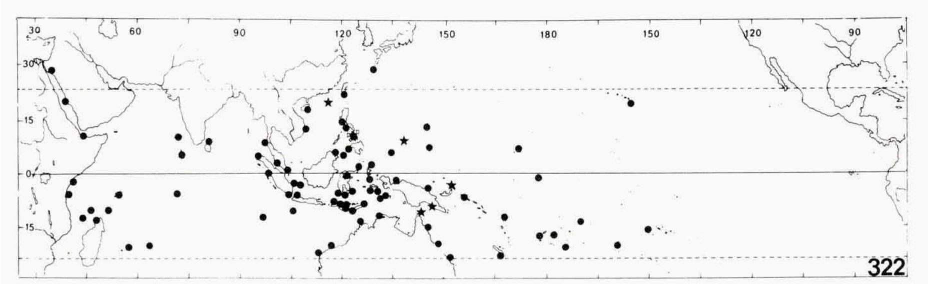


Fig. 322. The range of *Fungia (Fungia) fungites*. Records are from examined material (●) and published illustrations (★).

The colour of the animal is usually brown, sometimes green, depending on the environment (figs. 14-15). At parts of the body where growth or regeneration takes place, such as at the periphery, the animals may be pinkish violet. The margin of the mouth ("lips") is usually radially striped in violet and white. The small tentacles are transparent white.

Geographical distribution (fig. 322). — The species has a wide range, from the Gulf of Aqaba and East Africa to the Hawaiian Islands and the Society Islands. Northward the distribution area extends to southern Japan.

Remarks. — In his description of the species, Linnaeus (1758) refers to corals described or illustrated by other authors, such as Rumphius (1750: 247, pl. 88 figs. 1), who figured a specimen of "*Fungus saxeus*". The specimen is mentioned in a published abstract (Martelli, 1903: 181) of a handwritten catalogue of the Rumphius collection originally curated in the "Museo di Fisica e Storia naturale di Firenze" (Targioni-Tozzetti, ms.). In the introduction of the abstract, Martelli (1903) explains that it was published to facilitate the rediscovery of Rumphius' specimens because they became lost. Whether the particular specimen of "*Fungus saxeus*" has been retrieved is unknown; a letter to the Director of the Museum at Florence concerning this matter was not answered. Because Rumphius' illustration is not very clear, and because neither this specimen nor any of the other syntypes can be located, a specimen from Indonesia is designated neotype (figs. 312-313, 318, 321).

A specimen of *F. fungites* in the LSL collection which very probably belonged to Linnaeus (see note of Wells, 1966: 237), is not mentioned in Linnaeus' (1758) 10th edition, but in his 12th (1767). Therefore it cannot have the status of holotype, as suggested by Wells (1966).

The syntypes of *Fungia patella* Ellis & Solander, 1786 are probably lost. They are not mentioned in Young's (1877) list of corals figured by Ellis & Solander that are present at the HMG (see also Cornelius & Wells, 1988). However, they are well enough illustrated to be identifiable as *F. fungites*. The holotypes of *F. crassilamellata* and *F. lacera* could not be traced. Their descriptions correspond with that of the above described species. The type specimens of all other taxa mentioned above belong to *F. fungites*. These "species" were already synonymized by other authors.

The morphological variability of *F. fungites* has lead several authors to describe different forms within the species. These ecophenotypical forms are not related to any geographic area, it is not possible to distinguish them clearly. As a result of this variability some specimens are difficult to distinguish from forms of *F. (D.) scruposa*, particularly when they were sampled in shallow water. In that habitat type, large specimens of *F. fungites* may develop irregularly formed septal and costal ornamentations. The septa of such coralla are often thickened and their lower order costae are ornamented by relatively thick spines. Further, these specimens usually lack the ridges on the septal sides (fig. 320), a character which is thought to be typical of the species (fig. 318). Some specimens living in shallow water produce supernumerary mouths (fig. 314).

Systematically, *F. (F.) fungites* is classified with a monotypical subgenus. It cannot be placed in *F. (Danafungia)* because it lacks the almost spineless costae of high orders typical for that subgenus. The septal and costal ornamentations are rather similar to those of *F. (D.) scruposa*, the only *F. (Danafungia)* species with a perforated corallum wall. The septal dentations of *F. (F.) fungites* may be distinguished from those of *F. (D.) scruposa* because they are usually sharper and because they show typical rows of granulations on their sides. The granulations on the spines are concentrated at the tips in *F. (F.) fungites*, whereas they are more or less evenly distributed over the whole spine length in *F. (D.) scruposa*.

Subgenus **Wellsofungia** subgen. nov.

Type species: *Fungia granulosa* Klunzinger, 1879.

Fungia (Verrillofungia) (partim) Wells, 1966: 238-239; Veron & Pichon, 1979: 146; Ditlev, 1980: 56; Chevalier & Beauvais, 1987: 706; Veron & Kelley, 1988: 31.

Characters. — Adult animals are free-living, monostomatous and discoidal. Their corallum wall is perforated. The septal and costal ornamentations are relatively fine. The septa remain perforated, except those of higher orders in large specimens. The granulations on the septal sides are arranged in rows parallel or perpendicular to the septal margins.

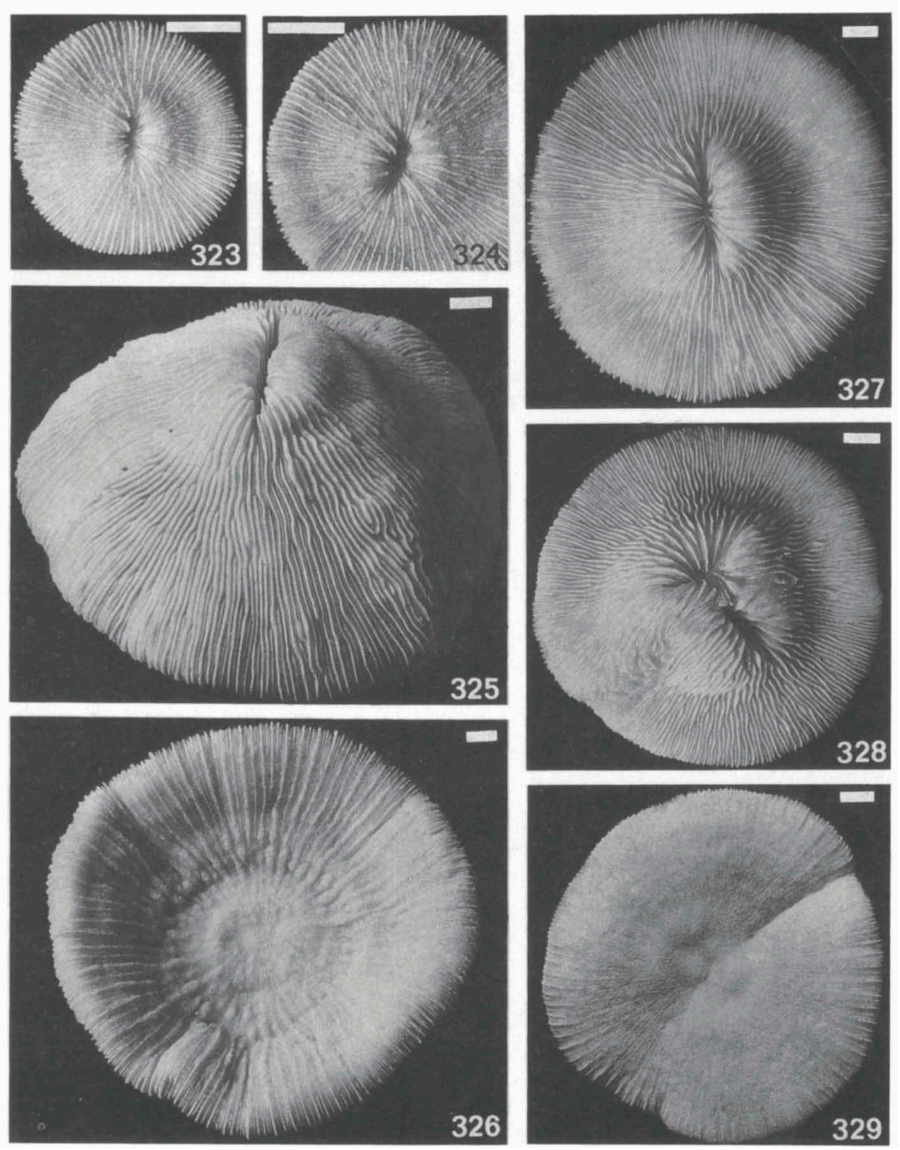
Remarks. — The single species of the subgenus was considered to belong to the subgenus *Verrillofungia* (see e.g. Veron & Pichon, 1979), before Wells' (1966) revision known as the *repanda* -group (Döderlein, 1901). The species was originally placed in that group by Döderlein (1902: 108) from which it differs in the structure and ornamentation of its septa and costae. These structures are much more similar to those of *F. (Pleuractis)*. *F. granulosa* does not fit in *F. (Pleuractis)* because, unlike the three presently recognized species of that subgenus, it has a round corallum outline instead of a distinctly oval-elongate one (Wells, 1966: 238).

Fungia (Wellsofungia) granulosa Klunzinger, 1879
(figs. 18, 323-335, 638-639)

Fungia granulosa Klunzinger, 1879: 65, pl. 7 fig. 3, pl. 8 fig. 3 (Koseir, Red Sea); Döderlein, 1902: 108-110, pl. 11 figs. 1-1b; Von Marenzeller, 1907: 89; Gardiner, 1909: 276; Van der Horst, 1921: 64, pl. 1 fig. 8; Boschma, 1925: 216-217; Hanzawa, 1931: pl. 2 fig. 2; Yabe & Sugiyama, 1935: 396; Nemenzo, 1955: 69-70, pl. 11 fig. 6; Schuhmacher, 1979: figs. 5, 19; Chevalier, 1980: 66; Nemenzo, 1981: 194, fig. 215; Lamberts, 1983: 9; Scheer & Pillai, 1983: 80, pl. 18 fig. 2; Schuhmacher & Mergner, 1985: 428; Nakamori, 1986: pl. 14 figs. 1a-b; Nemenzo, 1986: 149, fig. 173; Veron, 1986a: 32; Veron & Marsh, 1988: 84 (partim); Hoeksema & Moka, 1989: fig. 11. Not: Vaughan, 1906; Ma, 1937.
Fungia crassitentaculata — Gardiner, 1898: 527.
Fungia costulata — Ma, 1937: 142, pl. 61 figs. 2-3.
Fungia döderleini Yabe & Sugiyama, 1941: 77 (partim), pl. 66 figs. 9-9d. Not: Nemenzo, 1971; 1981; 1986.
Not *Fungia döderleini* Von Marenzeller, 1907.
Fungia distorta — Umbgrove, 1946b: 533, pl. 81 figs. 3-4.
Fungia (Heliofungia) granulosa — Ditlev, 1976: 6.
Fungia (Verrillofungia) granulosa — Veron & Pichon, 1979: 156-159, figs. 257-263; Ditlev, 1980: 56, fig. 235; Sakai & Yamazato, 1987: 46; Wood & Tan, 1987: 197; Veron & Kelley, 1988: 28, 32, fig. 10b.
Cycloseris c.f. *erosa* — Scheer & Pillai, 1983: 75-76, pl. 16 figs. 5-7.
Cycloseris distorta — Scheer & Pillai, 1983: 76, pl. 16 figs. 8-11.
Fungia (Verrillofungia) scabra — Randall & Myers, 1983: 17, figs. 356-357.
Cycloseris sinensis — Veron & Marsh, 1988: 82 (partim).

Type material examined. — MZB 2158 (holotype of *Fungia granulosa*; type loc. Koseir, RED SEA).

Other material. — RED SEA: BMNH 1885.1.26.1-2. Gulf of Aqaba: HSC 2/2 (1), RMNH 16021, 16022 (2), 18068, USNM 78252, 78417. DJIBOUTI: USNM 77743. N MADAGASCAR: USNM 77732. MASCARENE IS. Agalega: WAM 290.81. MALDIVES: RMNH 14245, YPM 7828, 7860. S CHINA SEA. Macclesfield Bank: BMNH 1892.10.17.85. MALAYSIA. Sabah: USNM 47946. PHILIPPINES. SW Luzon: USNM 77937. E Mindoro: UPZD 560. Cebu: UPSMI. Mindanao: USNM 77974 (3). Sulu Is.: USNM 77991. INDONESIA. Java: RGM 77645 (3, fossil), 77650-77651 (4, fossil), 167669 (fossil). NW Java: RMNH 16113-16124 (12). SW Sulawesi: RMNH 15680, 15683-15684 (3), 20754, 20827 (5), 20855, 20857 (25), 20869-20870 (18), 20874 (6), 20879 (9), 20893, 20895, 20954, 21018 (2). Tiger Is.: RMNH 20596 (6), 21070 (2), 21117 (2). Komodo: RMNH 20381, 21409 (2). N Sumbawa: RMNH 20502, 20944, 20946 (6), 21616 (8), 21639 (3), 21695 (2). E Flores: RMNH 9483. Tukang Besi Is.: RMNH 20188. S Moluccas: WAM 1378.88.



Figs. 323-329. Corals (anthocyathi) of *Fungia (Wellsofungia) granulosa* from Indonesia. Scale bars: 1 cm. Figs. 323-324. Upper surface of two small corals (Banda): RMNH 16023, 16024. Figs. 325-326. Upper and lower surface of a strongly arched coral (RMNH 16114; NW Java). Fig. 327. Upper surface of a flat coral with a slightly humped centre (RMNH 16113; NW Java). Figs. 328-329. Upper and lower surface of two fused corals (RMNH 16116; NW Java).

Banda: RMNH 8362, 16023-16025. AUSTRALIA. Christmas I.: WAM 264.87, 274.87. Kimberley: WAM 177.85, 180.85, 929.86. N Great Barrier Reef: AIMS 15130, QMB G8066. PAPUA NEW GUINEA. Bismarck Sea: ULB. MARIANA IS. Guam: USNM 80443. FIJI: QMB. SOCIETY IS.: MNHN.

Characters. — Adult animals are free-living, monostomatous and discoidal. Although the corals may form fragmentation slits in the corallum wall (Hoeksema & Moka, 1989: fig. 11), no fragmented specimens have been observed. The specimens vary in thickness; their shape varies from flat to highly arched. The diameter of the specimens ranges between 2.0 and 18.5 cm.

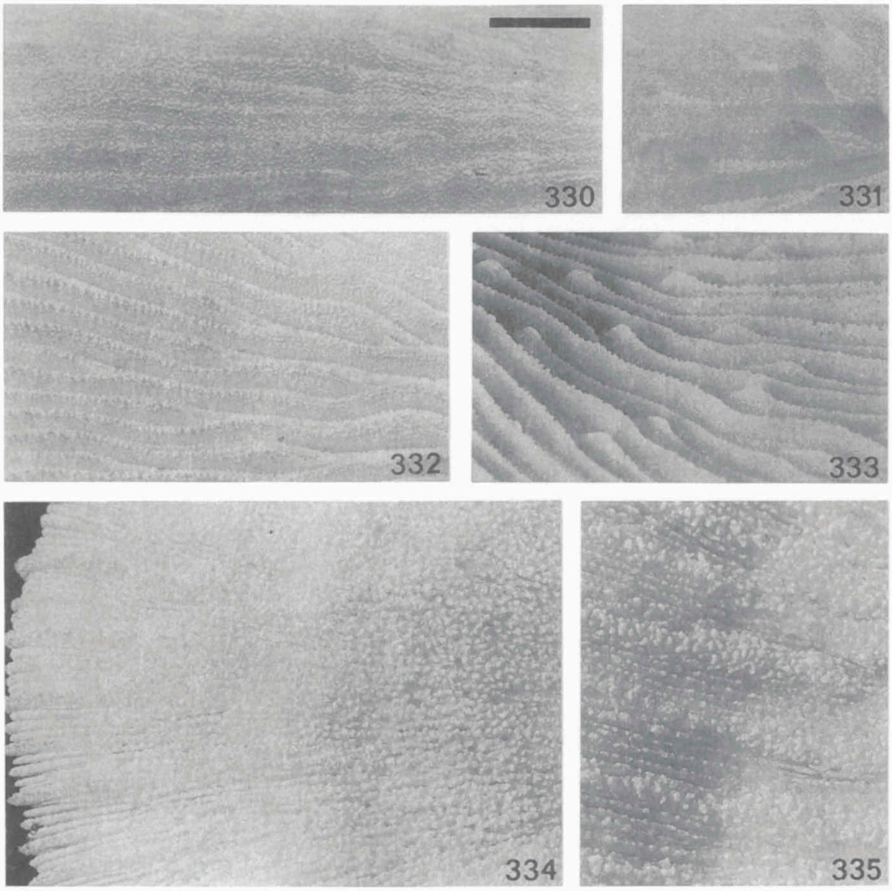
The length of the central fossa, measured at its bottom, is 1/10 to 1/3 of the coral length. The septal edges along its sides stand upright, whereas those at both of its ends diverge away from it. The columella is formed by a mingled mass of loosely or tightly packed trabeculae and paliform lobes with the tips either pointing upwards or in various directions.

The septa are tightly packed and usually straight; they become wavy after the development of a tentacular lobe on the adjacent septa of higher orders (fig. 332). Higher order septa are perforated; those of lower orders also (fig. 638), except the thick septa of very large specimens. The lower order septa are thicker and more exsert than those of higher orders. Most specimens have a tentacular lobe above the inner edge of each septum (figs. 331-333). The septal margins are ornamented with fine, irregularly granular dentations (figs. 330-333). Their number varies from 30 to 60 per cm. The septal sides are densely granulated. The granulations are either evenly distributed or arranged in crossing rows, parallel and perpendicular to the septal margin. The compound synapticulae connecting the septa laterally cannot easily be detected, because of the tight septal arrangement.

The corallum wall is usually perforated in adult specimens, but may still be solid in immature anthocyathi. The corallum wall is not granulated (fig. 639). A detachment scar is distinct at the aboral side of small specimens in anthocyathus phase. The costae are usually of equal thickness (fig. 329), whereas in some specimens the lower order costae are thicker than the other ones (fig. 326). The costae are straight and distinct near the corallum margin, but less prominent and wavy near the centre. All costae are finely ornamented with blunt, granulate spines (figs. 334-335, 639). Their number varies from 30 to 60 per cm.

The living animal is brown or ochre-coloured (fig. 18). It has small, colourless tentacles.

Geographical distribution (fig. 336). — The species is known to occur from the Gulf of Aqaba and northern Madagascar towards southern Japan, Guam and the Society Islands.



Figs. 330-335. Close-ups of *Fungia (Verrillofungia) granulosa* corals (NW Java, Indon.). Scale bar: 0.5 cm. Fig. 330. Septa of the coral in fig. 325. Fig. 331. Septa of a coral with distinct tentacular lobes (RMNH 16120). Fig. 332. Septa of the coral in fig. 328. Fig. 333. Septa of a juvenile with tentacular lobes (RMNH 16122). Fig. 334. Costae of the coral in fig. 329. Fig. 335. Costae of the coral in fig. 326.

Remarks. — Yabe & Sugiyama (1941: 77) decided to give the new name *F. doederleini* to Döderlein's (1902) specimen of *F. costulata* because they (erroneously) thought it was unsimilar to the holotype of this species. The illustrations of the paratype of *F. doederleini* (Yabe & Sugiyama, 1941: pl. 66 figs. 9-9d) are clear enough to show that it belongs to *F. granulosa*. The specimen has a perforated corallum wall and therefore does not resemble Döderlein's (1902) specimen of *F. costulata*, which was designated holotype. Yabe & Sugiyama (1941: 77) supposed that the characters shown by the paratype were "quite identical" to those of the holotype, but they did not study

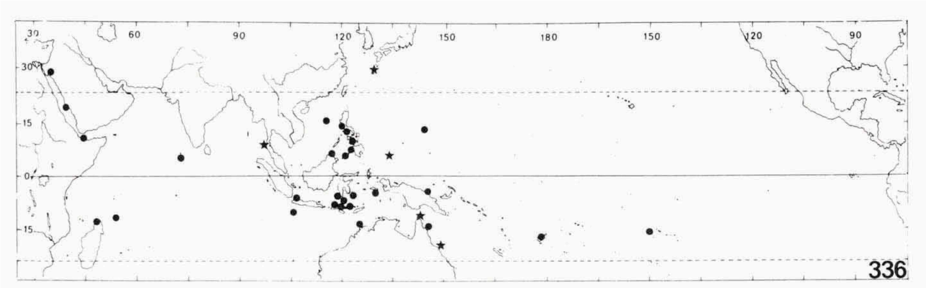


Fig. 336. The range of *Fungia (Wellsofungia) granulosa*. Records are from examined material (●) and published illustrations (★).

the latter specimen otherwise than from the text and illustrations given by Döderlein (1902).

Juvenile specimens of the species may resemble corals belonging to the subgenus *Cycloseris*, because their wall is often not yet perforate. Superficially many coralla look like those of *F. (C.) costulata*, whereas very small specimens in anthocyathus stage are almost identical to corals of *F. (C.) sinensis* or *F. (C.) distorta* because of their strongly perfortated septa.

Subgenus **Lobactis** Verrill, 1864

Type species: *Fungia dentigera* Leuckart, 1841 (= *Fungia scutaria* Lamarck, 1801). By original designation.

Lobactis Verrill, 1864: 52.
Fungia (Pleuractis) (partim) — Wells, 1966: 238; Veron & Pichon, 1979: 159; Ditlev, 1980: 55; Chevalier & Beauvais, 1987: 706; Veron & Kelley, 1988: 32.

Characters. — Adult animals are free-living and monostomatous. Their outline is oval-elongate. The corallum wall is perforated in adult specimens. The lower order septa are solid; those of higher orders are perforated. The septal dentations are fine and angular. The granulations on the septal fringe are arranged in rows perpendicular to the septal margin. Each septum bears a distinct tentacular lobe at its inner edge. The costal spines are long; they are covered by acute granulations.

Remarks. — *F. (Lobactis)* is part of Döderlein's (1901: 355) *"Scutaria-Gruppe"*. *Lobactis* was considered synonymous with *Pleuractis* by Wells (1966), with which it has an oval-elongate shape and a perforated corallum wall in common. These characters are probably the result of convergent evolution, because the septal and costal ornamentations of the two groups differ much in morphology and do not suggest a very close phylogenetic relationship (figs. 640-647). In the present revision the two are therefore separated again, and *Lobactis* is now considered a subgenus within *Fungia*.

Fungia (Lobactis) scutaria Lamarck, 1801
(figs. 19-20, 337-347, 640-641)

Fungia scutaria Lamarck, 1801: 370 (no locality given); 1815, 1816: 236-237 ("les mers de l'Inde"); Blainville, 1830: 303; 1834: 337; Ehrenberg, 1834: 50; Lamarck, 1836: 372-373; Leuckart, 1841: 49-50; Dana, 1846: 301-302, pl. 19 figs. 10-10a; Milne Edwards & Haime, 1851: 85; 1860: 16; Haeckel, 1876: pl. 2 fig. 1; Klunzinger, 1879: 65; Studer, 1880: 45; Döderlein, 1902: 91-97, pl. 8; Vaughan, 1907a: 131-132, pl. 28 fig. 3-3b, pls. 29-32; Gardiner, 1909: 272-274, pl. 34 fig. 8; Vaughan, 1918: 128; Van der Horst, 1921: 61-62; Boschma, 1925: 215; Faustino, 1927: 175-176, pl. 50 figs. 1-2; Boschma, 1929: 44-45; Yonge, 1930: 37; Thiel, 1932: 63-64, pl. 8 fig. 3; Edmondson, 1933: 43, figs. 20b-c; Yabe & Sugiyama, 1935: 396; Ma, 1937: 130-132, pl. 46 figs. 1-2, pl. 47 figs. 1-4, pl. 48 figs. 3-4; Eguchi, 1938: 360-361; Umbgrove, 1939: 43; 1940: 291-292, pl. 29 figs. 1-2; Yabe & Sugiyama, 1941: 78, pl. 61 fig. 6-6a, pl. 67 figs. 3-5, pls. 68-69; Vaughan & Wells, 1943: pl. 18 figs. 1-2; Wells, 1950: 44; Crossland, 1952: 152; Salter, 1954: 92; Wells, 1954: 447-448, pl. 95 fig. 1; Nemenzo, 1955: 61, pl. 11 fig. 5a; Boschma, 1959: 266-267; Wells & Davies, 1966: 48; Loya & Slobodkin, 1971: 123; Pillai, 1971a: 324; 1971b: 8; Reed, 1971: 38, figs. 1-2; Pillai, 1972: 203; Maragos, 1973: fig. 22; Pichon, 1974: 176; Zou, 1978: 101, pl. 7 figs. 5-6; Chevalier, 1979: 132; 1980: 65; Shirai, 1980: 529; Wijsman-Best, Faure & Pichon, 1980: 612; Boshoff, 1981: 22; Nemenzo, 1981: 189, fig. 206; Lamberts, 1983: 9; Pillai, 1983: 86; Scheer & Pillai, 1983: 79, pl. 17 figs. 6-7; Zou & Chen, 1983: 91; Wallace, 1984: 38, fig. 22.3; Schuhmacher & Mergner, 1985: 428; Johnston, 1986: 159; Nakamori, 1986: pl. 24 fig. 2; Nemenzo, 1986: 145, fig. 166; Veron, 1986a: 32; Fielding & Robinson, 1987: fig. 24; Nishihira, Yanagiya & Sakai, 1987: 56; Veron & Marsh, 1988: 84. Not: Duncan, 1883; Quelch, 1886; Utinomi, 1975.

Fongia scutaria — Blainville, 1820: 216.

Fungia dentigera Leuckart, 1841: 48-49, pl. 3 figs. 1-2 (Red Sea); Dana, 1846: 301, pl. 18 fig. 4; Milne Edwards & Haime, 1851: 86-87; 1860: 17-18; Klunzinger, 1879: 64; Ortmann, 1888: 178-179; 1889: pl. 18 fig. 12d; 1892: 653; Gardiner, 1898: 527; 1905: 938-940.

Fungia paumotensis — Dana, 1846: 300, pl. 19 figs. 1-9.

Lobactis danae Verrill, 1864: 52 (Sandwich Islands).

Lobactis conferta Verrill, 1864: 52 ("Kingsmills Islands").

Pleuractis scutaria — not: Verrill, 1864.

Fungia placunaria Klunzinger, 1879: 64, pl. 7 fig. 1, pl. 8 fig. 6 (Red Sea).

Fungia verrilliana Quelch, 1886: 30 (Honolulu, Sandwich Islands); Studer, 1901: 404-405.

Fungia tenuidens Quelch, 1886: 30, pl. 6 fig. 1-1a (Ternate, Moluccas); Whitelegge, 1898: 355.

Fungia oahensis Döderlein, 1901: 357-358 (Oahu, Sandwich Islands); 1902: 97-99, pl. 9 figs. 3-5; Vaughan, 1907a: 133, pls. 33-34.

Fungia (Pleuractis) scutaria — Rosen, 1971a: 75; Pillai & Scheer, 1973: 470; Maragos, 1974: 248; Scheer & Pillai, 1974: 36-37; Ditlev, 1976: 6; Pillai & Scheer, 1976: 43; Faure, 1977: 9; Maragos, 1977: 204, 208, figs. 4, 78-81; Maragos & Jokiel, 1978: 61; Rosen, 1979a: 12; Veron & Pichon, 1979: 159-162, figs. 264-268; Ditlev, 1980: 55, figs. 41, 232; Faure, 1982: 100; Randall & Myers, 1983: 18, figs. 94, 352-353; Hamilton & Brakel, 1984: 252; Faure, 1985: 271; Maragos & Jokiel, 1986: 144; Veron, 1986b: 343; Sakai & Yamazato, 1987: 46; Veron & Kelley, 1988: 28, 32.

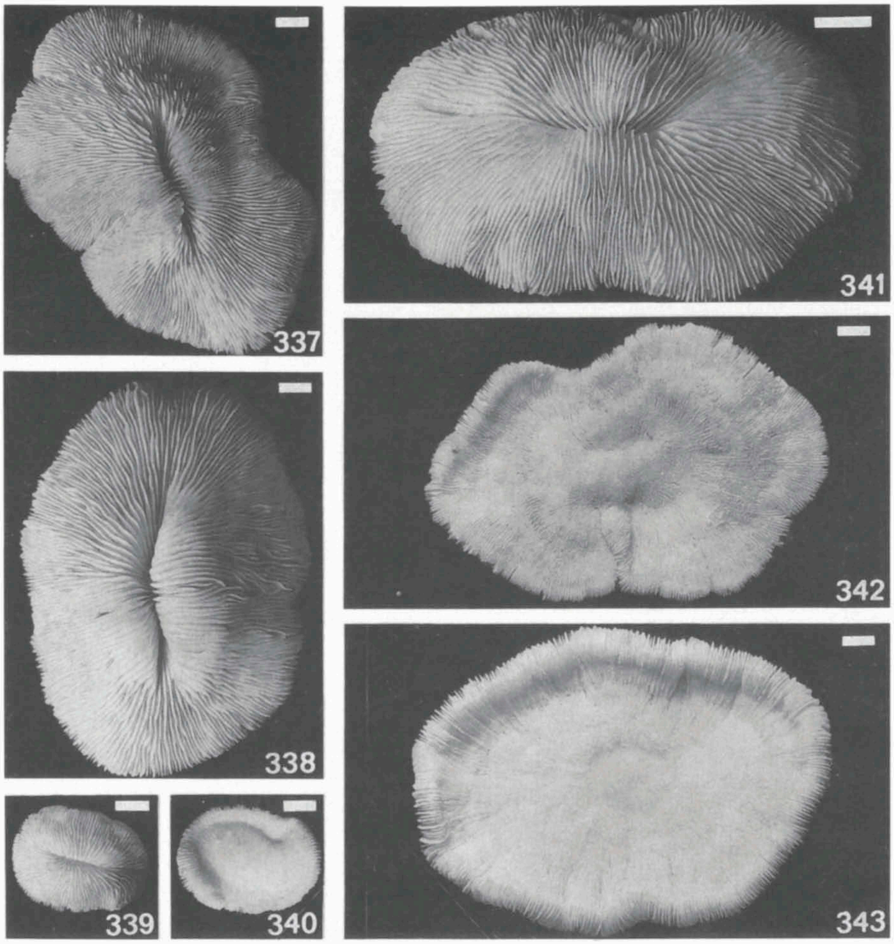
Fungia (Pleuractis) oehaensis — Ditlev, 1980: 55. (Incorrect spelling).

Type material examined. — MNHN 297 (neotype [present designation] of *Fungia scutaria*; type loc. RED SEA); MCZ 5396 (3), MNHN Fun37 (syntypes of *Lobactis danae*; type loc. HAWAII); MCZ 5294 (33), YPM 1803 (2), (syntypes of *Lobactis conferta*; type loc. Apiang, KINGSMILL IS.); MNHN Fun84 (holotype of *Fungia placunaria*; type loc. RED SEA); BMNH 1886.12.9.197 (holotype of *Fungia tenuidens*; type loc. Ternate, INDONESIA); ZMB 790 (holotype of *Fungia oahensis*; type loc. Oahu, HAWAII IS.).

Other material. — RED SEA: BMNH 1898.8.1.33, 1950.1.11.171/305/649, MNHN Fun90, 237, 264, RMNH 9532 (2), USNM 77739 (3), 77747. Gulf of Aqaba: BMNH 1965.12.30.1, USNM 78248 (2), ZMA 5596 (3). KENYA: RMNH 17090-17091. ALDABRA: BMNH 1986.10.6.131-132. MASCARENE IS.: BMNH 1876.5.5.39 (2). SEYCHELLES: RMNH 12094, YPM 7883. LACCADIVE IS.: BMNH 1937.11.17.414/1044-1045. MALDIVES: BMNH 1937.11.17.390/407, MCZ (1), RMNH 14228, 22153 (3), USNM 45602, 78288 (4), YPM 7830, 7833, 7836, 7838, 7841, 7846, 7853-7854, 7856-7858. CHAGOS IS.: BMNH 1891.4.9.17, 1970.3.6.118, YPM 7846. S SRI LANKA: RMNH 22208 (3). COCOS (KEELING) IS.: USNM 44333, 77927-77928. PHILIPPINES. Sulu Is.: ZMA 608 (2). INDONESIA. Belitung (Billiton): BMNH 1883.7.24.86. NW Java: RMNH 16036. N Sulawesi: ZMA 609. SW Sulawesi: RMNH 15677-15678, 15735, 20127 (2), 20133, 20143 (6), 20144 (2), 20147 (10), 20831 (2), 20884 (3), 20905, 20985. Tiger Is.: RMNH 20592, 20637, 21075 (5). Tukang Besi Is.: RMNH 15733, 20191. N Sumbawa: RMNH 21619. Komodo: RMNH 21385 (2), 21515 (2), 21580 (2). Ternate: BMNH 1897.3.9.143. Maisel Is.: PPPO 1125. Obi Latu: RMNH 15734. Banda: RMNH 15780. AUSTRALIA. Christmas I.: WAM 273.87, 277.87. Pilbara: WAM 552.78. Torres Str.: BMNH 1897.3.9.148/164. N Great Barrier Reef: QMB G8056, GL3619. C Great Barrier Reef: BMNH 1934.5.14.159, MCZ 3920, QMB G2855, G6731, G7479, GBR288-290. S Great Barrier Reef: QMB G2856, G6154-6156 (4), G6601, G6779, QMT. PAPUA NEW GUINEA. Bismarck Sea: ULB. MARIANA IS.: USNM 77762-77765 (28), 77917-77922, 78352-78353, 80087 (2). NEW CALEDONIA: USNM 78070, ZMA 6268-6270. MARSHALL IS.: RMNH 14619, 14621, USNM 44839-44849 (40), 49228, 49237, 78310-78313 (12), 77824-77825, 77862. GILBERT IS.: USNM 77899-77905 (63), 78351. CAROLINE IS.: ANSP 980 (14), USNM 77797, 78055 (2). TONGA IS.: BMNH 1891.3.6.118, USNM 77810. SAMOA IS.: USNM 77829, 77835. TAKELAU IS.: USNM 78067. PHOENIX IS.: USNM 78263. HAWAII IS.: AMNH 297-299, 873-874 (5), 956, 1015 (21), 1043 (31), 1045, 1670, 1681, 1683-1684 (3), ANSP 2060 (2), MCZ 248 (2), 1394 (7), 5297 (29), 5299 (2), 5384, MNHN Fun37, 81, RMNH 8344, 15781 (2), USNM 20838-20840 (6), 20961-20965, 22005-22006 (7), 78043 (4), 78046-78047 (13), 78054, 78324, YPM 1282, 1851, 1956, 4308. MIDWAY: USNM 78317-78323 (62). LINE IS.: USNM 78044-78045 (6), 78309 (2). SOCIETY IS.: BMNH 1973.4.17.4-5, MNHN, RMNH 8987 (16), 15782 (3), USNM 77817 (4), YPM 1953 (3), TUAMOTU IS.: MCZ 584 (3), USNM 97-103, 77801-77802 (7).

Characters. — Adult animals are free-living and monostomatous. Their outline varies from oval to elongate with ends either rounded or tapering. Although the corals may form rudimentary fragmentation slits at the periphery of the corallum wall (figs. 337, 342), no fragmented specimens have been observed. The coralla are usually thick; they vary from flat to highly arched. The length of the central fossa, measured at its bottom, is 1/8 to 1/4 of the coral length. The septal edges along the central fossa stand upright, but those at both ends of the mouth incline away from it. The columella is formed by loosely packed trabeculae and paliform lobes with the tips pointing in various directions. In full-grown specimens they may be strongly reduced. The length of the specimens varies between 2.5 and 18.0 cm.

The septa are densely packed and wavy, particularly along the tentacular



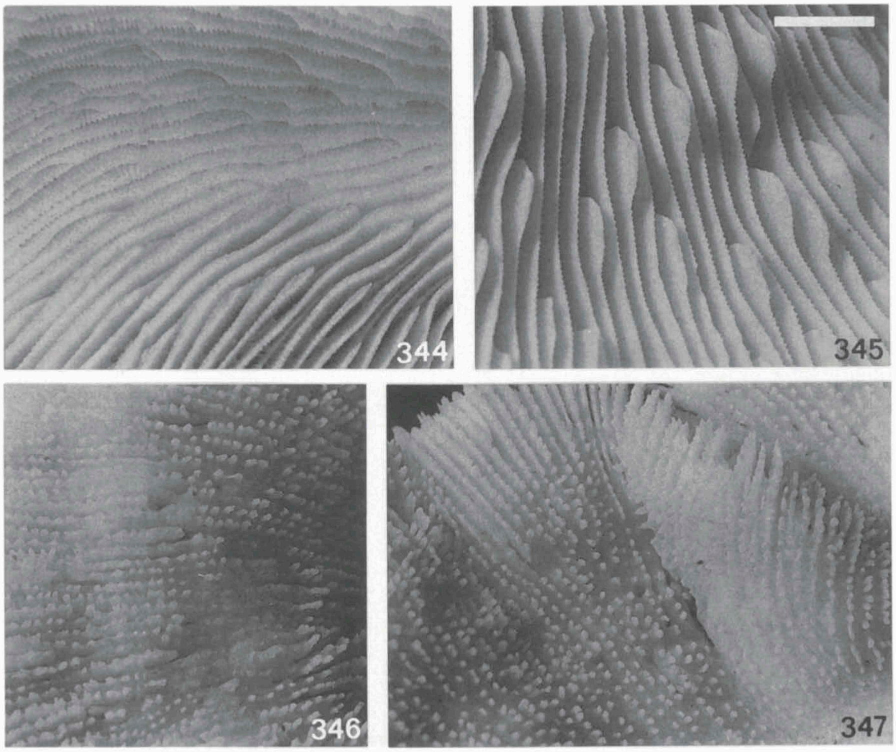
Figs. 337-343. Corals (anthocyathi) of *Fungia (Pleuractis) scutaria* from Indonesia. Scale bars: 1 cm. Fig. 337. Upper surface of a flat coral (RMNH 15677; SW Sulawesi). Fig. 338. Upper surface of a slightly arched coral (RMNH 16036; NW Java). Figs. 339-340. Upper and lower surface of a juvenile (RMNH 15678; SW Sulawesi). Fig. 341. Upper surface of the holotype of *Fungia tenuidens* (BMNH 1886.12.9.197; Ternate, Moluccas). Fig. 342. Aboral surface of the coral in fig. 337. Fig. 343. Aboral surface of the coral in fig. 338.

lobes of higher order septa. The septa are almost of equal thickness and height. The solid septa of lower orders are slightly thicker and higher than the perforated septa of higher orders. Above the inner edge of each septum there usually is a prominent tentacular lobe (figs. 344-345). The septal margins are finely ornamented with angular, sharp dentations. Their number varies from 30 to 50 per cm. The septal sides are thinly granulated. The granulations are arranged in rows or fused in ridges perpendicular to the septal margin (fig.

640). The compound synapticulae connecting the septa laterally can be detected, in spite of the tight septal arrangement.

The corallum wall is perforated in adult specimens, but may still be solid in small specimens. In many specimens the corallum wall near the periphery is partly folded or it contains short clefts. A detachment scar is usually only distinct at the aboral side of small specimens in anthocyathus stage. The wall is not granulated. The costae are almost equal in size; they are usually straight and distinct near the corallum margin, but less prominent near the centre. The costae of most specimens are not regularly built and straight (such as in fig. 342) but wavy and irregularly arranged (fig. 343). All costae are finely ornamented with blunt or elongate spines which are granulated at the tips (figs. 346-347, 641). Their number varies from 8 to 25 per cm.

The living animal is usually brown with irregularly formed pink or violet patches (fig. 19). The tentacles are small but conspicuous because of the supporting tentacular lobes (fig. 20). They are transparent and slightly white



Figs. 344-347. Close-ups of *Fungia (Pleuractis) scutaria* corals. Scale bar: 0.5 cm. Fig. 344. Septa of the holotype of *F. tenuidens* (see fig. 341). Fig. 345. Septa of the coral in fig. 337. Figs. 346-347. Costae of the coral in fig. 342.

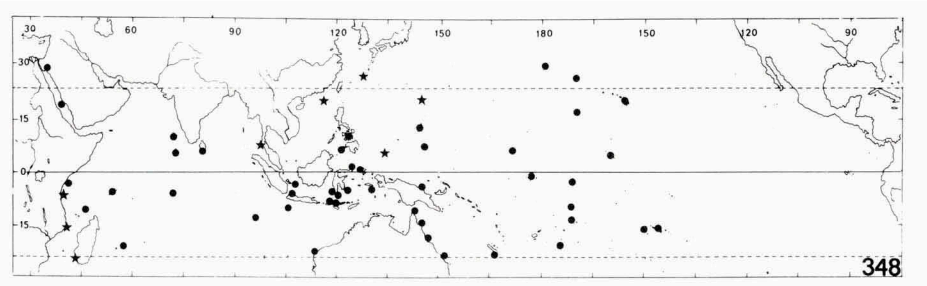


Fig. 348. The range of *Fungia (Pleuractis) scutaria*. Records are from examined material (●) and published illustrations (★).

or green. The mouth is brown or violet.

Geographical distribution (fig. 348). — In the western Indian Ocean the species has been found from the Gulf of Aqaba (Red Sea) towards southern Madagascar. In the eastern part of the Indian Ocean there are also several localities known, some of which are very isolated. From the Central Indo-Pacific the distribution extends further towards the Ryukyu Islands (Japan), the Marianas, the Hawaiian and Line Islands (including Midway where it is the only fungiid known) and the Society Islands.

Remarks. — The original material of *F. scutaria* referred to by Lamarck (1801) are three specimens illustrated by Seba (1759: pl. 112 figs. 28-30). One of these (Seba's fig. 29) resembles only slightly the species currently known as *F. scutaria*. In Lamarck's collection at the MNHN there are two corals from the Red Sea which belong to the species. One of these corals (MNHN 264) came from the Michelin collection while of the other (MNHN 297, the specimen designated neotype) it is unknown how Lamarck obtained it. These specimens were neither mentioned by Lamarck (1801), nor in a later publication by the same author (1815), where he still cites: "Habite les mers de l'Inde. Mon cabinet". Besides the specimens from the Red Sea no other specimens identified as *F. scutaria* were found in Lamarck's collection. It is not certain whether these were identified by Lamarck or by one of his successors.

The holotypes of *Fungia dentigera* and *F. verrilliana* could not be traced. However, the descriptions and illustrations leave no doubt that they belong to *F. scutaria*. The eliptical outline of the corallum and the large tentacular lobes are very characteristic of the species. Only in very large, coarsely built specimens from the Hawaiian Islands may the tentacular lobes become less clear.

The septal ornamentations of *F. scutaria* resemble those of the subgenus *Cycloseris*. The septal dentations of *F. scutaria* are sharper than those of *Pleuractis* species, which lack the distinct vertical rows of granulations on their septal sides. Both, the septal and the costal ornamentations, are very similar to those of the polystomatous *Herpolitha*.

Subgenus **Pleuractis** Verrill, 1864

Type species: *Fungia scutaria* Lamarck, 1801, sensu Verrill, 1864 [= *Fungia paumotensis* Stutchbury, 1833]. By monotypy.

Pleuractis Verrill, 1864: 52.
Fungia (Pleuractis) (partim) — Wells, 1966: 238; Veron & Pichon, 1979: 159; Ditlev, 1980: 55; Chevalier & Beauvais, 1987: 706; Veron & Kelley, 1988: 32.

Characters. — Adult animals are free-living and monostomatous. Their outline varies from oval to elongate. The corallum wall is solid in juvenile specimens, perforated in adults. It is not granulated. The blunt costal spines are either simple and granular or fused and laterally compressed. The septal dentations vary from fine and granular to coarse and angular. The septa are usually solid, but in some species they are slightly perforated at the fringe. The granulations on the septal sides are either irregularly arranged or they form zigzag rows or ridges.

Remarks. — The subgenus is part of Döderlein's (1901) "*Scutaria*-Gruppe". Although the nominal type species of *F. (Pleuractis)* is *F. scutaria*, it is not the species that Verrill (1864) identified as such. Examination of Verrill's material revealed that he used *F. paumotensis* as type species for *Pleuractis*. In his misidentification Verrill (1864) followed his compatriot Dana (1846), who also switched the names of both species. *F. paumotensis* will be proposed as neotype of *Pleuractis* (Hoeksema, in press). *F. scutaria* must be removed and be placed in *Lobactis*. The differently shaped septal and costal ornamentations suggest that the two subgenera do not have a very close phylogenetic relationship (figs. 640-647). Three species recognized as belonging to *Pleuractis* will remain.

The septal dentations and costal spines of *Pleuractis* are more similar to those of *Verrillofungia* and those of the new subgenus *Wellsofungia* than to the septo-costal ornamentations of *Lobactis*, with which it has in common an oval-elongate corallum outline and a perforated corallum wall.

Fungia (Pleuractis) moluccensis Van der Horst, 1919
(figs. 21, 349-358, 642-643)

Fungia moluccensis Van der Horst, 1919: 65, pl. 1 (Moluccas); 1921: 60-61, pl. 2 figs. 1-2; Boschma, 1925: 210-214 (partim), pl. 7 figs. 75-76, pl. 10 fig. 128; Boschma, 1929: 43-44, pl. 1; Loo & Chou, 1988: 28.
Fungia somervillei — Van der Horst, 1921: 58-59: pl. 1 fig. 2; Matthai, 1924: 41 (partim), pl. 9 figs. 1, 3, pl. 10 fig. 7; Schuhmacher, 1979: fig. 3.

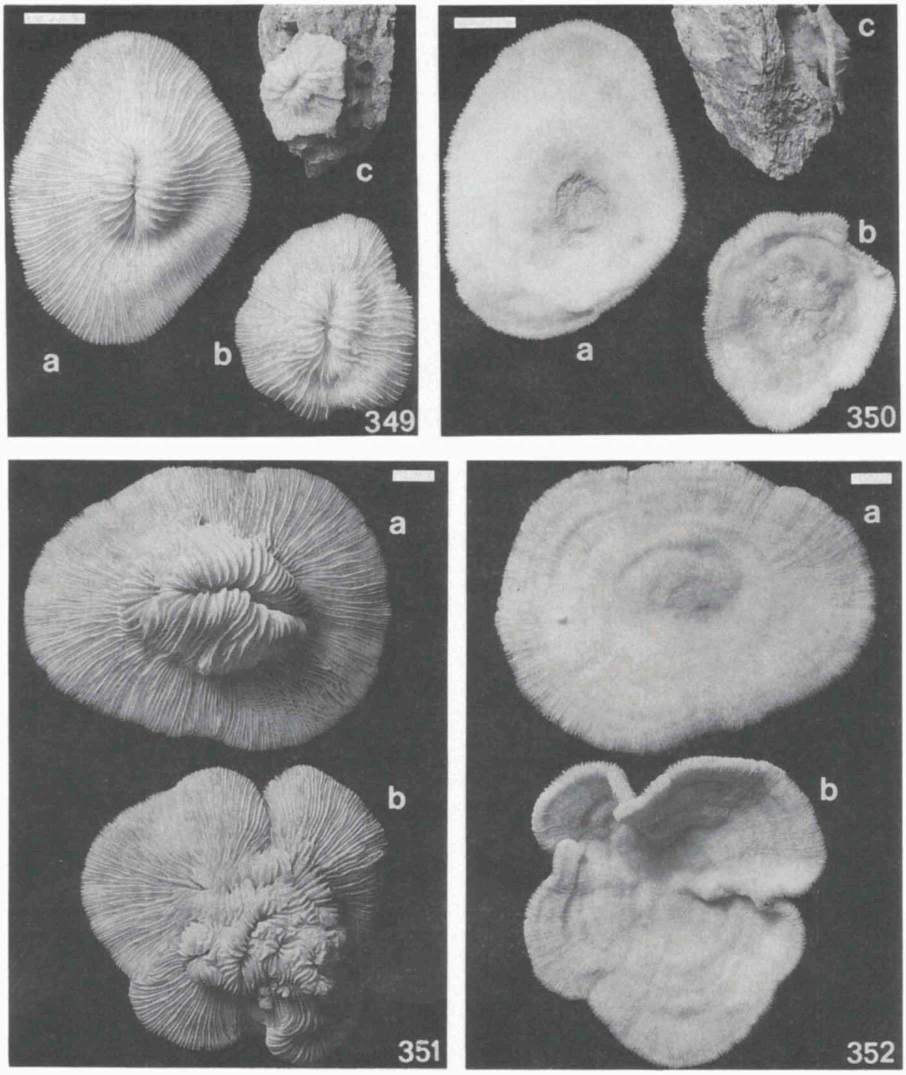
Fungia laciniosa Boschma, 1925: 198-199 (partim).
Fungia (Cycloseris) pseudoechinata Gerth, 1925: 40-41, pl. 6 fig. 2-2a (Miocene, "Goenoeng Linggapadang bei Margasari", Java). (New synonymy).
Fungia pseudoechinata — Umbgrove, 1945: 341; 1946b: 534.
Fungia (Pleuractis) somervillei — Scheer & Pillai, 1974: 37, pl. 18 figs. 1-2; Ditlev, 1976: 6.
Fungia (Pleuractis) moluccensis — Veron & Pichon, 1979: 165-166, figs. 273-282, 758; Faure, 1982: 102-103; Nemenzo & Ferraris, 1982: 119-120, fig. 8; Scheer & Pillai, 1983: 79-80, pl. 17 figs. 8-9, pl. 18 fig. 1; Veron, 1986b: 345; Veron & Kelley, 1988: 29.
Fungia (Pleuractis) somervelli — Ditlev, 1980: 55, figs. 40, 231. (Incorrect spelling).
Fungia somervilli — Pillai, 1983: 86. (Incorrect spelling).
Fungia granulosa — Veron & Marsh, 1988: 84 (partim).

Type material examined. — RMNH 9484-9485 (syntypes of *Fungia moluccensis*; type loc. Moluccas, INDONESIA); RGM 3891 (lectotype [present designation] of *Fungia pseudoechinata*; type loc. Margasari, Java, INDONESIA).

Other material. — RED SEA. Gulf of Aqaba: HSC 2/10 (1), USNM 78259. SINGAPORE: MCZ 5397. PHILIPPINES: MNHN Fun15. Cebu: UPMSI 325, USNM 77940. Sulu Is.: USNM 77780. INDONESIA. NW Java: RMNH 16058-16061 (10), 16063, 16068, USNM 77784. SW Sulawesi: RMNH 20312 (2), 20319 (4), 20321 (6), 20326, 20336 (3), 20340-20341 (23), 20346 (57), 20351 (30), 20365 (7), 20481 (3), 20833, 21023. Tiger Is.: RMNH 21087 (4). Komodo: RMNH 21411 (6), 21465 (3). N Sumbawa: PPPO 1026, RMNH 21337 (6), 21643, 21672 (3). Paternoster Is.: ZMA 5512. Banda: RMNH 8357, 8359 (3), 8373, 15771. Talaud Is.: RMNH 15729. PAPUA NEW GUINEA. Bismarck Sea: ULB. AUSTRALIA. Kimberley: WAM 206.85. N Great Barrier Reef: NTM 6781, 6788. C Great Barrier Reef: QMB GL3491-3492. PALAU IS.: USNM 47088. FIJI IS.: USNM 78348 (6). SAMOA IS.: USNM 77832-77833 (3). SOCIETY IS.: MNHN, RMNH 8982.

Characters. — Adult animals are free-living and have an irregularly oval-elongate corallum outline with rounded or tapering ends. They are usually monostomatous, but they may form supernumerary mouths by intra- or circumstomadaeal budding (fig. 351). The animals do not form fragmentation clefts in the corallum wall. The corals vary in thickness; their shape varies from flat to highly arched. The oral surface is very convex, especially around the central mouth. The length of the central fossa, measured at its bottom, is 1/7 to 1/2 of the corallum length. The septal edges along the central fossa stand upright, but those at both ends diverge away from it. The columella is formed by a mingled mass of tightly packed, sometimes fused paliform lobes and trabeculae with their tips pointing in various directions. The length of the specimens varies between 2.0 and 18.5 cm.

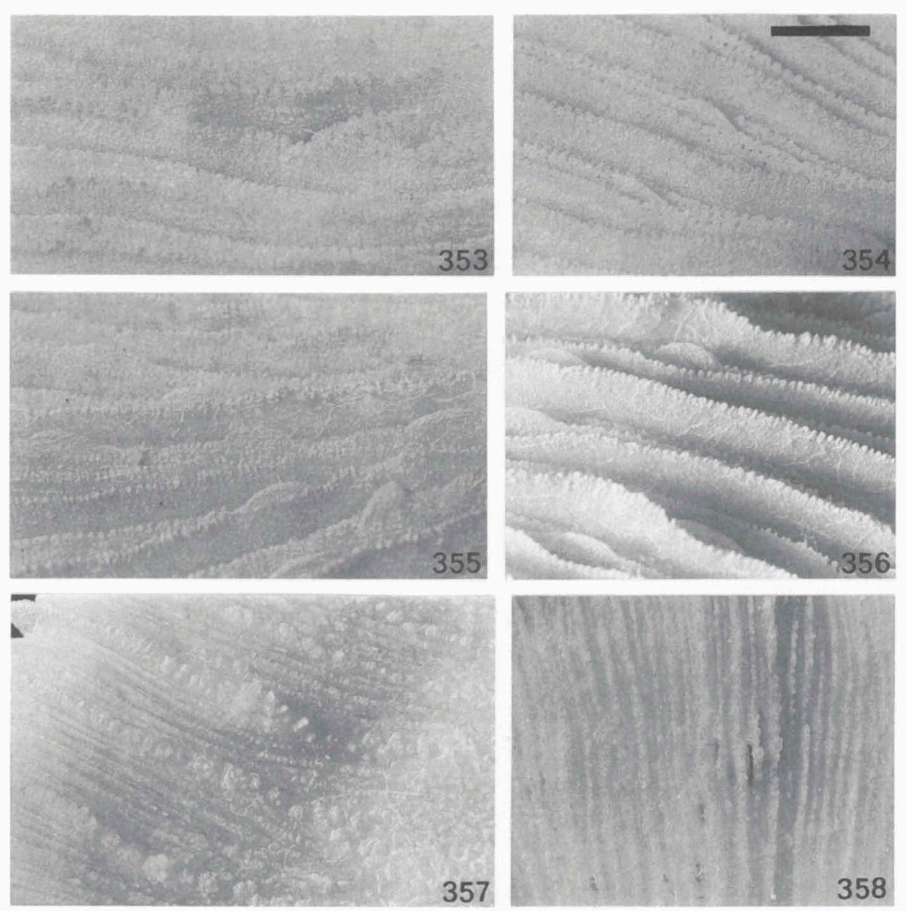
The septa are densely packed and straight. The septa of lower orders are thick and either perforated or solid, those of higher orders are relatively thin and always perforated (fig. 642). The septa of low order cycles are the most exsert. Tentacular lobes may be present (figs. 355-356). The septal margins are finely ornamented with septal dentations which are either blunt and irregularly granular or slightly angular and sharp (figs. 353-356). Their number varies from 20 to 90 per cm. The septal sides are densely granulated. The granulations are almost evenly distributed. The compound synapticulae connecting



Figs. 349-352. Corals of *Fungia (Pleuractis) moluccensis* from NW Java, Indonesia. Scale bars: 2 cm. Figs. 349-350. Upper and lower surface of three small to intermediate sized corals: (a) RMNH 16068, (b) RMNH 16061, both with a clear detaent scar and (c) an anthocaulus, RMNH 16058. Figs. 351-352. Upper and lower surface of two large corals (anthocyathi): (a) a coral with a supernumerary fossa and a clear detachment scar (RMNH 16059) and (b) an irregularly shaped coral with several supernumerary fossae and a slightly visible detachment scar (RMNH 16063).

the septa laterally cannot easily be detected, because of the tight septal arrangement.

The corallum wall is normally solid in immature specimens and perforated in adults, although in the latter the perforations may be rare or absent. A large detachment scar (diameter > 1 cm) is distinct at the aboral side of small anthocyathi, and usually it is discernible in large specimens as well. The underside usually shows concentric, irregularly undulating growth lines (fig. 352). The wall is not granulated. The costae are unequal in size, often thickened, straight and distinct near the corallum margin, but less distinct near the centre. In the smallest coralla they are not always clearly visible. The costae are finely ornamented with spines which are usually granular, blunt and erect



Figs. 353-358. Close-ups of *Fungia (Pleuractis) moluccensis* corals. Scale bar: 0.5 cm. Figs. 353-354. Septa of the coral in fig. 351a; some of the higher order septa are perforated. Figs. 355-356. Septa with small dentations and large tentacular lobes of a coral from the same area (RMNH 16060). Fig. 357. The same coral with unequally exsert costae and only one visible perforation in the corallum wall. Fig. 358. Equally sized costae of the coral in fig. 352a with several perforations in the corallum wall.

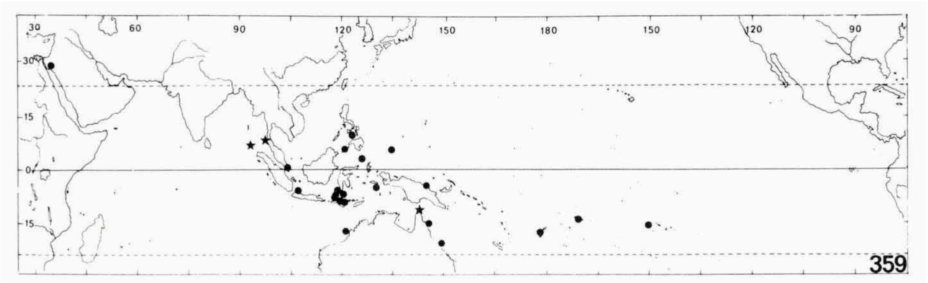


Fig. 359. The range of *Fungia (Pleuractis) moluccensis*. Records are from examined material (●) and published illustrations (★).

(fig. 358). On the thicker low order costae the spines point in various directions (figs. 357, 643). Their number varies from 40 to 70 per cm.

The animals vary from dark brown (fig. 21) to an ochre shade of yellow when mature, whereas anthocauli or small anthocyathi may be partly whitish. The small tentacles are either colourless and transparent or indistinctly white.

Geographical distribution (fig. 359). — The species occurs in the Gulf of Aqaba (Red Sea) and eastward from the Central Indo-Pacific towards the Society Islands. It has rarely been found in the Indian Ocean (apart from the Red Sea, off Western Australia and in the Andaman Sea). The species has not been found north of the Philippines.

Remarks. — In the literature, there is much confusion about the identity of *F. moluccensis* because it displays such variability in shape. For example, a specimen of *F. moluccensis* was misidentified as *F. somervillei* by Van der Horst (1921), who earlier (1919) discovered the first species as new to science. He was misguided by the similarity in overall shape of these two species, whereas they differ distinctly in their septal and costal ornamentations, which explains why they are placed in different subgenera. Boschma (1925), who had access to the syntypes of *F. moluccensis*, described two juvenile specimens of *Fungia moluccensis* as a new species, *F. laciniosa*. Large collections of *F. moluccensis* corals were needed to study the morphological range of the species. These were not yet available to Van der Horst (1921) and Boschma (1925), which explains why they could not always recognize this species.

Not all of the small and abraded coral fragments described as *F. pseudoechinata* are easily identifiable; the most complete specimen, belonging to *F. moluccensis*, is therefore designated lectotype.

F. moluccensis has costae which are more unequal than those of other *Pleuractis* species. Therefore its underside is less smooth. The humped upper surface is more pronounced than that of *F. gravis*. Some adult corals of *F. moluccensis* are difficult to separate from irregularly formed specimens of *F. granulosa*, because of their almost similar septo-costal ornamentations.

Fungia (Pleuractis) gravis Nemenzo, 1955
(figs. 22, 360-370, 644-645)

Fungia paumotensis — Döderlein, 1902: 88-91 (partim), pl. 7 fig. 3; Yabe & Sugiyama, 1941: 77 (partim), pl. 67 figs. 1-1a; Veron & Marsh, 1988: 84 (partim).

Fungia gravis Nemenzo, 1955: 62, pl. 10 figs 1-2 (Guimares I., Iloilo, Panay); 1981: 189, fig. 207; 1986: 145-146, fig. 167.

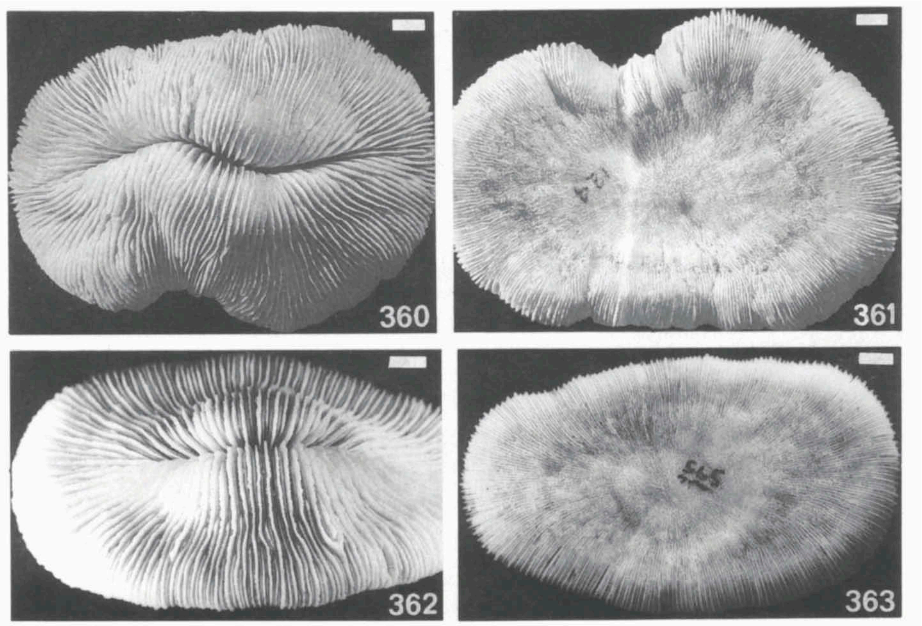
Fungia (Pleuractis) paumotensis — Veron & Pichon, 1979: 162-165 (partim), fig. 269; Veron, 1986b: 344 (partim).

Fungia alta Nemenzo, 1983: 272-273, fig. 2 (Mactan I., Cebu); ? Veron & Kelley, 1988: 28. (New synonymy).

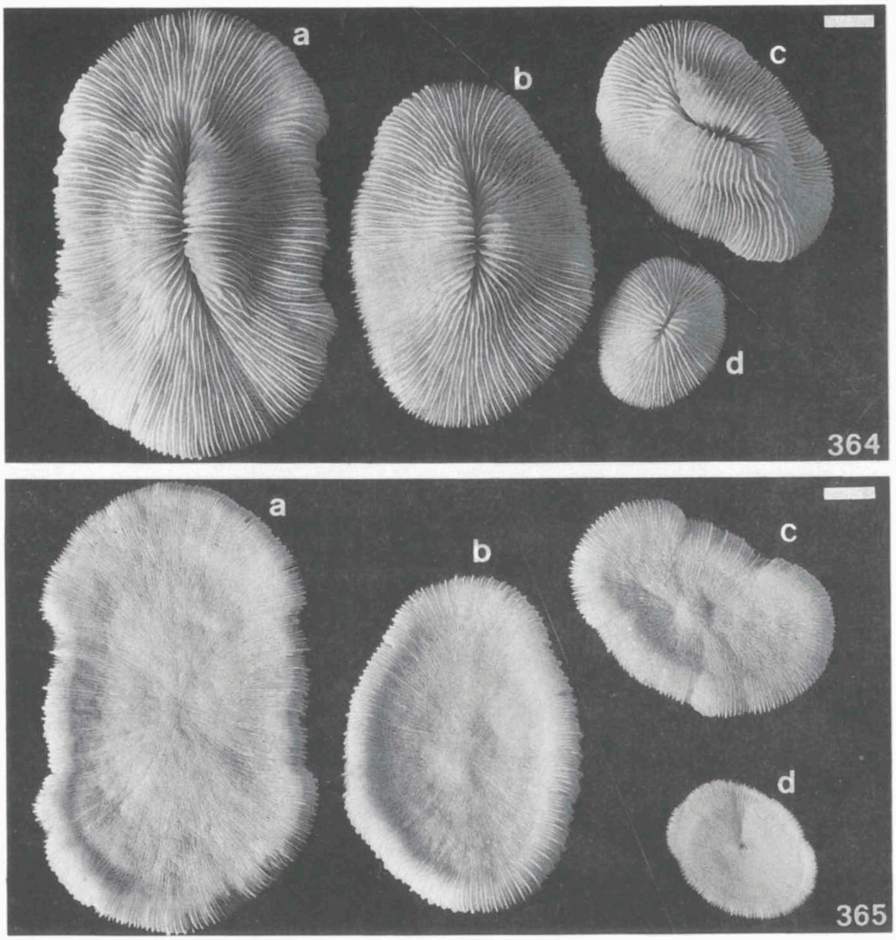
Fungia granulosa — Veron & Marsh, 1988: 84 (partim).

Type material examined. — UPZD 124 (holotype of *Fungia gravis*; type loc. Guimares I., Iloilo, Panay, PHILIPPINES); UPMSI 565 (holotype of *Fungia alta*; type loc. Mactan I., Cebu, PHILIPPINES).

Other material. — SEYCHELLES: USNM 78293. ANDAMAN IS.: USNM 77789. S CHINA SEA. Tizard Bank: BMNH 1889.9.24.135. MALAYSIA. Sabah: USNM 47955. PHILIPPINES: BMNH 1923.12.7.3. INDONESIA. SW Sulawesi: RMNH 20202 (2), 20204-20205, 20211, 20213 (5), 20218-20220 (14), 20231 (2), 20247 (22), 20253 (18), 20254 (2), 20370 (4), 20378 (2), 20391 (3), 20957, 21021. Tiger Is: RMNH 21074, 21097 (4), 21170 (3). N Sumbawa: RMNH 20508 (2), 20530 (3), 20807-20808 (3), 21673. Komodo: RMNH 21072. AUSTRALIA. Kimberley: WAM 175.85, 696.86. C Great Barrier Reef: AIMS 5789, QMB (2). PAPUA NEW GUINEA. Bismarck Sea: ULB. SOCIETY IS.: BMNH 1886.12.9.189, MNHN.



Figs. 360-363. Holotypes from the Philippines. Scale bars: 1 cm. Figs. 360-361. Upper and lower surface of the holotype of *Fungia (Pleuractis) gravis* (UPZD 124; Guimares I., Iloilo, Panay). Figs. 362-363. Upper and lower surface of the holotype of *Fungia alta* (= *F. (P.) gravis*, UPMSI 565; Mactan I., Cebu).

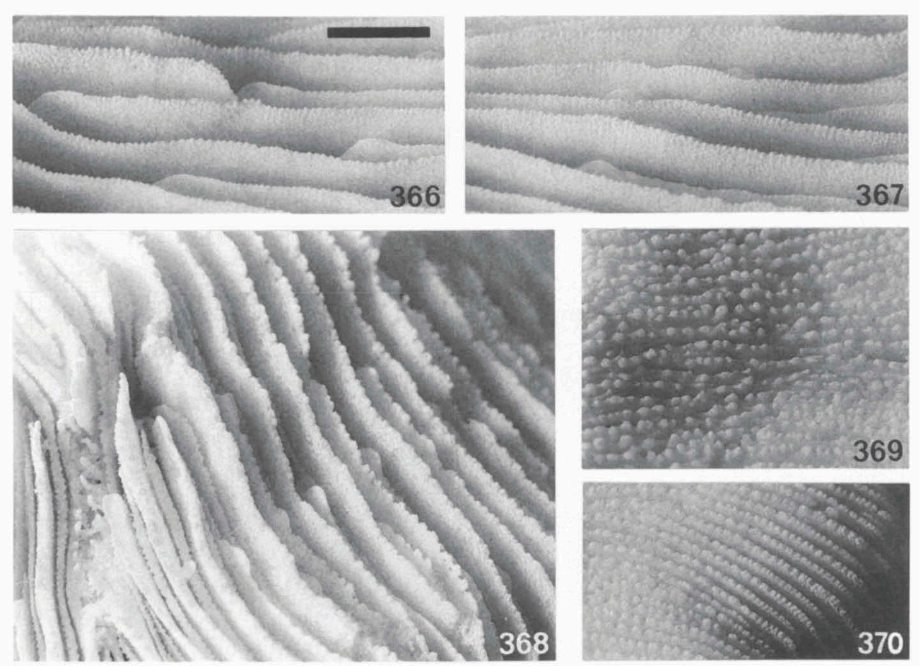


Figs. 364-365. Upper and lower surface of corals (anthocyathi) of *Fungia (Pleuractis) gravis* from SW Sulawesi, Indonesia (RMNH 20218). Scale bars: 2 cm.

Characters. — Adult animals are free-living. The polyps are usually monostomatous, but they may grow supernumerary stomata by circumstomadaeal budding. Their outline is oval-elongate with rounded, blunt (rarely tapering) ends. The animals do not form fragmentation clefts in the corallum wall. The coralla vary in thickness and are either flat or arched. The length of the central fossa, measured at its bottom, is 1/10 to 1/3 of the coral length. The septal edges along its sides stand upright, whereas those at both ends diverge away from it. The columella is formed by a mingled mass of loosely packed trabeculae and paliform lobes with the tips pointing in various directions. The length of the specimens ranges between 2.5 and 17.5 cm.

The septa are densely packed and usually straight, or otherwise wavy or slightly bending. The septa of lower orders are usually thick and either solid or perforated (fig. 644); those of higher orders are thin and always perforated. In juvenile specimens all septa are perforated. The septa of lowest orders are most exsert. Tentacular lobes may be present above the inner edges of the septa (figs. 366-368). The septal margins are finely ornamented with septal dentations which may vary from granular to slightly angular (figs. 366-368). Their number varies from 25 to 50 per cm septum. The septal sides are densely granulated. The granulations are coarse and irregularly distributed at the septal base, whereas at the septal fringe, they are more or less evenly arranged (fig. 644). The compound synapticulae connecting the septa laterally cannot easily be detected, because of the tight septal arrangement.

The corallum wall is solid in relatively small specimens whereas it is perforated in large specimens. A detachment scar is only present at the aboral side of specimens in early anthocyathus-phase (fig. 365d). The corallum wall is not granulated (fig. 645). The costae are almost of equal size, straight and distinct from the corallum margin towards the centre. The costae are finely to coarsely



Figs. 366-370. Close-ups of *Fungia (Pleuractis) gravis* corals. Scale bar: 0.5 cm. Figs. 366-367. Septa of the coral of fig. 364b with small dentations and distinct tentacular lobes. Fig. 368. Septa of a polystomatous coral from the same sample showing a supernumerary fossa, fine dentations and distinct tentacular lobes. Figs. 369-370. Costae of the coral in fig. 365c.

ornamented. The costal spines are blunt, granular and when fused, flattened at the costal sides (fig. 369-370, 645). Their number varies from 15 to 40 per cm costa.

The colour of the living animal varies from dark brown to ochre (fig. 22). The small tentacles are transparent or indistinctly white.

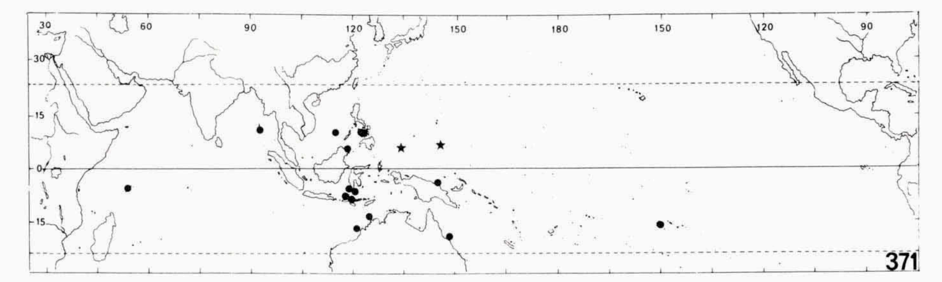


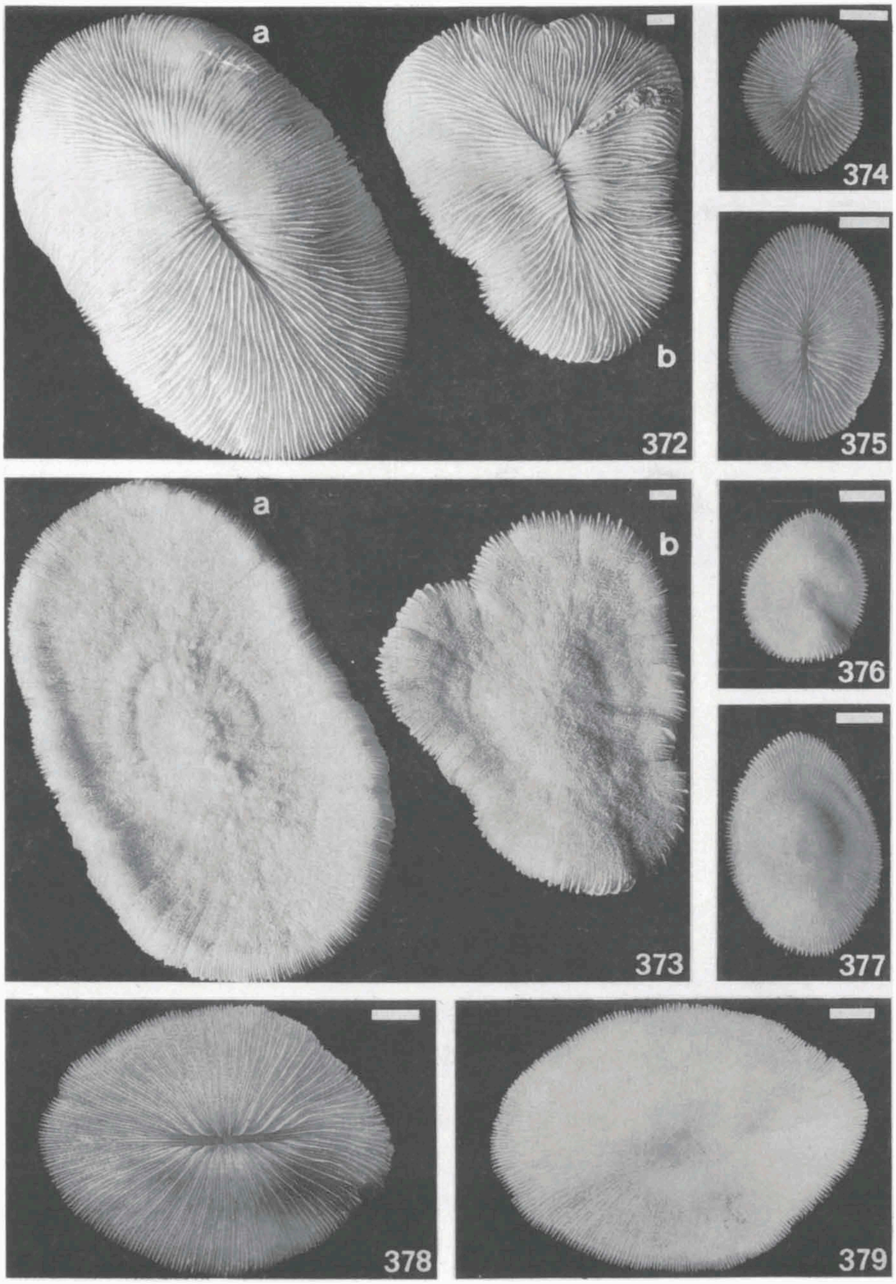
Fig. 371. The range of *Fungia (Pleuractis) gravis*. Records are from examined material (●) and published illustrations (★).

Geographical distribution (fig. 371). — The species occurs from the Seychelles towards the Society Islands. Most specimens were collected in the Central Indo-Pacific and at the Andaman Islands, Palau, the Caroline Islands and the Great Barrier Reef.

Remarks. — *F. alta* belongs in the synonymy of this species. Its holotype is flatter, with a more regular shape and with a more distinct oral hump than that of *F. gravis* (see figs. 360-363). Morphologically the relatively unknown *F. gravis* is situated in between *F. moluccensis* and *F. paumotensis*; its septa are similar to those of *F. moluccensis*, its costae to those of *F. paumotensis* (see figs. 642-647). Compared to *F. moluccensis*, *F. gravis* is much more regular in shape and its underside is much smoother, like that of *F. paumotensis*. Compared to the latter species, *F. gravis* has the septa more tightly arranged and with finer dentations. At some oceanic locations, especially at the periphery of the known distribution range (Seychelles and Society Is.) the corals of *F. gravis* tend to look more like those of *F. scutaria*, with costae which are less regularly arranged and the lower side less smooth. In the Central Indo-Pacific, however, the species can easily be distinguished.

Fungia (Pleuractis) paumotensis Stutchbury, 1833
(figs. 23, 372-385, 646-647)

Fungia paumotensis Stutchbury, 1833: 495, pl. 32 figs. 6a-b ("Paumotos"); Milne Edwards & Haime, 1851: 86; 1860: 16-17; Quelch, 1886: 137; Döderlein, 1902: 88-91 (partim), pl. 7 figs.



Figs. 372-379. Corals (anthocyathi) of *Fungia (Pleuractis) paumotensis* from NW Java, Indonesia. Scale bars: 1 cm. Figs. 372-373. Upper and lower surface of two corals (RMNH 16070): (a) a single coral and (b) two fused individuals. Figs. 374-375. Juveniles (RMNH 16079). Figs. 376-377. Aboral surface of the corals in figs. 374-375. Figs. 378-379. Upper and lower surface of an immature specimen (RMNH 16079).

1-2, 4-5a; Bedot, 1907: 218; Vaughan, 1907a: 134, pl. 35; Van der Horst, 1921: 61; Matthai, 1924: 42; Boschma, 1925: 214-215, pl. 7 fig. 77; Hoffmeister, 1925: 34-35; Umbgrove, 1926: 42; Faustino, 1927: 174-175, pl. 49 figs. 1-2; Boschma, 1929: 44; Yabe & Sugiyama: 1935: 396; Ma, 1937: 133, pl. 48 figs. 1-2; Eguchi, 1938: 362; Umbgrove, 1940: 292; Yabe & Sugiyama, 1941: 77 (partim), pl. 65. fig. 4, pl. 67 figs. 2-2a; Crossland, 1952: 153; Nemenzo, 1955: 60-61, pl. 11 figs. 4, 5b; Stephenson & Wells, 1955: 26; Pillai, 1972: 203; Pichon, 1974: 176; Chevalier, 1979: 132; 1980: 66; Shirai, 1980: 530; Nemenzo, 1981: 188, fig. 205; Pillai, 1983: 86; Zou & Chen, 1983: 91; Wallace, 1984: 38, fig. 22.7; Johnston, 1986: 159; Nemenzo, 1986: 145, fig. 165; Veron, 1986a: 32; Veron & Marsh, 1988: 84 (partim). Not: Dana, 1846; Montanaro, 1932; Zou, Song & Ma, 1975.

Fungia carcharias Studer, 1877: 649-650, pl. 4 fig. 14 ("Kaiserin Augusta-Bai, Bougainville-Insel").

Fungia scutaria — Duncan, 1883: pl. 5 figs. 3-8; Quelch, 1886: 137.

Pleuractis scutaria — Verrill, 1864: 52.

Lobactis conferta Verrill, 1864: 52 (partim).

Fungia plana Studer, 1877: 650 (partim).

Fungia placunaria — Ortmann, 1888: 178.

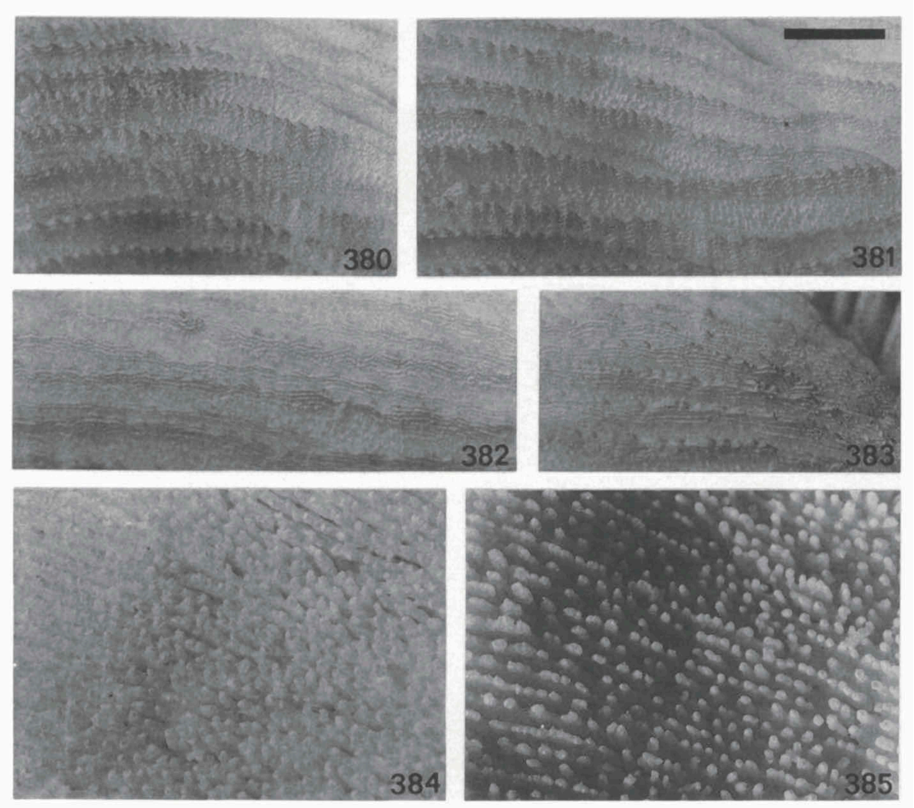
Fungia proechinata Döderlein, 1901: 358 ("? Jaluit, Marschallinseln"); 1902: 100-101, pl. 10 fig. 6-6a. (New synonymy). Not: Van der Horst, 1921.

Fungia subpaumotensis Umbgrove, 1946b: 534, pl. 80 fig. 5 (Early Pliocene, Prupuk, Java). (New synonymy).

Fungia (Pleuractis) paumotensis — Scheer & Pillai, 1974: 36; Maragos & Jokiel, 1978: 61; Rosen, 1979a: 12; Veron & Pichon, 1979: 162-165 (partim), figs. 270-272; Ditlev, 1980: 55; Faure, 1982: 100-101; Randall & Myers, 1983: 18, figs. 346-347; Veron, 1986b: 344 (partim); Sakai & Yamazato, 1987: 46; Wood & Tan, 1987: 197; Veron & Kelley, 1988: 28, 32.

Type material examined. — BMNH 1939.1.2.31 (neotype [present designation] of *Fungia paumotensis*; type loc. Aku Maru, Gambier Is., TUAMOTU ARCHIPELAGO); MCZ 5294 (paralectotype of *Lobactis conferta*; Apiang, KINGSMILL IS.); ZMB H484 (holotype of *Fungia proechinata*; type loc. Jaluit, MARSHALL IS. ?); RGM 77653 (holotype of *Fungia subpaumotensis*; type loc. Prupuk, Java, INDONESIA).

Other material. — RED SEA: RMNH 9430. SINGAPORE: AMNH 295-296, BMNH 1891.8.9.5, MCZ 5398 (10). MALAYSIA. Sabah: USNM 47953. PHILIPPINES: USNM 20841, 77962. E Mindoro: UPZD 116. Burias: USNM 78006. Cebu: UPZD 530. Bohol: UPZD 548-549. SW Mindanao: BMNH 1886.12.4.188, 1959.8.6.24. INDONESIA: ZMA 448. Belitung (Billiton): BMNH 1883.7.24.85. NW Java: RMNH 15784, 16070 (2), 16071-16079 (23), ZMA 365. SW Sulawesi: RMNH 15679, 15764 (3), 20121, 20256-20257 (6), 20266 (8), 20277 (2), 20298 (4), 20706, 20847, 20900 (2), 20958, 21024. Tiger Is: RMNH 21315, 21641. Togian Is: RMNH 9442, 9492, 9535. Komodo: RMNH 20440 (2). N Sumbawa: RMNH 20512, 21618 (2). Tukang Besi Is: RMNH 20101, 20137, 20198. Moluccas: RMNH 9488-9489. Ambon: RMNH 9491, ZMA 445. Banda: RMNH 8360-8361, 8366-8367 (4), USNM 78327 (4), 78334 (9). Obi: RMNH 15730, USNM 78330. N Halmahera: USNM 78043, 78065. Talaud Is: RMNH 15731 (2). Kei Is: RMNH 8368 (5). PAPUA NEW GUINEA. Bismarck Sea: ULB. SOLOMON IS. Bougainville: AMNH. AUSTRALIA. Kimberley: WAM 190.85, 191.85. N Great Barrier Reef: QMB G8068. C Great Barrier Reef: BMNH 1892.12.1.408/421/426/435, QMB GBR294, GL3197, GL3612. S Great Barrier Reef: QMB G6602, QMT. PALAU IS: USNM 78013. CAROLINE IS.: USNM 77822. MARSHALL IS.: RMNH 14620, USNM 77863-77864, 78242-78243, 78315 (6). GILBERT IS.: MCZ 5417 (2), USNM 77891-77892. SAMOA IS.: USNM 77834. TONGA IS.: BMNH 1891.3.6.77. PHOENIX IS.: USNM 78264. HAWAII IS: MNHN FUN 82-83. SOCIETY IS.: BMNH 1886.12.9.183-185/190-191/373-374/377, 1892.10.16.11, 1922.1.21.62, 1959.8.6.22-23/62, 1973.4.17.1-3, MCZ 5393, MNHN, RMNH 8983 (3), 8986 (2), 15783, 15785, USNM 77815 (2), 77854.



Figs. 380-385. Close-ups of *Fungia (Pleuractis) paumotensis* corals. Scale bar: 0.5 cm. Figs. 380-381. Septa of the coral in fig. 372b. Figs. 382-383. Septa of the coral in fig. 372a. Fig. 384. Costae of the coral in fig. 375b. Fig. 385. Costae of the coral in fig. 375a.

Characters. — Adult animals are free-living and monostomatous. Their outline is oval-elongate with rounded ends. They do not form fragmentation clefts in the corallum wall. The coralla vary in thickness; their shape varies from flat to arched. The septal edges along the central fossa stand upright, whereas those at both ends diverge away from it. The length of the central fossa, measured at its bottom, is 1/8 to 1/4 of the corallum length. The columella is formed by a mingled mass of loosely packed trabeculae and paliform lobes with the tips pointing in various directions. The length of the specimens ranges from 3.0 to 21.5 cm.

The septa are more or less loosely packed and straight. The solid septa of low order cycles are thicker and more protruding than the perforated septa of higher orders. Tentacular lobes are absent. The septal margins are finely to coarsely ornamented with irregularly angular dentations (figs. 380-383). Their number varies from 12 to 30 per cm. The septal sides are thinly granulated. The granulae are coarse and irregularly dispersed at the septal base, but more upwards, at the septal fringe, they are fused in ridges parallel to the septal margin (fig. 646). The compound synapticulae connecting the septa laterally cannot be detected easily in all specimens.

The corallum wall is solid in immature specimens and perforated in adults. A detachment scar is distinct at the aboral side of specimens in early anthocyathus-stage. The corallum wall is not granulated. The costae are almost equal in size; they are straight and distinct from the corallum margin towards the centre. The costae are finely to coarsely ornamented with blunt, granular spines which may appear to be laterally compressed when fused (figs. 384-385, 647). Their number varies from 15 to 50 per cm.

The living animal is usually brown (fig. 23). The small tentacles are transparent and either colourless or green. Their tips may be white. The mouth is either brown or violet.

Geographical distribution (fig. 386). — In addition to a single specimen from the Red Sea, no specimens are known to have been collected west of Singapore. Eastward the range extends from the Central Indo-Pacific towards the Ryukyu Islands (S Japan), the Hawaiian Islands and the Tuamoto Islands.

Remarks. — The holotype (from the Tuamotu Archipelago = Paumotu Islands) is lost. It is not clear from the description, whether it was collected and deposited in a museum, or thrown away after being described and illustrated in the field. At present the specimen is in neither the BMNH nor the LSL. The illustrations given by Stutchbury (1833) are not clear enough to show to which species the holotype belongs. Because no material from the type locality is available, a coral from Aku Maru, Gambier Islands, Tuamotu Archipelago is designated as neotype.

The holotype of *F. carcharias* (ZMB 1793), from Bougainville Island (Solomons), cannot be traced in the ZMB any longer. A clear photograph of the

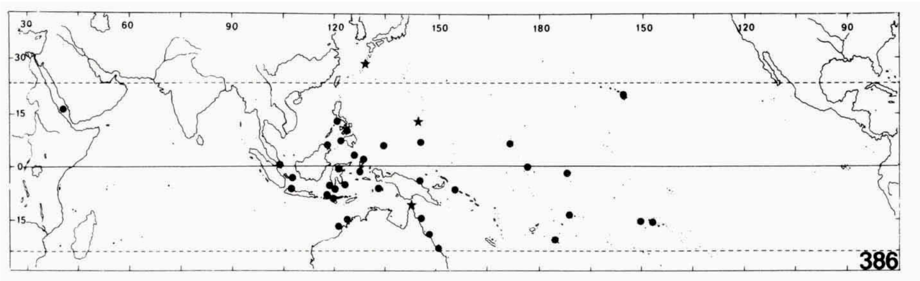


Fig. 386. The range of *Fungia (Pleuractis) paumotensis*. Records are from examined material (●) and published illustrations (★).

specimen has been given by Döderlein (1902; pl. 7 fig. 2). The specimen does not differ distinctly from *F. paumotensis* corals and therefore *F. carcharias* was synonymized with this species by Döderlein (1902). The holotype of *F. proechinata* has frayed septal margins, which give it a slight resemblance to that of *Ctenactis echinata*. The frayed septal margins are considered an abnormality which is not specific for *F. paumotensis*, because occasionally it is observed in other *Fungia* species as well. Otherwise, the septal and costal ornamentations are very much like those of *F. paumotensis*. The fossil *F. subpaumotensis* does not differ clearly from *F. paumotensis* and therefore both have to be considered conspecific.

The species has been misidentified as *F. scutaria* by several coral taxonomists. It differs from the latter species mainly by its larger septal dentations covered by zigzag ridges of granulations. These ridges resemble closely ridges typical of some *F. (Verrillofungia)* species.

F. paumotensis, morphologically the closest ally of *F. gravis*, differs from the latter by its looser septal arrangement and its coarser septal dentations. Additionnally, *F. paumotensis* is the only species of *Pleuractis* in which the animals are not able to develop tentacular lobes.

Heliofungia Wells, 1966

Type species: *Fungia actiniformis* Quoy & Gaimard, 1833. By original designation.

Fungia (Heliofungia) Wells, 1966: 239-240; Ditlev, 1980: 57; Chevalier & Beauvais, 1987: 706, 710.
Heliofungia — Veron & Pichon, 1979: 125; Veron, 1986b: 328.

Characters. — Adult animals are free-living and monostomatous. Their outline varies from circular to oval; the coralla vary from flat to slightly arched. The corallum wall is solid and granulated. The septal margins are ornamented with lobate dentations. The sides of the dentations are covered by granulations which are radially arranged. The costal spines are laterally flattened with either a single row of granulations or several rows, each being oriented perpendicularly to the costal margin. The polyp is fleshy with thick, relatively long tentacles which give the animal an actinian-like appearance. The tentacles have knobbed tips (acrospheres).

Remarks. — Döderlein (1901: 355; 1902: 82) classified the single species of this genus as a member of the "*Actiniformis* -Gruppe" within *Fungia*. Wells (1966) established the group as the subgenus *Fungia (Heliofungia)* after which Veron & Pichon (1979) raised it to genus level. Besides the skeleton, with its unique characters (e.g. the septo-costal ornamentations, figs. 648-649), the fleshy tissue is also different from that in other genera. The affinities of the genus are not clear.

Heliofungia actiniformis (Quoy & Gaimard, 1833)
(figs. 24, 387-399, 648-649)

Fungia actiniformis Quoy & Gaimard, 1833: 180-182, pl. 14 figs. 1-2 ("sur l'île aux Cocos, au havre Carteret de la Nouvelle-Irlande"); Lamarck, 1836: 374; Leuckart, 1841: 46-47; Dana, 1846: 299; Milne Edwards & Haime, 1851: 83; 1860: 13-14; Studer, 1877: 648-649, pl. 3 figs. 12a-b, pl. 14 fig. 2c; Döderlein, 1902: 82-88, pl. 6 (including var. *singapurensis* Döderlein, 1902 [Singapore]; var. *suluensis* Döderlein, 1902 [Mindanao]; var. *palawensis* Döderlein, 1902 ["Palau-Inseln"; sometimes misspelled *palauensis*]; var. *salawattensis* Döderlein, 1902 ["Salawatti bei Neu-Guinea"]); Bedot, 1907: 218; Gerth, 1921: 422; Van der Horst, 1921: 61; Boschma, 1925: 210; Faustino, 1927: 172-174, pl. 47 figs. 1-2, pl. 48 figs. 1-7; Yonge, 1930: 37-38, fig. 21b; Thiel, 1932: 62-63; Ma, 1937: 144, pl. 65 figs. 1-4; Abe, 1938: 470-478, figs. 1a, 2-3; Eguchi, 1938: 360; Umbgrove, 1939: 43; Yabe & Sugiyama, 1941: 77, pl. 66 figs. 1-7; Crossland, 1952: 52; Nemenzo, 1955: 70-72, pl. 12 fig. 1; Stephenson & Wells, 1955: 25; Purchon, 1956: 157; Searle, 1956: 17, pls. 14B, 19A; Sisson, 1973: 790-791; Sukarno, 1974: 14; Coleman, 1977: 60; Phillipps, 1978: 101; Zou, 1978: 100, pl. 8 figs. 1-4; Green, Harris, Robertson & Santavy, 1979: 298; Shirai, 1980: 530; Betterton, 1981: 204-205, pls. 84-85; Nemenzo, 1981: 196-198, figs. 219-221; Zou & Chen, 1983: 91; Nemenzo, 1986: 151-152, figs. 175a-b. Not: Montanaro, 1932; Vaughan & Wells, 1943; Boshoff, 1981.

Fungia crassitentaculata Quoy & Gaimard, 1833: 182-183, pl. 14 figs. 3-4 (Vanikoro); Lamarck, 1836: 374-375; Milne Edwards, 1836-1849: pl. 82 figs. 1-1a; Leuckart, 1841: 47-48; Dana, 1846: 299-300; Milne Edwards & Haime, 1851: 88; 1860: 19; Ortmann, 1888: 178; 1889: pl. 18 fig. 12e; Rehberg, 1892: 27-28; Saville-Kent, 1893: 173-176, pl. 23, pl. 24 fig. 2, chromo pl. 6 figs. 13-14; Vaughan & Wells, 1943: pl. 2 fig. 1. Not: Gardiner, 1909.

Fungia diversidens Milne Edwards & Haime, 1851: 87-88 ("Patrie inconnue"); 1860: 18.

Fungia granulicostata Umbgrove, 1946b: 533, pl. 80 fig. 6 (Lower Pliocene, Prupuk, Java). (New synonymy).

Fungia actinodiscus Umbgrove, 1950: 647, pl. 82 figs. 11-12 (Lower Pleistocene, Putjangan, Java). (New synonymy).

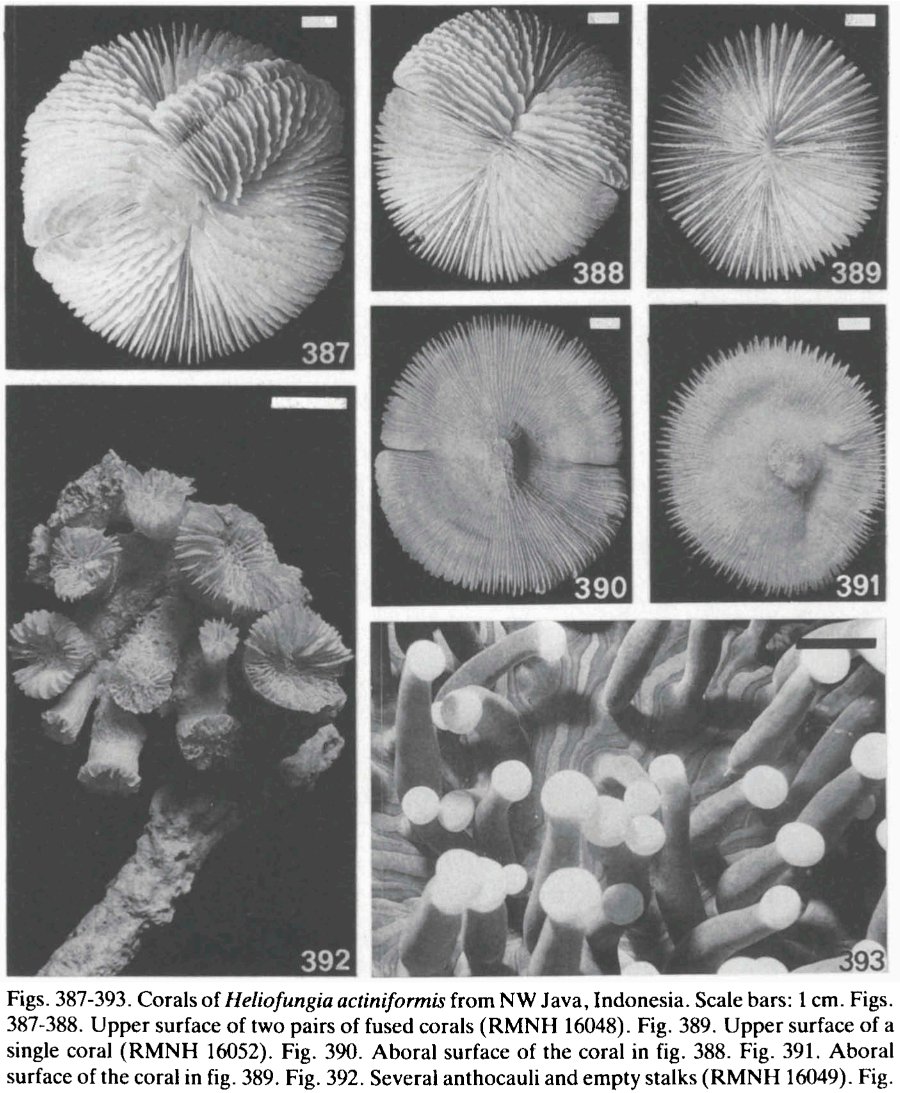
Fungia sp. — Zou, 1978: pl. 9 figs. 5-6.

Fungia (Heliofungia) actiniformis — Ditlev, 1980: 57.

Heliofungia actiniformis — Faulkner & Chesher, 1979: 287-288, pls. 103-104; Veron & Pichon, 1979: 125-128, figs. 202-205, 754; Wood, 1983: 118-119, 144; Wallace, 1984: 38; Johnston, 1986: 159; Veron, 1986a: 31; 1986b: 328-329; Wood & Tan, 1987: 197, pl. 7h; Loo & Chou, 1988: 28; Veron & Kelley, 1988: 28, 31; Veron & Marsh, 1988: 82.

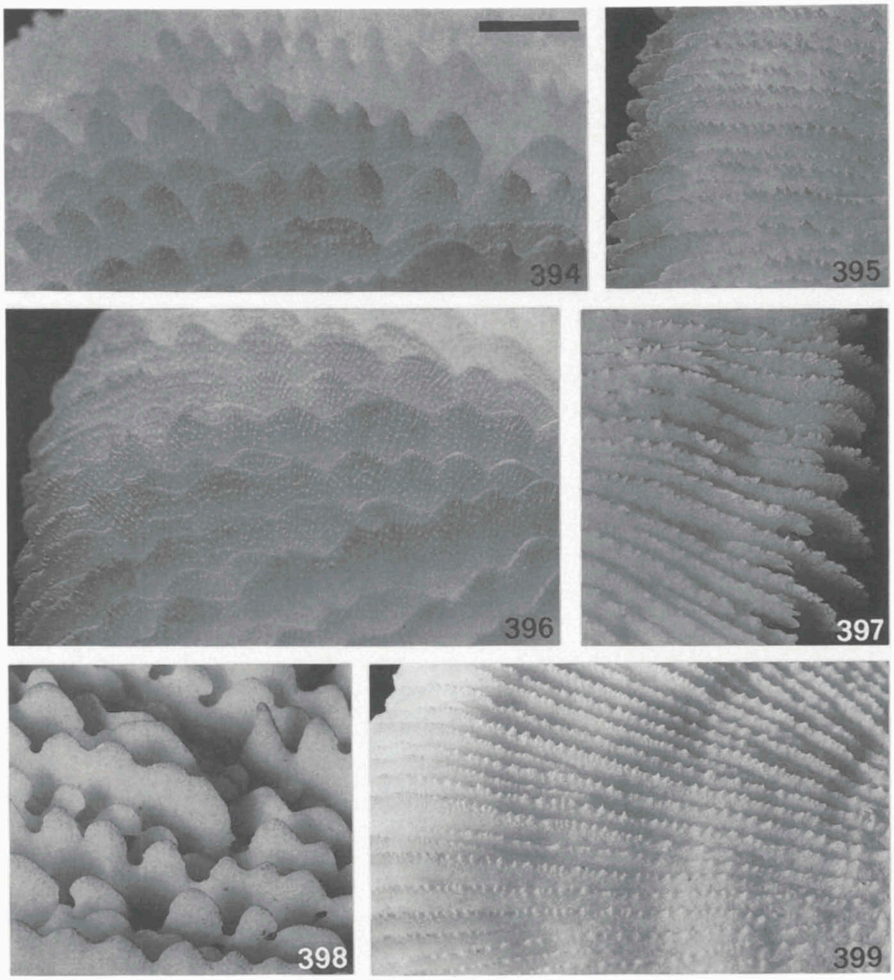
Type material examined. — MNHN (holotype of *Fungia actiniformis*; type loc. Carteret, New Ireland, BISMARCK IS.); MNHN Fun35 (holotype of *Fungia crassitentaculata*; type loc. Vanikoro, Santa Cruz Is., NEW HEBRIDES [VANUATU]); RGM 77646 (holotype of *Fungia granulicostata*; type loc. Prupuk, Java, INDONESIA); RGM 77987 (holotype of *Fungia actinodiscus*; type loc. Putjangan, Java, INDONESIA).

Other material. — SINGAPORE: BMNH 1898.12.1.6, 1953.11.9.3, ZMA 464, 598. MALAYSIA. Sabah: BMNH. PHILIPPINES: USNM 77942 (8). E Mindoro: UPZD 81, 110. Cebu: UPZD 25. SW Mindanao: USNM 45445, 45600 (6), 77981. Sulu Is.: USNM 77980 (2), ZMA 596-597 (5), 599 (12). INDONESIA. Java: RGM 3875 (fossil). NW Java: RMNH 8353, 8355, 8556 (many small), 15769 (5), 16048-16052 (5 + many small), 16236-16240 (62), ZMA 334-335 (many small), 5499 (many small), 5513, 5596. N Sulawesi: ZMA 600, 719. SW Sulawesi: RMNH 15675-15676, 20165 (3), 20887, 21009 (2). Tiger Is.: RMNH 21258. Paternoster Is.: ZMA 343. N Sumbawa: RMNH 21317. Obi Latu: RMNH 15752. Maisel Is.: RMNH 20089. Banda: RMNH 8354, 9543 (4). Biak: RMNH 15765. PALAU IS.: USNM 47091, 78027-78028 (6), 78096. PAPUA NEW GUINEA. Bismarck Sea: ULB, USNM 78232. AUSTRALIA. Kimberley: WAM 185.85, 595.87 (5). Northern Territory: NTM 1831, 6945. N Great Barrier Reef: QMB G8058, GL3604. C Great Barrier Reef: BMNH 1892.12.1.440, 1934.5.14.164, QMB GL3618, USNM 5391-5392 (14). S Great Barrier Reef: QMB G2851-2852, G6153 (2), G6614 (3), G7366 (6). NEW CALEDONIA: ZMA 6277.



Figs. 387-393. Corals of *Heliofungia actiniformis* from NW Java, Indonesia. Scale bars: 1 cm. Figs. 387-388. Upper surface of two pairs of fused corals (RMNH 16048). Fig. 389. Upper surface of a single coral (RMNH 16052). Fig. 390. Aboral surface of the coral in fig. 388. Fig. 391. Aboral surface of the coral in fig. 389. Fig. 392. Several anthocauli and empty stalks (RMNH 16049). Fig. 393. Close-up of a fleshy polyp with long tentacles; note the knobbed tips (acrospheres).

Characters. — Adult animals are unattached and monostomatous. Their outline varies from circular to slightly oval. The corallum wall is solid; it does not contain fragmentation clefts. When slits are present, they are the result of fusion of two or more polyps in anthocaulus stage (compare fig. 392 with figs. 387, 388 and 390). The coralla are thick; they vary from flat to slightly arched. The length of the central fossa, measured at its bottom, is 1/5 to 2/7 of the corallum length. The septal edges at the sides of the fossa stand upright,



Figs. 394-399. Close-ups of *Heliofungia actiniformis* corals from NW Java, Indonesia. Scale bar: 0.5 cm. Fig. 394. Septa of a coral with relatively sharp dentations (RMNH 16049). Fig. 395. Costae of the same coral. Fig. 396. Septa of the coral in fig. 387 with rounded dentations. Fig. 397. Costae of the coral in fig. 391. Fig. 398. Fenestrate septa of a coral from NW Java (RMNH 16236). Fig. 399. Costae of the coral in fig. 390.

whereas those at its ends diverge away from it. The columella is formed by a mingled mass of loosely packed trabeculae and paliform lobes with the tips pointing upwards. The diameter of the specimens varies between 0.5 and 21.0 cm.

The septa are loosely packed and straight. The septa are of almost equal thickness; in particular high order septa may be perforated. Between two adjacent septal dentations the septa may be fenestrate (fig. 398). The primary septa are more exsert than those of the last orders. Clear tentacular lobes are absent. The septal margins are coarsely ornamented with lobate, rounded dentations (figs. 394, 396, 398). Their number varies from 3 to 5 per cm septum. They are finely granulated at their margin and on their sides, where the granulations are arranged in radial patterns (fig. 396, 648). At the base of the septa, the granulations are evenly distributed. The compound synapticulae connecting the septa laterally can easily be distinguished by the loose septal arrangement (fig. 389).

The corallum wall is solid, although at the corallum margin it may not yet be complete and seem perforated. A detachment scar is distinct at the aboral side of all specimens in anthocyathus-stage (figs. 390-391). The wall is granulated; the costae are covered by distinct rows of granulations perpendicular to the costal margin (fig. 649). The costae are almost equal in size; they are straight and distinct from the centre to the corallum margin (figs. 395, 397, 399). They are finely ornamentated by costal projections (spines) which are laterally flattened with sharp granulations at their margin. The spines are either single and angular-granulate or composed-lobate with several granulations at their tips (fig. 649). Their number varies from 20 to 30 per cm.

The living animal with its long tentacles resembles a sea-anemone (fig. 24). The polyp is usually brown with white knobbed tentacle tips, acrospheres (fig. 393). More occasionally it is brightly green with yellow radial stripes and yellow tentacle tips or greyish violet with pink acrospheres.

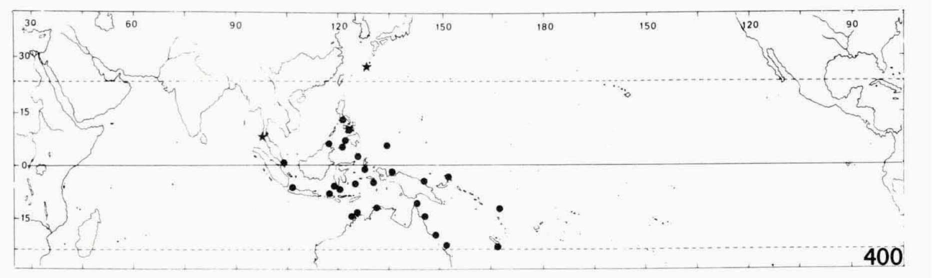


Fig. 400. The range of *Heliofungia actiniformis*. Records are from examined material (●) and published illustrations (★).

Geographical distribution (fig. 400). — The species has a clearly outlined range, which is restricted to the central Indo-Pacific. Along the Indian Ocean it is bordered by the Malayan peninsula, Indonesia and NW Australia. In the Pacific, the species has not been observed eastward from a line which runs from the Ryukyu Islands towards Palau, the Solomons, the New Hebrides and New Caledonia.

Remarks. — The holotype of *Fungia crassitentaculata* does not differ distinctly from that of *F. actiniformis* (both in the MNHN; the latter without an administration number). According to Milne Edwards & Haime (1851) the syntypes of *F. diversidens* were in museums at Bristol and Bowerbank, but whether they are still there is not known. The description leaves no doubt that it concerns *Heliofungia actiniformis*. Although the holotypes of the fossil *Fungia granulicostata* and *Fungia actinodiscus* are heavily damaged, they still do show the typical costae of *H. actiniformis*. Because no characters which distinguish them from the latter species were observed, the three taxa are considered identical.

In *H. actiniformis* the tentacles and the other soft parts of the polyp differ from those of any other fungiid known. The skeleton of this species displays also characters which are unique or rare within the Fungiidae (e.g. the shapes of the septo-costal structures, the presence of a detachment scar). Therefore it is difficult to discern with which other species it is phylogenetically most closely related.

Ctenactis Verrill, 1864

Type species: *Madrepora echinata* Pallas, 1766. By original designation.

Ctenactis Verrill, 1864: 51; Scheer & Pillai, 1983: 85-86.
Fungia (Ctenactis) — Wells, 1966: 238; Veron & Pichon, 1979: 168; Ditlev, 1980: 56; Chevalier & Beauvais, 1987: 706.
Herpetoglossa Wells, 1966: 241-242; Veron & Pichon, 1979: 173; Ditlev, 1980: 57; Chevalier & Beauvais, 1987: 710 (as a subgenus of *Herpolitha*). (Type species: *Herpolitha simplex* Gardiner, 1905 [= *Ctenactis crassa* (Dana, 1846)]. By monotypy).

Characters. — Adult animals are free-living and either mono- or polystomatous. Polystomatism is achieved by intrastomadaeal budding. The outline of juveniles (either anthocauli or anthocyathi) is oval; it is elongate in adult anthocyathi. The corallum wall is granulated and perforated. The septal dentations are coarse and either angular or rounded-lobate. The costal spines are relatively large and echinose.

Remarks. — In the literature, *Ctenactis* was not directly accepted after its establishment by Verrill (1864). The three *Ctenactis* species recognized by

Verrill (1864) were considered to belong to *Fungia* by other authors. Döderlein (1901: 356; 1902: 100) classified these species and some others as the " *Echinata* -Gruppe" within *Fungia*. *Ctenactis* was rehabilitated by Wells (1966), as a subgenus in *Fungia*, including the single species *C. echinata*.

Wells (1966) considered *Herpetoglossa* a separate, monospecific genus of the Fungiidae because of the polystomatous character of the corals. Animals of its single species are sometimes hard to distinguish from *C. echinata* specimens because a considerable part of these (> 10%), usually larger ones, prove to be polystomatous as well.

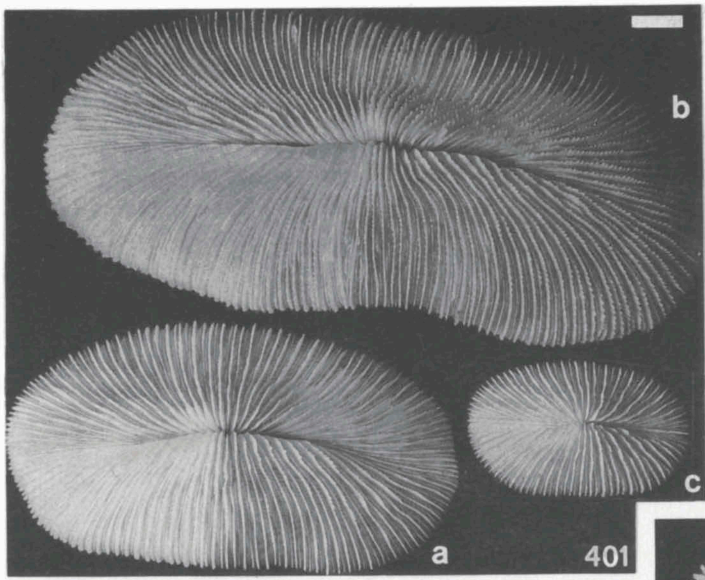
In the present revision, besides the occasionally polystomatous *C. echinata* and the consistently polystomatous *C. crassa* (= *Herpetoglossa simplex*), the almost consistently monostomatous *C. albitentaculata* spec. nov. is recognized. Together the three species constitute a genus which can easily be separated from *Fungia* by a combination of characters: (1) the coralla are more elongate and become much larger and heavier; (2) the septal and costal ornamentations are coarser and more spinose; (3) there exists a clear tendency from monostomatism to polystomatism, in which *C. albitentaculata* and *C. crassa* are the extremes and *C. echinata* an intermediate form. Of these three species *C. albitentaculata* shows most similarities with *Fungia*, by being almost consistently monostomatous, by being the least elongate and by having smaller septal dentations than the other two species.

Ctenactis albitentaculata spec. nov.
(figs. 25, 401-414)

Fungia echinata — Boschma, 1925: 215-216 (partim); Yabe & Sugiyama, 1941: 78 (partim), pl. 71 figs. 1-1d; Faulkner & Chesher, 1979: 287 (partim), pl. 101; Veron, 1986a: 32 (partim); Veron & Marsh, 1988: 84-85 (partim).
Fungia (Ctenactis) echinata — Veron & Pichon, 1979: 169-171 (partim), fig. 283.
Fungia sp. — Laboute & Magnier, 1978: fig. 32.

Type material examined. — RMNH 16098 (holotype of *Ctenactis albitentaculata*; type loc. S coast of Pulau Payung, Kepulauan Seribu [Thousand Islands], NW Java, INDONESIA); RMNH 16095, 16102-16103 (10), (paratypes of *Ctenactis albitentaculata*; Pulau Tikus, Kepulauan Seribu).

Other material. — SINGAPORE: MCZ, YPM 1439, 1736. INDONESIA. Belitung (Billiton): BMNH 1883.7.24.90. NW Java: ZMA 336. SW Sulawesi: RMNH 15704, 16054 (6), 16056-16057, 16062 (2), 16064-16067 (17), 16093-16094 (4), 16096-16097 (3), 16099-16100 (8), 20074 (5), 20083, 20086, 20090, 20832, ZMA 405, 428. Tiger Is.: RMNH 21217 (2). Komodo: RMNH 21466. N Sumbawa: RMNH 21674. NE Sumba: RMNH 20238 (2). W Timor: ZMA 417. Talaud Is.: RMNH 15732. Banda: RMNH 15773. AUSTRALIA. Kimberley: WAM 242.85. N Great Barrier Reef: AIMS 12604. PAPUA NEW GUINEA. Bismarck Sea: ULB. PÁLAU IS.: USNM 47089. MARIANA IS. Guam: USNM 80086. MARSHALL IS.: USNM 77866.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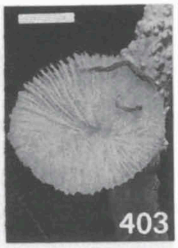
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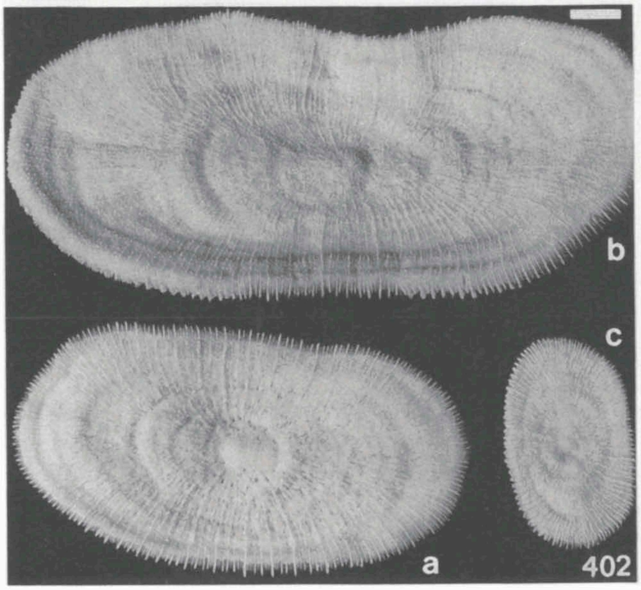
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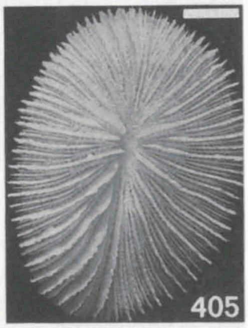
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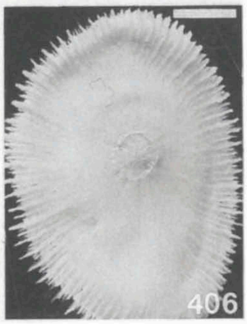
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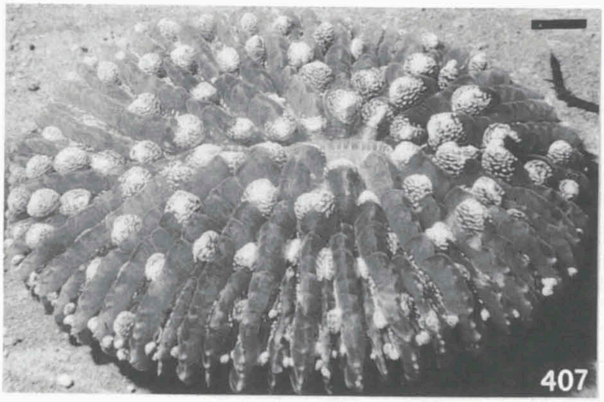
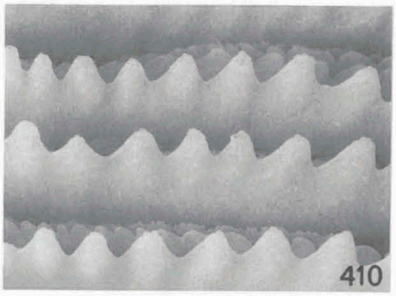
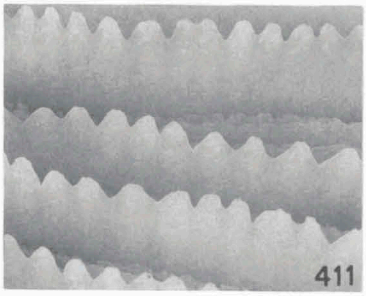
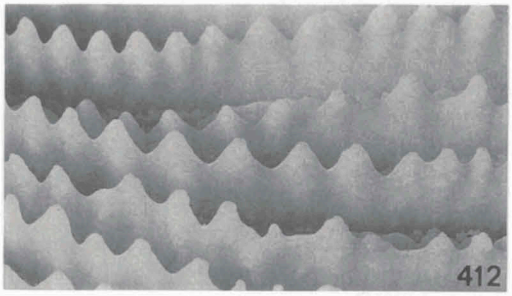
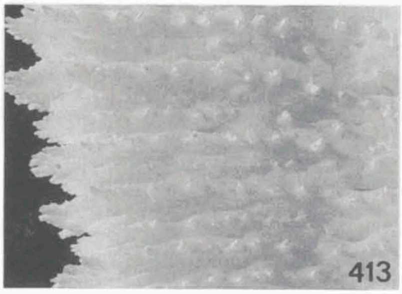
Figs. 401-406. Holotype and paratypes of *Ctenactis albitentaculata* (Kepulauan Seribu, NW Java, Indonesia. Figs. 401-402. Upper and lower surface of three corals: (a) the holotype from Pulau Payung (RMNH 16098) and (b-c) two paratypes from Pulau Tikus (RMNH 16103). Scale bars: 2.5 cm. Figs. 403-404. Upper surface and lateral view of an anthocaulus (RMNH 16103). Scale bars: 1 cm. Figs. 405-406. Upper and lower surface of a recently detached anthocyathus with a distinct detachment scar (RMNH 16103). Scale bars: 1 cm.

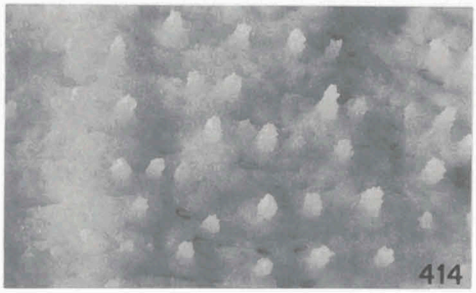












Figs. 407-414. Close-ups of *Ctenactis albitentaculata* corals. Scale bars: 0.5 cm. Fig. 407. A living immature anthocyathus showing white tentacles (coral in fig. 405). Fig. 408. Septa of the juvenile in fig. 401c. Fig. 409. Septal arrangement of the holotype in fig. 401a from above. Fig. 410. Septa of the coral in fig. 401b. Fig. 411. Septa of the holotype (fig. 401a). Fig. 412. Septa of the coral in fig. 401b. Fig. 413. Costae of the juvenile in fig. 402c. Fig. 414. Costae of the holotype (fig. 402a).

Characters. — Adult animals are unattached and practically always monostomatous (very few have two mouths instead of one; less than 1 %, n > 200). The corallum outline varies from oval to elongate with rounded ends. There are no fragmentation clefts in the corallum margin. The coralla are thick and vary from flat to slightly arched. The length of the central fossa, measured at its bottom, is 1/8 to 1/5 of the corallum length. The columella is formed by a mingled mass of loosely packed, partly fused trabeculae and paliform lobes with the tips pointing in various directions. The septal edges along the central groove stand upright, whereas those at its ends diverge strongly away from it. The length of the specimens varies between 3.0 and 40.0 cm.

The septa are relatively loosely packed and either straight or slightly bending (fig. 409). The septa of lower orders are solid, whereas those of higher orders are perforated. Septa of lowest orders are higher and thicker than those of highest orders. Tentacular lobes are absent. The septal margins are coarsely ornamented with long dentations which taper towards their tips and are either slightly rounded or pointed (figs. 408-412). Some of them may be partly fused in pairs (figs. 411-412). Their number varies from 7 to 12 per cm. The septal sides are thinly granulated. The granulations are coarse and indistinctly arranged in rows which are either more or less perpendicular (fig. 408: a relatively small specimen) or parallel (figs. 410-412: relatively large specimens) to the septal margin. The compound synapticulae connecting the septa laterally can easily be detected, because of the relatively loose septal arrangement.

The corallum wall is perforated and covered by granulations. A detachment scar is distinct at the aboral side of small specimens in anthocyathus-stage. The costae are unequal in size; they are straight and distinct near the corallum margin, whereas they are less distinct near the centre. All costae are coarsely ornamented with slightly echinose spines which are either short and blunt or elongate (figs. 413-414). Their number varies from 7 to 11 per cm.

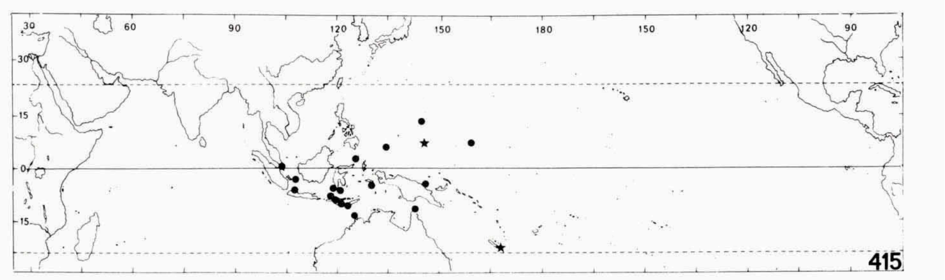


Fig. 415. The range of *Ctenactis albitentaculata*. Records are from examined material (●) and published illustrations (★).

The living animal is usually brown and can easily be recognized because of its distinct white tentacles which already show up in small specimens (figs. 25, 407).

Geographical distribution (fig. 415). — The species occurs from the Indo-Malayan region and NW Australia towards Palau, Guam, the Caroline Islands, the Marshall Islands and New Caledonia.

Remarks. — Specimens have been collected and photographed at several locations (see the literature mentioned above), but have not been recognized as belonging to a still undescribed species. However, the consistently white tentacles, which make the species easily recognizable in the field, are not the only character distinguishing it from other species. These additional characters concern mainly the skeleton, i.e. the tapering septal dentations, the relatively loose septal arrangement and a relative wide appearance (the length/width ratio of the coralla seems small). Apparently few coral taxonomists have studied Fungiidae in the field and because of its relatively rare occurrence the species is difficult to notice (Hoeksema & Moka, 1989).

Specimens of this species may resemble the syntypes of *C. echinata* f. *gigantea*, but the latter have larger septal dentations and a denser septal arrangement. The species can further be distinguished from *C. echinata*, its closest ally, by: (1) its tentacles, which are white instead of colourless; (2) the septal dentations are sharper; (3) it has almost always one stoma; (4) the animals are less elongate.

Etymology. — The epithet "albitentaculata" indicates that the species has white tentacles.

Ctenactis echinata (Pallas, 1766)
(figs. 26, 416-428, 650-651)

Madrepora echinata Pallas, 1766: 284 ("Oceanus Indicus"); Boddaert, 1768: 352-353; Wilkens, 1787: 25. Not: Esper, 1791.

Fungia limacina — Lamarck, 1815, 1816: 237 (partim, including var. *lobata subfurcata* Lamarck, 1815); Blainville, 1830: 303 (partim), pl. 34 figs. 3-3a; 1834: 337 (partim), pl. 51 figs. 3-3a.

Fongia limacina — Blainville, 1820: 216 (partim).

Fungia pectinata Ehrenberg, 1834: 50 (Red Sea); Leuckart, 1841: 49; Dana, 1846: 302.

Haliglossa echinata — Ehrenberg, 1834: 50-51 (partim); Klunzinger, 1879: 67; Studer, 1880: 45.

Herpetolithas ehrenbergii Leuckart, 1841: 52-54, pl. 2 figs. 1-3 (Red Sea).

Herpetolithas ruepellii Leuckart, 1841: 54-55, pl. 1 figs. 1-3; Dana, 1846: 304 (Indian Ocean).

Fungia ehrenbergii — Dana, 1846: 303, pl. 19 fig. 11 (including var. *gigantea* Dana, 1846 ["the Feejees"]); Milne Edwards & Haime, 1851: 83-84; 1860: 14; Verril, 1864: 51; Studer, 1877: 647; Ortmann, 1888: 178; 1889: 521; Gardiner, 1899b: 168.

Fungia gigantea Dana, 1846, pl. 19 fig. 12 ("the Feejees"); Milne Edwards & Haime, 1860: 15 (New synonymy).

Fungia asperata Dana, 1846: 303-304, pl. 19 fig. 14 (Red Sea).

Fungia echinata — Milne Edwards, 1836-1849: pl. 82 fig. 2; 1851: 84-85; 1860: 15; Studer, 1877: 648; Duncan, 1883: 149-152, pl. 5 figs. 1-2; 1886: 15; Studer, 1901: 405; Döderlein, 1902: 101-105, pl. 10 figs. 1-5 (including var. *parvispina* Döderlein, 1902 [Red Sea]; var. *undulata* Döderlein, 1902 [New Ireland]); Bedot, 1907: 218; Gravier, 1907: 342; Von Marenzeller, 1907: 89; Vaughan, 1907a: 134, pls. 36-37; 1907b: 261; Gardiner, 1909: 274 (partim); Gravier, 1911: 62; Van der Horst, 1921: 10-11; Gerth, 1923: 101; Matthai, 1923: 78; 1924: 42-43 (partim); Boschma, 1925: 215-216 (partim), pl. 7 figs. 66-67, 71-72, pl. 10 fig. 126; Umbgrove, 1926: 42; Faustino, 1927: 176, pls. 51-52; Thiel, 1932: 67-69 (partim); Boschma, 1934: 4201-4202, fig. 3; Yabe & Sugiyama, 1935: 396; Ma, 1937: 134-135, pl. 68 figs. 1-2, pl. 69 figs. 1-2; Abe, 1938: 481-482, figs. 1c, 6; Eguchi, 1938: 361; Umbgrove, 1939: 43; 1940: 290-291; Yabe & Sugiyama, 1941: 78 (partim), pl. 70 figs. 1-2d, pl. 71 figs. 3-3a, pl. 72 figs. 1-1c; Vaughan & Wells, 1943: pl. 17 fig. 11; Umbgrove, 1946a: 91; 1946b: 533-534; Crossland, 1952: 152; Wells, 1954: 448; Stephenson & Wells, 1955: 25; Nemenzo, 1955: 59-60, pl. 10 figs. 3-4; Purchon, 1956: 157; Searle, 1956: 17, pl. 17A; Wells & Davies, 1966: 48; Scheer, 1967: 428; Loya & Slobodkin, 1971: 123; Pillai, 1972: 203; Sukarno, 1974: 14; Zou, Song & Ma, 1975: 29, pl. 1 fig. 10, pl. 8 fig. 4; Pillai & Scheer, 1976: 43; Coleman, 1977: 61; Zou, 1978: 100; Green, Harris, Robertson & Santavy, 1979: 298; Shirai, 1980: 531; Betterton, 1981: 204, pl. 82; Nemenzo, 1981: 188, fig. 204; Lamberts, 1983: 8; Pillai, 1983: 86; Zou & Chen, 1983: 91; Werner, 1984: pl. 3; Schuhmacher & Mergner, 1985: 428; Johnston, 1986: 159; Nakamori, 1986: pl. 13 figs. 7-7a; Nemenzo, 1986: 143, fig. 164; Veron, 1986a: 32 (partim); Veron & Marsh, 1988: 84-85 (partim). Not: Dana, 1846.

Ctenactis echinata — Verrill, 1864: 51; Scheer & Pillai, 1983: 86-87 (partim), pl. 20 fig. 9.

Ctenactis ehrenbergii — Verrill, 1864: 51.

Ctenactis gigantea — Verrill, 1864: 51.

Haliglossa pectinata — Klunzinger, 1879: 66-67; Studer, 1880: 45-46.

Fungia (Ctenactis) echinata — Scheer & Pillai, 1974: 37; Ditlev, 1976: 6; Faulkner & Chesher, 1979: 287 (partim); Veron & Pichon, 1979: 169-171 (partim), figs. 284-289; Ditlev, 1980: 56, figs. 42, 233; Randall & Myers, 1983: 18, figs. 95, 350-351; Veron, 1986b: 346; Sakai & Yamazato, 1987: 46; Wood & Tan, 1987: 197; Veron & Kelley, 1988: 29, 32, fig. 10d.

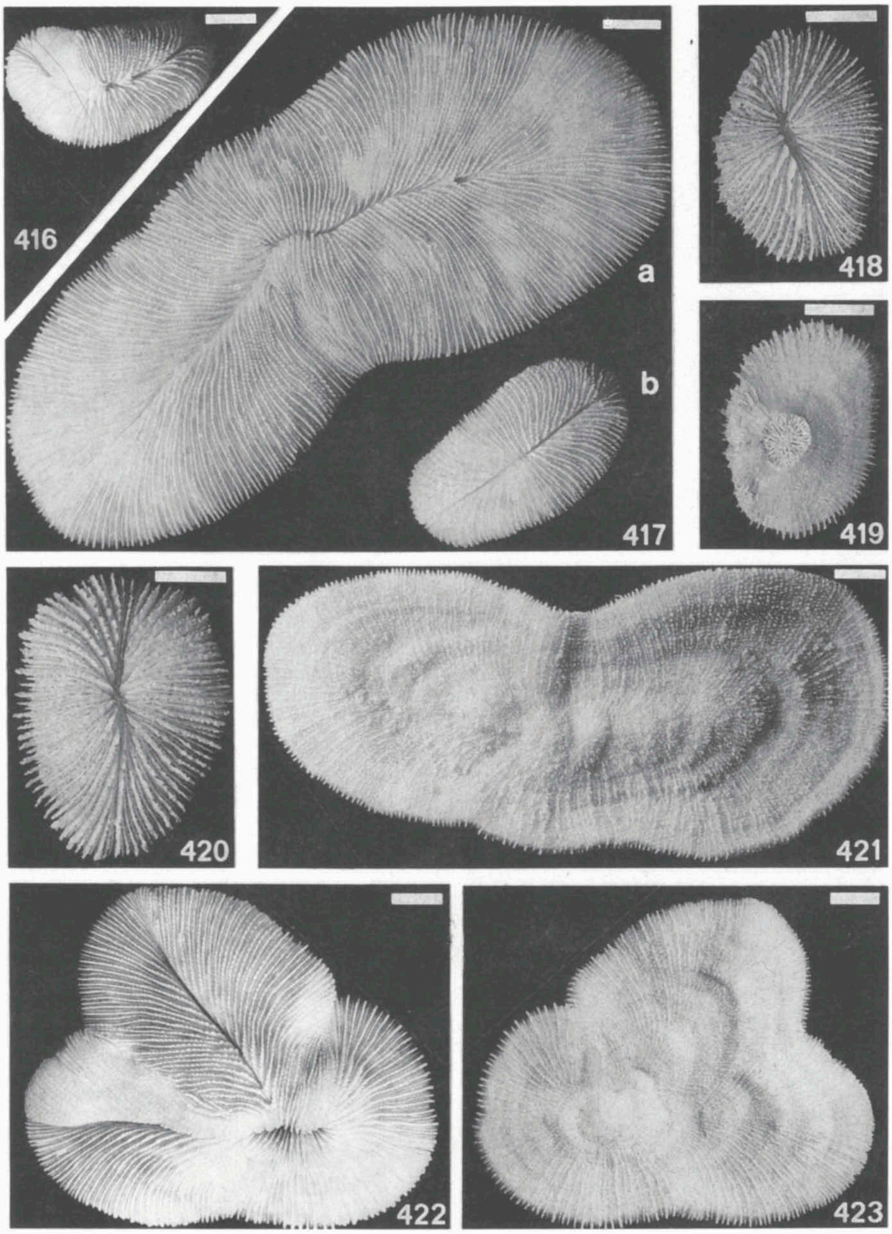
Fungia scutaria — Utinomi, 1975: 71.

Fungia paumotensis — Zou, Song & Ma, 1975: 30-31, pl. 13 fig. 5, pl. 15 fig. 9.

Zoopilus echinatus — Wood, 1983: 130, 145 (partim).

Type material examined. — RMNH 16083 (neotype [present designation] of *Madrepora echinata*; type loc. Pulau Seribu, NW Java, INDONESIA); MCZ 526, 5284, MNHN Fun219, YPM 1952 (syntypes of *Fungia gigantea*, FIJI); USNM 141, YPM 1951 (syntypes of *Fungia gigantea*, EAST INDIES).

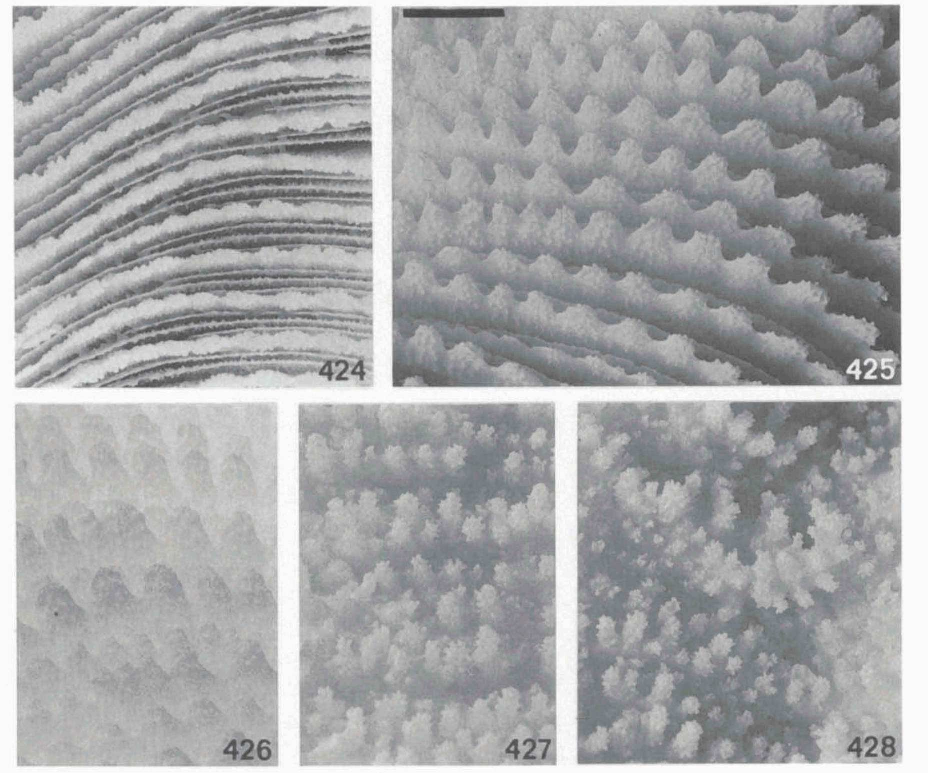
Other material. — RED SEA: BMNH 1898.8.1.27, 1937.11.17.398/1051, 1950.1.11.322, RMNH 9431-9432, 9434, USNM 77741 (2). Gulf of Aqaba: BMNH 1961.5.16.15. RMNH 13871-13872, 13874. Jeddah: RMNH 9433. DJIBOUTI: MNHN 3517-3518, Fun286. SINGAPORE: MCZ 30-31, ZMA 427. MALAYSIA. Malaya: BMNH 1979.4.24.99. Sabah: USNM 47948, 47957. PHILIPPINES: BMNH 1923.12.7.1. Cebu: UPMSI 245, UPZD 532. Bohol: UPZD 553. INDONESIA: Belitung (Billiton): ZMA 432. Java: RGM 77747 (fossil). NW Java: RMNH 9314, 15779 (2), 16082-16092 (12), USNM 77758 (2). SW Sulawesi: RMNH 9439, 10794, 15705-15707, 15738, 20166, 20169 (4), 20172 (10), 20885 (2), 20960, ZMA 405. Togian Is.: RMNH 9440-9441, 9443-9444. N Sumbawa: RMNH 20476. W Flores: PPPO 1145. W Timor: ZMA 421. Kera: RMNH 14452 (2). Tukang Besi Is.: RMNH 20041. Moluccas: RMNH 9428 (3), 9435-9438, ZMA 416, 429. Ambon: BMNH 1946.1.1.10, RMNH 8363 (4), 8372, 9429, ZMA 425. Obi: RMNH 15736, USNM 78329. Banda: RMNH 8364, USNM 78331, 78335 (2). Tanimber Is.: RMNH 15737. Biak: RMNH 15777. PAPUA NEW GUINEA. Bismarck Sea: ULB. PALAU IS.: USNM 78012 (2), 78024, 78032-78036 (7), 78040 (3), 78294. AUSTRALIA. Pilbara: WAM 529.81. Torres Str.: MCZ 5290-5291 (4). N Great Barrier Reef: QMB G2861, G8049, G8187, GBR293, GBR338.



Figs. 416-423. Corals (anthocyathi) of *Ctenactis echinata* from NW Java, Indonesia. Fig. 416. A small polystomatous coral (RMNH 16088). Scale bar: 2.5 cm. Fig. 417. Upper surface of: (a) a large polystomatous coral and (b) a small monostomatous one (both RMNH 16092). Scale bar: 2.5 cm. Figs. 418-419. A small anthocyathus with a distinct detachment scar (RMNH 16085). Scale bars: 1 cm. Fig. 420. A small anthocyathus (RMNH 16089). Scale bar: 1 cm. Fig. 421. Aboral surface of the coral in fig. 417a. Scale bar: 2.5 cm. Figs. 422-423. Upper and lower surface of two fused individuals (RMNH 16082). Scale bars: 2.5 cm.

C Great Barrier Reef: BMNH 1879.3.9.132, MCZ 5292, QMB G2857-2860, G6716, G7627, GBR287, GBR303, GBR344-345, GL3644, USNM 78344. SOLOMON IS.: BMNH 1884.12.11.5, 1938.3.17.5. Bougainville I.: AMNH. NEW CALEDONIA: MNHN 1773, 1834, USNM 78069, 78285, ZMA 6261, 6265, 6273. FIJI IS.: MCZ 524. SOCIETY IS.: MNHN.

Characters. — Adult animals are free-living. They are usually monostomatous, although more than ten percent of the individuals (n > 200) produce supernumerary mouths by intrastomadaeal budding (figs. 416, 417a). The outline of the coralla varies from oval to elongate with ends which vary between tapering and rounded. There are no fragmentation clefts in the corallum wall. The coralla are thick and vary from flat to highly arched. The length of the central fossa or groove, measured at its bottom, is 1/5 to 1/2 of the corallum length. The septal edges along the sides of the groove stand upright whereas those at its ends diverge away from it. The columella is formed by a mingled mass of loosely to tightly packed, sometimes strongly fused trabeculae and paliform lobes with their tips pointing in various directions. The length of



Figs. 424-428. Close-ups of *Ctenactis echinata* corals from NW Java, Indonesia. Scale bar: 0.5 cm. Fig. 424. Septal arrangement of the coral in fig. 417a from above. Figs. 425-426. Septa of the coral in fig. 422. Figs. 427-428. Costae of the coral in fig. 423.

the specimens varies between 2.5 and 44.0 cm.

The septa are densely packed and either straight or slightly bending (fig. 424). The septa of low order cycles are thick and solid, those of higher orders thin and usually perforated. Those of the lowest orders are more protruding than those of higher orders. Tentacular lobes are absent. The septal margins are coarsely ornamented with irregularly rounded or lobate dentations (figs. 425-426). In the smallest specimens they are usually more acute or frayish. Their number varies from 4 to 8 per cm. The septal sides are thinly granulated. The granulations are coarse and more or less evenly distributed (figs. 425-426, 650). The compound synapticulae connecting the septa laterally can easily be detected in spite of the tight septal arrangement.

The corallum wall is perforated and covered by granulations. A detachment scar is distinct at the aboral side of small specimens in early anthocyathus stage (fig. 419). The costae are unequal in size; they are more or less straight and distinct from near the centre towards the corallum margin. All costae are coarsely ornamented with spines which vary from long and echinose to short and coarsely granulated (figs. 427-428, 651). Their number varies from 7 to 12 per cm.

The living animal is usually brown, sometimes with patches of lighter colour (fig. 26). The small tentacles are transparent and colourless.

Geographical distribution (fig. 429). — In the Indian Ocean, specimens have been collected only in the northern part (Red Sea and the Maldives) and in Western Australia (southern limit: Ningaloo Reefs). In the Pacific, the area extends from the Indo-Malayan region towards Japan and the Society Islands with, as southernmost location, New Caledonia.

Remarks. — Pallas (1766) refers to two illustrations in the description of his species. He undeniably was not convinced about the identity of the specimen illustrated by Rumphius (1750, pl. 88 fig. 2), because he added a question mark. (This specimen belongs to the species currently known as *Polyphyllia*

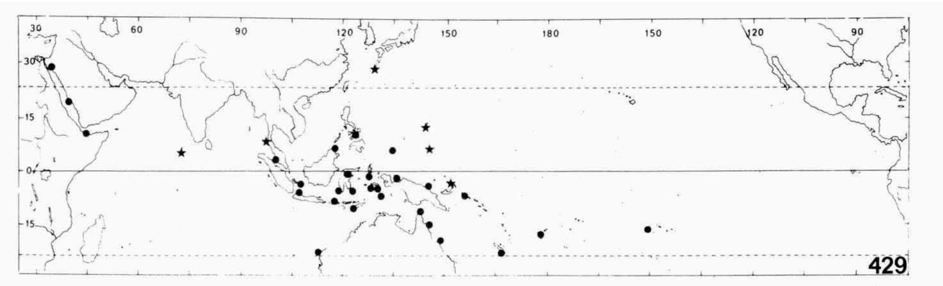


Fig. 429. The range of *Ctenactis echinata*. Records are from examined material (●) and published illustrations (★).

talpina). However, Pallas (1766) was sure that the identity of the coral illustrated by Seba (1759, pl.111 fig. 4) was a specimen belonging to the species he described as *Madrepora echinata*. Because this specimen cannot be traced, and because the illustration given by Seba is not clear enough to show to which *Ctenactis* species it actually belongs, a neotype from Indonesia is designated.

The type specimens of *Fungia pectinata*, *Herpolithus ehrenbergii* and *H. ruepelii* were originally reported to be kept in the ZMB. They may have already been lost for a long time as they would probably have been mentioned by Döderlein (1902) if they were available to him. According to Dana (1846), the holotype of *Fungia asperata* should be in the ANSP collection but it is no longer there.

Veron & Pichon (1979) stated that *C. echinata* has rarely more than one stoma, whereas in the present study much more than ten percent (n > 200) of the specimens prove to have secondary stomata. *C. echinata* can be distinguished from *C. crassa*, a consistently polystomatous species, by its less compact septal arrangement and by its rounder septal dentations.

Ctenactis crassa (Dana, 1846)
(figs. 27, 430-440)

Haliglossa echinata — Ehrenberg, 1834: 51 (including: ? var. *polystoma* Ehrenberg, 1834 [Red Sea]; ? var. *platystoma* Ehrenberg, 1834 [Red Sea]).

Fungia crassa Dana, 1846: 304-305, pl. 19 fig. 13 ("Feejee Islands"); Milne Edwards & Haime, 1860: 15; Duncan, 1886: 15.

Ctenactis crassa — Verrill, 1864: 51.

Herpolitha simplex Gardiner, 1905: 943, pl. 91 fig. 13 (S Nilandu, Maldives); Folkeson, 1919: 17; Boschma, 1925: 223-226, pl. 7 figs. 68-70; Nemenzo, 1955: 76-77, pl. 14 figs. 2, 4; Pillai, 1972: 203; Nemenzo, 1981: 228, fig. 227; 1986: 155, fig. 181. (New synonymy).

Fungia simplex — Gardiner, 1909: 274; Matthai, 1924: 44; Veron, 1986a: 32; Veron & Marsh, 1988: 85.

Fungia proechinata — Van der Horst, 1921: 62.

Fungia echinata — Matthai, 1924: 42-43 (partim), pl. 8 fig. 8; Thiel, 1932: 67-69 (partim), pl. 10 fig. 1; Yabe & Sugiyama, 1941: 78 (partim), pl. 71 figs. 2-2c, pl. 72 figs. 2-2d; Veron, 1986a: 32 (partim); Veron & Marsh, 1988: 84-85 (partim).

Fungia brachystoma Thiel, 1932: 65-67, pl. 8 fig. 5 ("Zwischen Banda-Neira und Goenoeng Api"). (New synonymy).

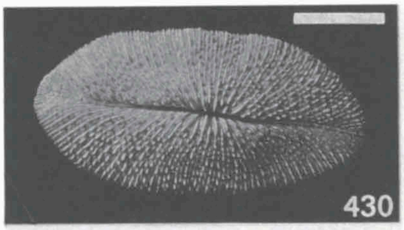
Herpetoglossa simplex — Wells, 1966: 241; Ditlev, 1976: 7; Veron & Pichon, 1979: 173-176, figs. 290-293; Ditlev, 1980: 57, fig. 239; Wood, 1983: 119.

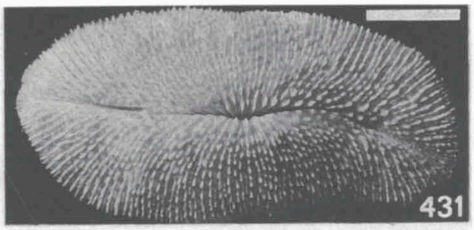
Ctenactis echinata — Scheer & Pillai, 1983: 86-87 (partim), pl. 20 figs. 6-8.

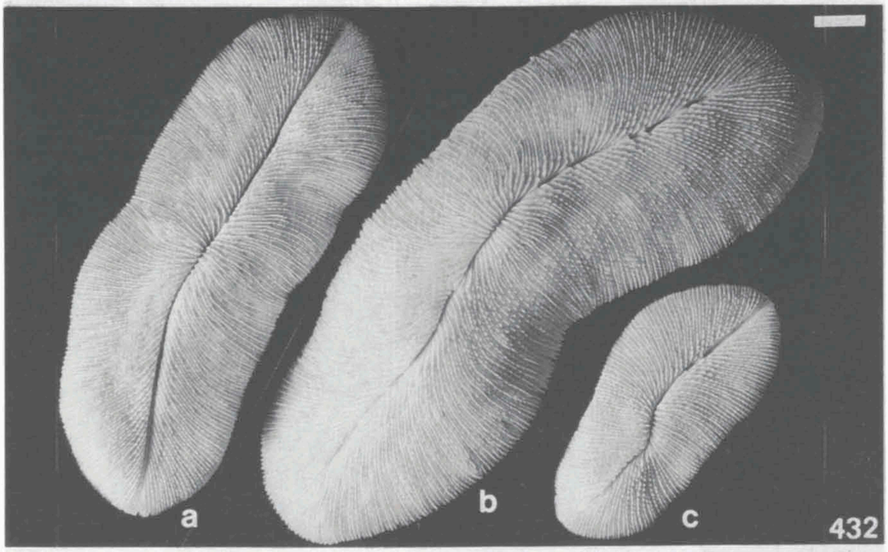
Fungia (Ctenactis) simplex — Veron, 1986b: 347.

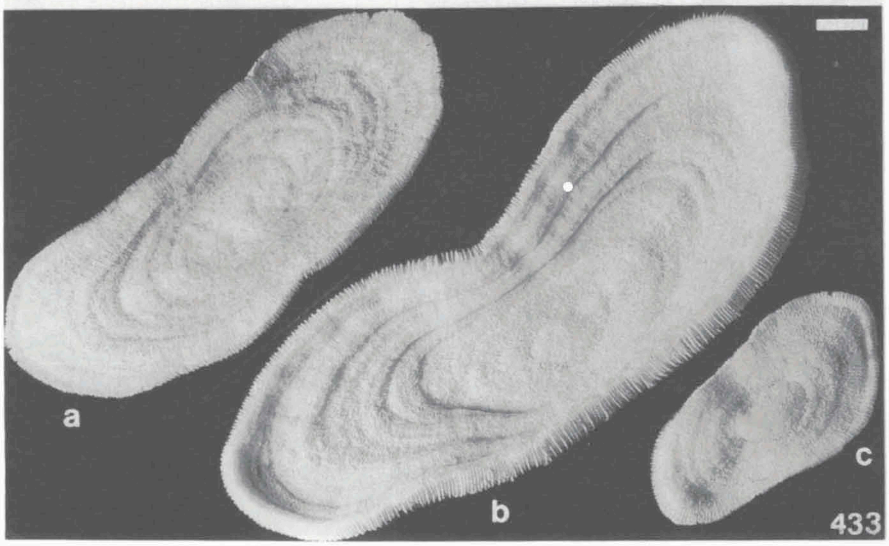
Type material examined. — USNM 139 (holotype of *Fungia crassa*; type loc. FIJI); UMZC (holotype of *Herpolitha simplex*; type loc. S Nilandu, MALDIVES); IRSNB/KBIN IG9223 (holotype of *Fungia brachystoma*; type loc. Banda, INDONESIA).

Other material. — RED SEA: BMNH 1886.10.5.1, 1937.11.17.410/418/1049, MNHN 491,









Figs. 430-433. Corals (anthocyathi) of *Ctenactis crassa* from Indonesia. Scale bars: 2.5 cm. Fig. 430. A small anthocyathus (RMNH 8389; Banda) with a single fossa. Fig. 431. A small polystomatous coral (RMNH 8391; Banda). Figs. 432-433. Upper and lower surface of three large polystomatous corals (NW Java): (a) RMNH 16055, (b) RMNH 16053, (c) RMNH 16080.

ZMA 418. DJIBOUTI: USNM 21980. MALDIVES: USNM 78287. COCOS (KEELING) I.: USNM 75153. PHILIPPINES: UPMSI. INDONESIA. Belitung (Billiton): BMNH 1884.7.24.84. NW Java: RMNH 16053, 16055 (3), 16080. SW Sulawesi: PPPO 1193, RMNH 20000 (3), 20006 (4), 20012 (2), 20033 (9), 20035, 20061 (8), 20071, 20175 (2), 20189 (2), 20199 (2), 20833 (3), 20852 (2). Tiger Is.: RMNH 20621, 21076 (3), 21171. N Sumbawa: RMNH 20809, 21620 (2). W Timor: ZMA 444, 538. Tukang Besi Is.: RMNH 20042. Banda: RMNH 8389-8392. PALAU IS.: USNM 47083. PAPUA NEW GUINEA. Bismarck Sea: ULB. SOLOMON IS.: BMNH 1938.3.1.20. AUSTRALIA. Kimberley: WAM 164.77, 202.85, 868.81. N Great Barrier Reef: QMB GL3635. C Great Barrier Reef: BMNH 1897.3.9.142/160, QMB G2048, GL3632. NEW CALEDONIA: ZMA 6266. CAROLINE IS.: USNM 77796, 78350. MARSHALL IS.: RMNH 14617, 14622, USNM 77865. SOCIETY IS.: MNHN.

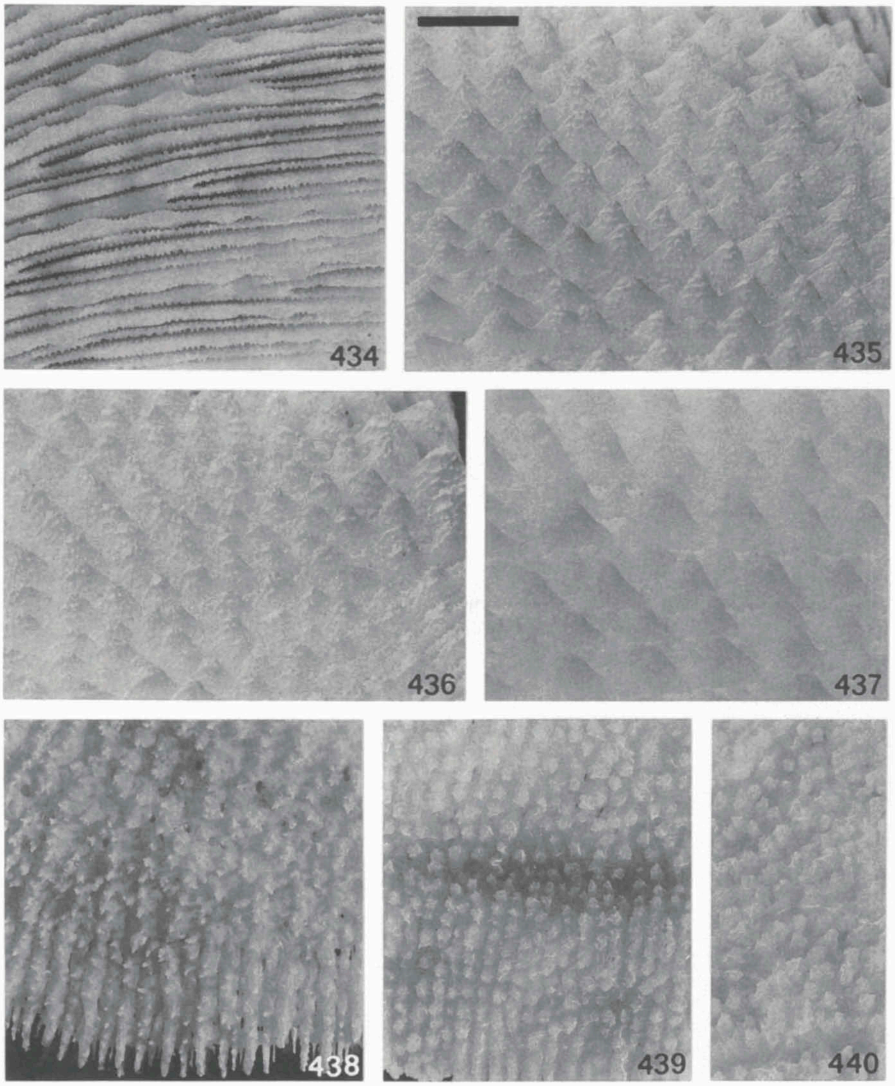
Characters. — Adult animals are free-living. Juvenile specimens have a single mouth. After detachment the polyps become polystomatous by intrastomadaeal budding inside the axial groove. The outline of the corals is elongate with the ends varying between tapering and rounded. There are no fragmentation clefts in the corallum wall. The coralla are thick and vary from flat to highly arched. The length of the central fossa (or axial groove), measured at its bottom, is 1/4 to 2/3 of the corallum length. The columella is formed by a mingled mass of loosely packed trabeculae and paliform lobes with their tips pointing in various directions. The length of the specimens varies between 3.5 and 48.0 cm.

The septa are very densely packed and straight (fig. 434). The septa of lower orders are thick and solid, those of higher orders thin and perforated. The septa of the first orders are slightly more protruding than those of the last orders. Tentacular lobes are absent. The septal margins are coarsely ornamented with irregularly angular dentations (figs. 435-437). Their number varies from 2 to 8 per cm. The septal sides are thinly granulated. The granulations are coarse and evenly distributed. At the tips of the dentations they may partly fuse into ridges, parallel to the septal margin. The compound synapticulae connecting the septa laterally cannot easily be distinguished, because of the tight septal arrangement.

The corallum wall is perforated and covered with granulations. A distinct detachment scar may be observed at the aboral side of small specimen in early anthocyathus-phase. The costae are almost equal in size; they are straight and distinct near the corallum margin, but less distinct near the centre. All costae are coarsely ornamented with spines which vary from blunt and granular at the tips to spinose (figs. 438-440). Their number varies from 5 to 18 per cm.

The colour of the living animal usually varies between brown and ochre. Juvenile specimens are usually ochre with a pink outline (fig. 27). The inconspicuous tentacles are transparent and colourless.

Geographical distribution (fig. 441). — In the Indian Ocean, the species has been collected in the Red Sea, the Maldives and Cocos-Keeling. In the Pacific



Figs. 434-440. Close-ups of *Ctenactis crassa* corals from NW Java, Indonesia. Scale bar: 0.5 cm. Fig. 434. Septal arrangement of the coral in fig. 432b. Fig. 435. Septa of the coral in fig. 432a. Fig. 436. Septa of the coral in fig. 432c. Fig. 437. Septa of the coral in fig. 432b. Fig. 438. Costae of the coral in fig. 433c. Figs. 439-440. Costae of the coral in fig. 433b.

the distribution extends from the Indo-Malayan region towards southern Japan, the Marshall Islands and the Society Islands. The southernmost locations known are eastern Australia and New Caledonia.

Remarks. — In the literature, the name *Fungia crassa* Dana, 1846, has been

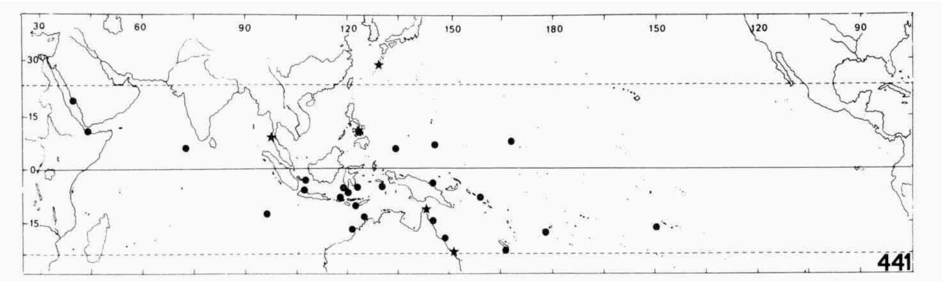


Fig. 441. The range of *Ctenactis crassa*. Records are from examined material (●) and published illustrations (★).

overlooked since 1886. The junior synonym *Herpolitha simplex* Gardiner, 1905, although currently in use, has not been cited frequently enough for preservation and therefore, in the present revision, the name *crassa* has to be introduced again. Its classification in *Ctenactis* was previously only done by Verrill (1864) when he established *Ctenactis* as a new genus.

The holotype of *Fungia brachystoma* is a juvenile anthocyathus with a single mouth which can be distinguished from small specimens of *C. echinata* by its angular septal dentations and its compact septal arrangement.

C. crassa can be distinguished from *C. echinata*, its closest ally, by several characters: (1) its septa are more densely packed; (2) its septal dentations are larger and more angular; (3) the adults are polystomatous.

Herpolitha Eschscholtz, 1825

Type species: *Herpolitha limacina* (Lamarck) (= *Madrepora limax* Esper, 1797). Designated by Milne Edwards & Haime, 1850.

Herpolitha Eschscholtz, 1825: 746 (partim); Milne Edwards & Haime, 1850: xlvii; Klunzinger, 1879: 67; Duncan, 1885: 145; Gardiner, 1905: 943 (partim); Gardiner, 1909: 282-284; Boschma, 1925: 222-223; Vaughan & Wells, 1943: 142; Wells, 1956: 389; Wells, 1966: 240; Veron & Pichon, 1979: 176, 178; Ditlev, 1980: 58; Nemenzo, 1981: 200; Scheer & Pillai, 1983: 87; Nemenzo, 1986: 154; Veron, 1986b: 348-349; Chevalier & Beauvais, 1987: 710.

Haliglossa Ehrenberg, 1834: 50; Klunzinger, 1879: 65-66. (Type species: *Madrepora limax* Esper, 1797 [designated by Wells, 1986]).

Herpetolithus Leuckart, 1841: 51-52 (partim); Dana, 1846: 306-307; Milne Edwards & Haime, 1849: 71. (Intentional change of spelling).

Herpetolitha Milne Edwards & Haime, 1851: 93; 1860: 23-24; Quelch, 1886: 143; Ortmann, 1889: 518; Vaughan, 1918: 129; Matthai, 1924: 47. (Intentional change of spelling).

Characters. — Adult animals are free-living. They are polystomatous by intra- and circumstomadaeal budding. The outline of the corals is elongate. The corals vary from flat to arched. The corallum wall is perforated and not covered by granulations. The septal and costal ornamentations are fine. The granulations on the septal sides are arranged in rows perpendicular to the septal margins.

Remarks. — In the present revision one species is recognized as belonging to *Herpolitha*. The septal and costal ornamentations of *Herpolitha* resemble those of *Fungia (Lobactis)*. In overall shape, *Herpolitha* most closely resembles *Polyphyllia*, except that the latter has more stomata, which are more evenly distributed over the coral upper surface.

Herpolitha limax Esper, 1797
(figs. 28, 442-459, 652-653)

Madrepora pileus — Pallas, 1766: 354 (partim); Boddaert, 1768: 353-356 (partim); Ellis & Solander, 1786: 159, pl. 45; Wilkens, 1787: 26-30 (partim), pl. 13 fig. 48; Gmelin, 1791: 3758 (partim); Esper, 1797: 90-91, pl. 73.

Madrepora trilinguis Boddaert, 1768: 613-614, pl. 14 (no locality given). (New synonymy).

Madrepora talpa Houttuyn, 1772: 116-117 (partim; no locality given); Müller, 1775: 677. (New synonymy).

Madrepora limax — Müller, 1775: 678 (partim), pl. 20 fig. 4.

Madrepora limax Esper, 1797: 77-79, pl. 63 ("Oceano Indiae orientalis").
Not *Madrepora limax* Houttuyn, 1772.

Fungia limacina Lamarck, 1801: 370; 1815, 1816: 237 (partim); Lamouroux, 1821: 52-53, pl. 45; Blainville, 1830: 303 (partim); Stutchbury, 1833: 496-497; Blainville, 1834: 337 (partim); Lamarck, 1836: 373.

Fongia limacina — Blainville, 1820: 216 (partim).

Fungia limax — Oken, 1815: 74.

Herpolitha limax — Eschscholtz, 1825: 746; Duncan, 1886: 16; Gardiner, 1909: 284-286, pl. 38 figs. 20-23, pl. 39 figs. 24-25; Van der Horst, 1921: 15-16; Boschma, 1925: 227-231, pl. 8 figs. 78-85, pl. 9 fig. 117; Faustino, 1927: 195-196, pl. 64 figs. 1-2; Boschma, 1929: 46; Boschma, 1934: 4202-4203, fig. 4; Crossland, 1935: 501; Ma, 1937: 146-148, pl. 73 figs. 1-2, pl. 74 figs. 1-2; Umbgrove, 1939: 45; Yabe & Sugiyama, 1941: 80, pls. 79-80; Crossland, 1952: 154-155; Wells, 1954: 449, pl. 62 figs. 3-4; Nemenzo, 1955: 75-76, pl. 14 fig. 3; Stephenson & Wells, 1955: 27; Purchon, 1956: 157; Searle, 1956: 17, pl. 17B; Loya & Slobodkin, 1971: 123; Rosen, 1971a: 76; Pillai, 1972: 203; Maragos, 1974: 248; Pichon, 1974: 176; Scheer & Pillai, 1974: 39; Sukarno, 1974: 14; Ditlev, 1976: 7; Pillai & Scheer, 1976: 45; Faure, 1977: 10; Maragos & Jokiel, 1978: 61; Zou, 1978: 101; Chèvalier, 1979: 132; Rosen, 1979a: 12; Veron & Pichon, 1979: 178-180, figs. 294-299; Chevalier, 1980: 65; Ditlev, 1980: 58, figs. 44, 240-241; Shirai, 1980: 533; Wijsman-Best, Faure & Pichon, 1980: 612; Betterton, 1981: 205, pl. 88; Boshoff, 1981: 22; Nemenzo, 1981: 201, fig. 226; Faure, 1982: 104-105; Lamberts, 1983: 9; Pillai, 1983: 86; Scheer & Pillai, 1983: 87, pl. 21 fig. 1; Randall & Myers, 1983: 20, figs. 98, 354-355; Wood, 1983: 119, 122, 144; Hamilton & Brakel, 1984: 252; Wallace, 1984: 38, fig. 22.6; Schuhmacher & Mergner, 1985: 428; Johnston, 1986: 159; Nakamori, 1986: pl. 14 fig. 3; Nemenzo, 1986: 155, fig. 180; Veron, 1986a: 32; 1986b: 350-351; Sakai & Yamazato, 1987: 46; Wood & Tan, 1987: 197; Veron & Kelley, 1988: 29, 32, 34; Veron & Marsh, 1988: 85.

Haliglossa limacina — Ehrenberg, 1834: 51.

Haliglossa interrupta Ehrenberg, 1834: 51 (Red Sea).

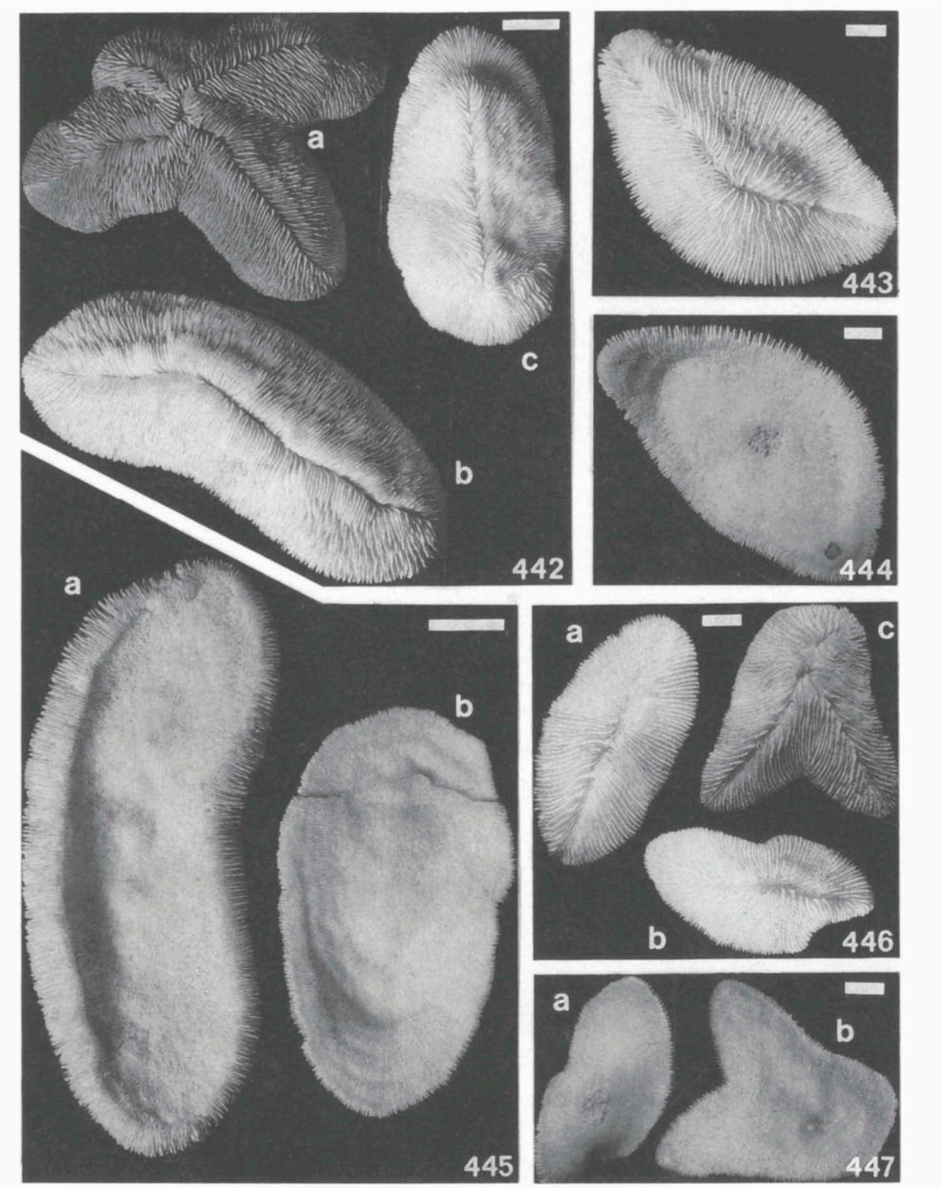
Haliglossa foliosa Ehrenberg, 1834: 51 (Red Sea).

Haliglossa stellaris Ehrenberg, 1834: 51-52 (Red Sea).

Herpetolitha limacina — Leuckart, 1841: 56-58; Dana, 1846: 307-308, pl. 20 figs. 2-2d; Milne Edwards & Haime, 1851: 94-95.
Herpetolitha interrupta — Leuckart, 1841: 58-59; Dana, 1846: 308.
Herpetolitha foliosa — Leuckart, 1841: 59; Dana, 1846: 308-309; Klunzinger, 1879: 68-69, pl. 8 figs. 4-5; Gravier, 1907: 342; Von Marenzeller, 1907: 89; Vaughan, 1907b: 262; Gardiner, 1909: 282-284, pl. 36 figs. 14-15, pl. 37; Gravier, 1911: 62; Matthai, 1924: 48.
Herpetolitha stellaris — Leuckart, 1841: 58.
Herpetolithus stellaris — Dana, 1846: 309.
Herpetolithus strictus Dana, 1846: 309-310, pl. 21 fig. 1 (Tahiti, Society Islands).
Herpetolithus crassus Dana, 1846: 310, pl. 20 figs. 5-5c ("Feejee Islands").
Herpetolitha limax — Milne Edwards & Haime, 1851: 94-95; 1860: 24-25; Verrill, 1864: 52; Studer, 1880: 46; Ortmann, 1888: 179; 1889: 518, pl. 18 fig. 12c; Bedot, 1907: 223-225, pl. 33 figs. 169-173; Vaughan, 1918: 130; Matthai, 1924: 47-48, pl. 8 figs. 7, 9; Crossland, 1931: 354-355, pl. 2 fig. 3, pl. 3; Thiel, 1932: 87-89; Yabe & Sugiyama, 1935: 397; Abe, 1938: 482-484, fig. 7; Eguchi, 1938: 362-363.
Herpetolitha ampla Verrill, 1864: 52 (Zanzibar). (New synonymy).
Herpolitha limosa — Duncan, 1883: 152, pl. 6 figs. 6-7. (Intentional change of spelling).
Herpetolitha crassa — Quelch, 1886: 143; Vaughan, 1918: 129, pl. 53 figs. 1-1a, pl. 54 fig. 1; Umbgrove, 1924: 13.
Herpolitha crassa — Gardiner, 1898: 529; 1909: 286-287; Lamberts, 1983: 9.
Herpetolitha stricta — Vaughan, 1918: 129-130, pl. 51 figs. 3-3b; Matthai, 1924: 48-49; Yonge, 1930: 38; Hanzawa, 1931: pl. 4.
Fungia weberi Van der Horst, 1921: 62, pl. 1 figs. 5-6 ("Anchorage East of Sailus Besar, Paternoster-islands"); Van Soest, 1979: 107. (New synonymy).
Fungia echinata — Matthai, 1924: 42-43 (partim), pl. 9 fig. 4, pl. 10 fig. 8.
Herpolitha weberi — Boschma, 1925: 226-227; 1934: 4203-4204, fig. 5; Yabe & Sugiyama, 1941: 80-81, pl. 81 figs. 2-2d; Ditlev, 1976: 7; Pillai & Scheer, 1976: 44-45, pl. 18 fig. 1; Zou, 1978: 101, pl. 8 figs. 5-6; Veron & Pichon, 1979: 180, 182, figs. 300-304; Randall & Myers, 1983: 20, figs. 358-359; Johnston, 1986: 159; Veron, 1986a: 32; 1986b: 351; Veron & Kelley, 1988: 29; Veron & Marsh, 1988: 85.
Herpolitha stricta — Vaughan & Wells, 1943: pl. 18 figs. 5-6; Nemenzo, 1955: 74-75, pl. 14 fig. 1; Shirai, 1980: 533; Nemenzo, 1981: 200, fig. 225; 1986: 154, fig. 179.
Herpolitha foliosa — Vaughan & Wells, 1943: pl. 18 fig. 7.
Fungia [Herpolitha ?] praecursor Umbgrove, 1946b: 535, pl. 81 fig. 1 (Lower Pliocene, Prupuk, Java). (New synonymy).
Herpolitha spec. — Phillipps, 1978: 101, pl. 7A; Green, Harris, Robertson & Santavy, 1979: 298-299.

Type material examined. — HMG ZC0015 (lectotype [present designation] of *Madrepora limax*; type loc. unknown); MNHN 78 (holotype of *Fungia limacina*; type loc. EAST INDIES); USNM 161, YPM 1960 (2 syntypes of *Herpetolithus strictus*; type loc. Tahiti, SOCIETY IS.); USNM 160, YPM 1961 (2 syntypes of *Herpetolithus crassus*; type loc. FIJI); MCZ 129 (2 syntypes of *Herpetolitha ampla*; type loc. ZANZIBAR); ZMA 6894-6895 (2 syntypes of *Fungia weberi*; type loc. Paternoster Is., INDONESIA); RGM 77663 (holotype of *Fungia praecursor*; type loc. Prupuk, Java, INDONESIA).

Other Material. — RED SEA: BMNH 1937.11.17.1059, RMNH 9624, USNM 48077. DJIBOUTI: MNHN 3522, 3525, Fun286, USNM 21987 (2). KENYA: RMNH 17092-17094. ZANZIBAR: BMNH 1955.10.11.9-11, MCZ 5283. N MADAGASCAR: USNM 77722, ZMA 1720. MASCARENE IS. Mauritius: ZMA 531. SEYCHELLES: BMNH 1981.3.5.464-465/468, RMNH 12096. CHAGOS IS.: BMNH 1891.4.9.13-14/18, 1970.7.30.28-29, USNM 77768. MALDIVES: RMNH 14242 (2). MALAYSIA. Malacca Str.: BMNH 1883.11.8.5/14. Sabah: USNM 47958-47959. SINGAPORE: AMNH 1749-1750, ANSP 4527, BMNH 1893.7.22.10, 1898.12.1.5, 1950.1.11.635, 1953.11.9.4, 1957.5.13.20, MCZ 10-11 (9), 519 (15), 5242 (6), 5282 (19), 5287 (5),



Figs. 442-447. Corals (anthocyathi) of *Herpolitha limax* from Indonesia. Fig. 442a-c. Upper surface of three corals: (a) RMNH 8430 (Banda), (b) RMNH 15740 (Obi Latu), (c) RMNH 16112 (NW Java) a regenerated coral. Scale bar: 2.5 cm. Figs. 443-444. Upper and lower surface of a juvenile with a detachment scar (RMNH 16111; NW Java). Scale bars: 1 cm. Fig. 445. Aboral surface of the corals in fig. 442b-c. Scale bar: 2.5 cm. Fig. 446. Upper surface of three small corals: (a-b) RMNH 16108, 16105 (NW Java) and (c) RMNH 8424 (Banda) two fused juveniles. Scale bar: 1 cm. Fig. 447. Aboral surface of the corals in fig. 446b-c showing a detachment scar. Scale bar: 1 cm.

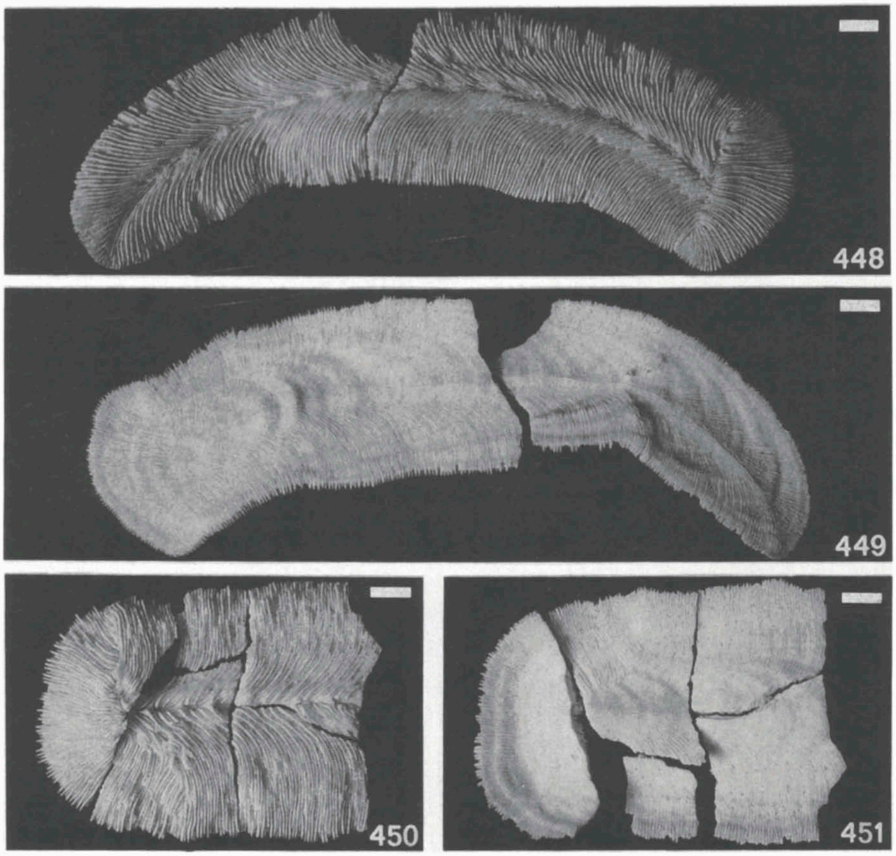
5293 (6), USNM 138, YPM 45, 47-48, 1434 (2). PHILIPPINES. S Luzon: USNM 77931. E Mindoro: UPZD 609. SE Panay: UPZD 42. S Mindanao: USNM 45399, 77997. INDONESIA. N Sumatra: ZMA 539. Belitung (Billiton): BMNH 1883.7.24.88/91, ZMA 527. Java: RGM 77662 (fossil). NW Java: RMNH 9329, 16104-16112, USNM 77759. SW Sulawesi: RMNH 9615, 15227-15228, 16069 (8), 16081 (3), 16142 (4), 20718, 20886 (2), 20961 (2), ZMA 526, 543. Tiger Is.: RMNH 21077, 21119, 21172. NE Sumba: RMNH 20269. Komodo, 20398, 21568 (4). N Sumbawa: RMNH 21338 (2), 21644. E Flores: ZMA 1841. Moluccas: ZMA 524, 527-530 (6), 532-533, 536-537, 540-541, 544, 546-548. Ambon: RMNH 8365, 9617, 9621 (2). Obi Latu: RMNH 15740. N Halmahera: USNM 78064. Banda: BMNH 1886.12.9.215, RMNH 8422, 8423-8431 (22), 15774-15775. Tukang Besi Is.: RMNH 20118, 20197. Talaud Is.: RMNH 15739. PALAU IS.: USNM 47090, 78010-78011, 78038 (2). MARIANA IS.: USNM 77772 (3). CAROLINE IS.: USNM 77792, 78059-78060 (3). PAPUA NEW GUINEA. Bismarck Sea: ULB. SOLOMON IS.: AMNH. NW AUSTRALIA: BMNH 1959.2.18.7. AUSTRALIA. Kimberley: WAM 709.86, 584.87. Pilbara: WAM 896.85. Northern Territory: NTM 1828, 6154, QMB GL3639. N Great Barrier Reef: QMB G8050-8051, GL3636-3637. C Great Barrier Reef: BMNH 1892.12.1.427, 1893.3.9.133-134/156, 1934.5.14.229, QMB G2933-2937, G6772, G6774, G7046-7047, G7608, G8052, GBR302, GBR343, GL3633, ZMA 6634. S Great Barrier Reef: QMB G6162, G6595. VANUATU (NEW HEBRIDES): USNM 78077-78078. NEW CALEDONIA: MNHN 1774, ZMA 6293 (2). MARIANA IS., GUAM: USNM 80088, 80094 (2), 80096, 80439, 80444. MARSHALL IS.: RMNH 14613-14616, 14618, USNM 44862-44864, 77818 (3), 77869 (3). GILBERT IS.: MCZ 5282, 5295 (8), USNM 77771, 77914-77915 (9). SAMOA IS.: QMT. TONGA IS.: USNM 77811 (2). SAMOA IS.: AMNH, USNM 77831. LINE IS.: USNM 78420. SOCIETY IS.: BMNH 1962.8.28.9, 1973.4.17.25-27, MNHN, RMNH 8988-8989, USNM 77803 (14), 77853 (2). TOAMOTU IS.: ANSP 4526 (3), USNM 77800.

Characters. — Adult animals are free-living. The corallum outline varies from elliptical to elongate, with tapering or rounded ends. As a result of fusion in anthocaulus stage, V-, Y- and X-shaped specimens may occur (figs. 442a, 446c). There are no fragmentation clefts in the corallum wall. The coralla are thick and vary from flat to highly arched. The length of the specimens varies between 2.5 and 62.0 cm.

Polystomatism is principally achieved by intrastomadaeal budding inside the axial groove. Juvenile specimens have a single mouth until two opposite septa grow towards each other through the mouth, and fuse. This process may repeat in other pairs of opposite septa until the animal reaches its maximum length, or perhaps even after this. The septa must reach a certain length to permit circumstomadaeal budding alongside the central axis. The lateral secondary mouths will appear in irregular rows parallel to the axial furrow, merely as invaginations in groups of adjacent septa. Eventually, they become more abundant than the more distinct stomata inside the axial groove and their distribution pattern becomes more irregular. The columellae inside the stomata are formed by tightly packed, partly fused trabeculae and paliform lobes with their tips pointing in various directions. In the lateral stomata the columellae may remain undeveloped and indistinct.

The septa are densely packed and straight. Interstomatous septa are situated in between the central axis and the newly formed lateral stomata. The septa of lower order cycles are thick and solid, those of higher orders thin and perforated. The septa alternate in height; those of lower orders being more protruding than those of higher orders. Tentacular lobes are absent. The septal margins are coarsely ornamented with irregularly angular and sharp dentations (figs. 452-453, 457). Their number varies from 15 to 35 per cm. The septal sides are thinly granulated. The granulations are coarse and arranged in rows or fused in ridges perpendicular to the septal margin (fig. 652). The compound synapticulae connecting the septa laterally can easily be distinguished, in spite of the tight septal arrangement.

The corallum wall is perforated. It is not covered with granulations (fig. 653). A detachment scar is distinct at the aboral side of small specimens in early anthocyathus phase (figs. 444, 447). The costae are straight and almost



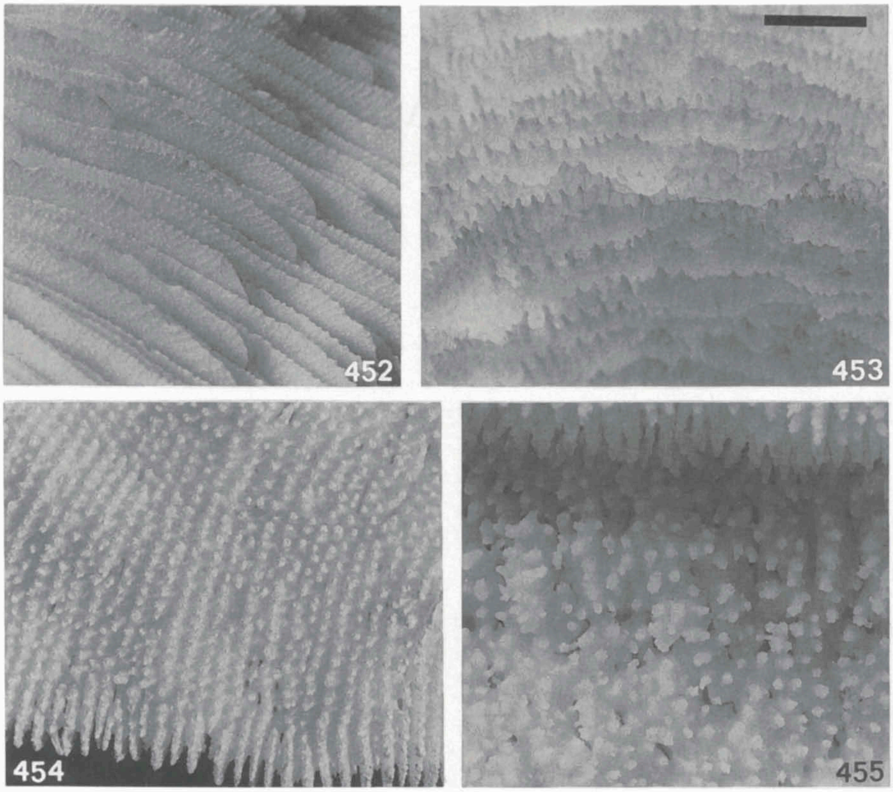
Figs. 448-451. The two syntypes of *Fungia weberi* (= *Herpolitha limax*, Paternoster Is., Indon.). Scale bars: 1 cm. Figs. 448-449. Upper and lower surface (ZMA 6894). Figs. 450-451. Upper and lower surface (ZMA 6895).

equal in size. They are distinct near the corallum margin, less distinct near the centre. All costae are finely to coarsely ornamented with spines which are either blunt and granular at the tips or elongate with acute points (figs. 454-455, 458-459, 653). The number of the spines varies from 15 to 40 per cm.

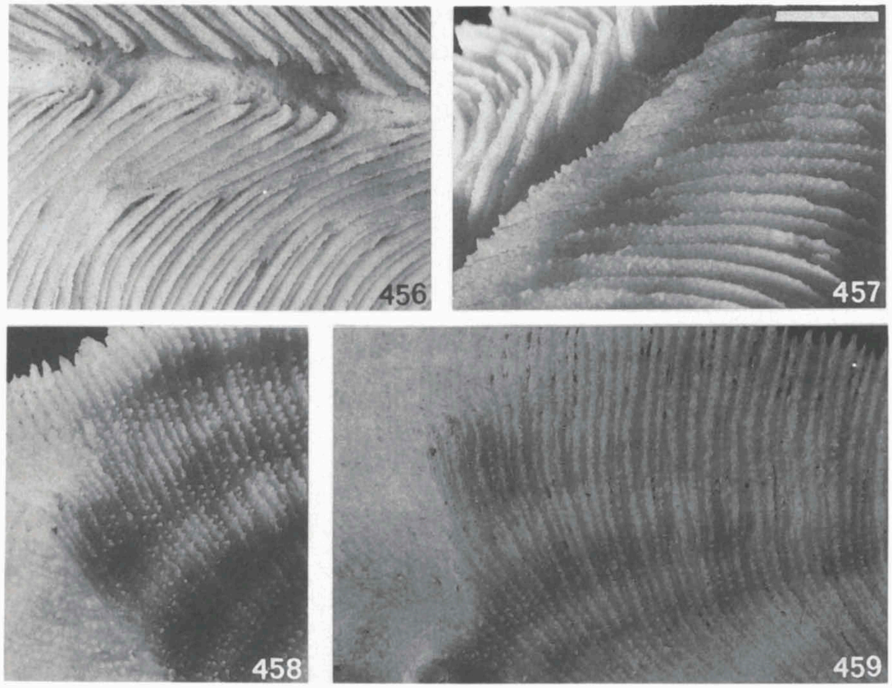
The living animal is usually brown (fig. 28). The small tentacles are usually translucent and colourless; less frequently, they are either white or green.

Geographical distribution (fig. 460). — The species is widely distributed, from the western Indian Ocean (Red Sea to Madagascar), through the Central Indo-Pacific, towards southern Japan, the Line Islands and the Tuamotu Archipelgo.

Remarks. — In the literature, there is much confusion about the use of the epithet *limax*. Hoeksema (1988) proposed a suppression of the epithet *limax* prior to its reintroduction by Esper (1797), as well as the epithets *trilinguis* Boddaert, 1768 and *talpa* Houttuyn, 1772. The epithet *limax* Houttuyn, 1772,



Figs. 452-455. Close-ups of *Herpolitha limax* corals from Indonesia. Scale bar: 0.5 cm. Fig. 452. Septa of the coral in fig. 442c. Fig. 453. Septa of the coral in fig. 442b. Fig. 454. Costae of the coral in fig. 445b. Fig. 455. Costae of the coral in fig. 445a.



Figs. 456-459. Close-ups of a syntype of *Fungia weberi* (= *Herpolitha limax*, ZMA 6894). Scale bar: 0.5 cm. Figs. 456-457. Fossae and septa. Figs. 458-459. Costae and wall perforations.

has originally been used for the species currently known as *Polyphyllia talpina* Lamarck, 1801. The holotype of *Madrepora limax* Houttuyn, 1772, is a specimen of *Polyphyllia talpina* figured by Seba (1759, pl. 112 fig. 31). Müller (1775) used the name *Madrepora limax* for the same species as Houttuyn (1772) did, but he did so inconsistently, which increased the confusion about its identity. Esper (1797) was the first author who used the name *Madrepora limax* unequivocally for the species currently known as *Herpolitha limax*.

The presently designated lectotype of *H. limax* (erroneously given the status of holotype by Hoeksema, 1988) is a coral in an illustration published by Ellis & Solander (1786: pl. 45), which was successively copied by Esper (1797: pl. 63). The specimen was later mentioned in a list of corals from the Ellis & Solander collection in the HMG (Young, 1877), and is at present still there. The holotype of *M. trilinguis* is an anomalously Y-shaped specimen resulting from the fusion of two or more anthocauli (Boddaert, 1768: pl. 14).

Both *Fungia weberi* and *F. praecursor* are synonymized in the present study because they cannot be separated from *H. limax*. The two syntypes of *F. weberi* show some indistinct lateral secondary stomata (figs. 448, 450, 456), which makes the presence of uninterrupted septa invalid as a diagnostic criterion for this species. The corals are relatively thin, a character which is commonly observed in specimens living in silty environments (Hoeksema & Moka, 1989). Besides, the number of lateral secondary stomata in *H. limax* is very variable because it is related to age and may also be influenced by environmental conditions (Hoeksema & Moka, 1989). It is not reported, however, from what kind of bottom the type specimens of *F. weberi* were dredged (Van der Horst, 1921). The holotype of *F. praecursor* is a thin fragment which contains a part of the central furrow, including several stomata.

Herpolitha limax has several characters in common with *Fungia (Lobactis) scutaria*. Although *H. limax* does not have the tentacular lobes of the latter, it has very similar septal and costal ornamentations. It differs from *F. (L.) scutaria* by being polystomatous and longer in shape. *H. limax* differs from *Polyphyllia talpina*, another polystomatous elongate species, by having longer interstomatous septa and by a more uneven distribution of its stomata.

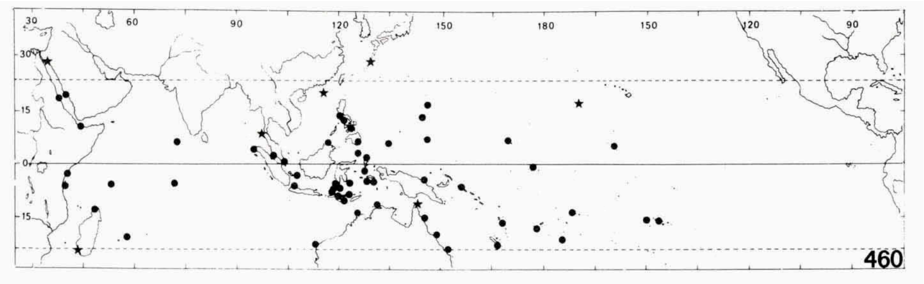


Fig. 460. The range of *Herpolitha limax*. Records are from examined material (●) and published illustrations (★).

Polyphyllia Blainville, 1830.

Type species: *Fungia talpa* Lamarck, 1815 [= *Polyphyllia talpina* (Lamarck, 1815)]. By monotypy.

Polyphyllia Blainville, 1830: 305-306; Quoy & Gaimard, 1833: 184; Blainville, 1834: 339-340; Ehrenberg, 1834: 52; Lamarck, 1836: 373-374; Leuckart, 1841: 60; Dana, 1846: 312-313; Milne Edwards & Haime, 1849: 72; 1850: xlviii; 1851: 98-99; 1860: 25-26; Duncan, 1885: 145-146; Gardiner, 1909: 287; Vaughan, 1918: 130; Van der Horst, 1921: 16; Matthai, 1924: 49; Boschma, 1925: 231; Vaughan & Wells, 1943: 142; Wells, 1956: 389; Wells, 1966: 240-241; Veron & Pichon, 1979: 182-183; Ditlev, 1980: 58; Nemenzo, 1981: 202; Lamberts, 1984: 18; Nemenzo, 1986: 155; Veron, 1986b: 352; Chevalier & Beauvais, 1987: 710.

Lithactinia Lesson, 1831: pl. 6; Milne Edwards & Haime, 1849: 71; 1850: xlviii; 1851: 100-101; 1860: 28; Duncan, 1885: 146; Quelch, 1886: 142; Lamberts, 1984: 20. (Type species: *Lithactinia novaehiberniae* Lesson, 1831. By monotypy).

Cryptabacia Milne Edwards & Haime, 1849: 71; 1850: xlvii; 1851: 95-96; 1860: 22; Duncan, 1885:

144; Quelch, 1886: 141. (Type species: *Fungia talpa* Lamarck, 1815 [= *Polyphyllia talpina* (Lamarck, 1801)]. By monotypy).

Characters. — Adult animals are free-living and polystomatous. They are elongate and have an axial row of stomata. Polystomatism is achieved by intra- and circumstomadaeal (especially peripheral) budding. The corallum wall is perforated. It is not covered by granulations. The coralla vary from flat to arched. The interstomatous septa are short; they are oriented parallel to each other or they diverge from the central axis towards the periphery. The septal dentations are fine; they are covered by irregular rows of granulations perpendicular to the septal margin. The costal spines are blunt and granulated.

Remarks. — *Polyphyllia* was established by Quoy & Gaimard in a manuscript that was used by Blainville (1830) for the description of the genus. Blainville (1830) classified several "species" with *Polyphyllia* of which *P. talpa* was the only available name. Hence, the type species was designated by monotypy.

Of the nominae nudae mentioned by Blainville (1830), *P. pelvis* was obtained from Quoy & Gaimard (ms.) and later used by themselves (1833) for the only species they attributed to the genus. *P. substellata*, introduced by Blainville (1830: 305; 1834: 339) to name a coral at the MNHN, was not validated before Milne Edwards & Haime (1851) used it to describe this specimen. The remaining numina nudae mentioned by Blainville (1830; 1834), i.e. *P. echinata* ("Mers de Ceilan"), *P. cristata* (no loc.) and *P. coadunata* (no loc.), were supposed to be represented by specimens in a collection at Caen (France) but Milne Edwards & Haime (1860: 27), who tried to locate these specimens in the museum of Caen, could not find them.

In this revision *Lithactinia* is considered synonymous with *Polyphyllia*, although recently Lamberts (1984) suggested that it should be maintained as separate genus. His main criterium for separation is that specimens of *Lithactinia* lack an axial row of stomata. Regenerated fragments of *Polyphyllia talpina*, however, may also lack an axial row of stomata (figs. 475-476). Corals of *P. novaehiberniae*, the only species Lamberts (1984) classified with *Lithactinia*, are more fragile and therefore lack the axial row of stomata more frequently than those of *P. talpina*.

In corallum shape, *Polyphyllia* is slightly similar to *Herpolitha*. The interstomatous septa of *Polyphyllia* are shorter and its stomata are more evenly distributed than in the other genus. In septal and costal ornamentation, however, *Polyphyllia* resembles *Sandalolitha*, a genus that does not show the intrastomadaeal budding observed in *Polyphyllia*.

Polyphyllia novaehiberniae (Lesson, 1831)
(figs. 461-471)

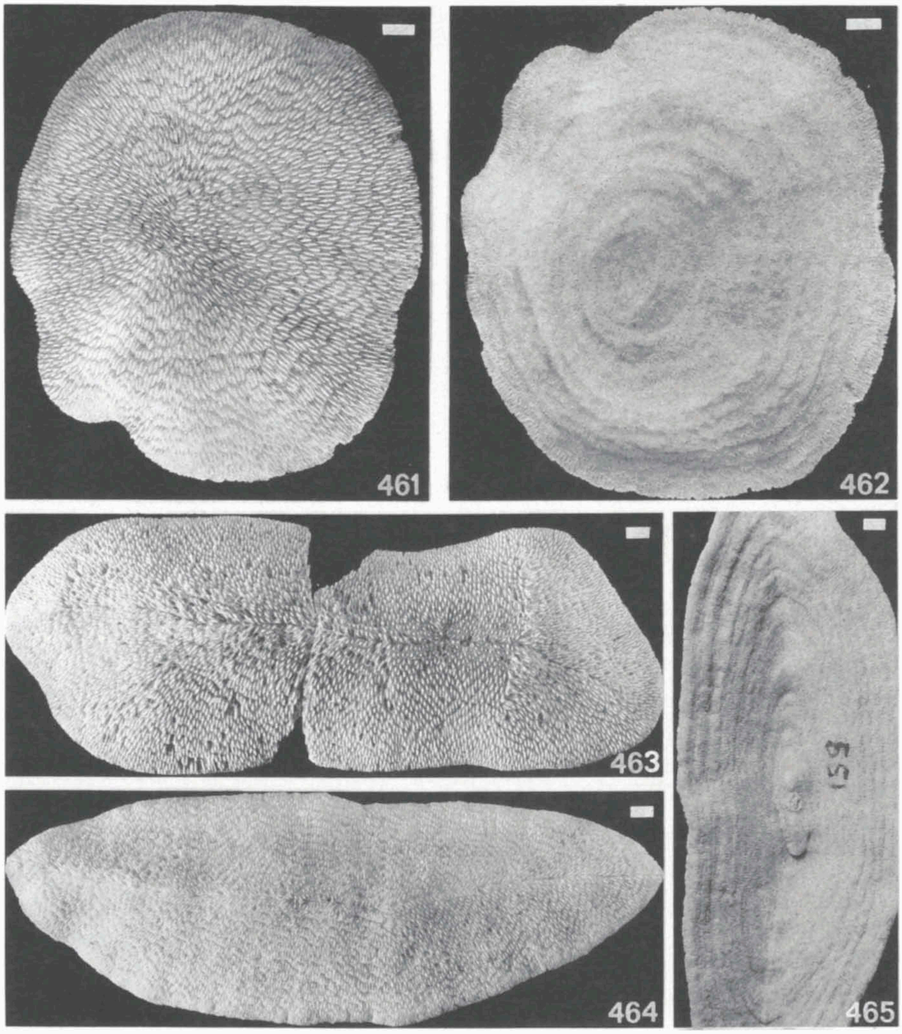
Lithactinia novae-hiberniae Lesson, 1831 : pl. 6, figs. 1-2 ("la Nouvelle-Irlande"); Dana, 1846: 316.
Polyphyllia pelvis Quoy & Gaimard, 1833: 185-187 (partim); Blainville, 1834: 339.
Polyphyllia pileiformis Dana, 1846: 317, pl. 21 fig. 4 ("Feejee Islands").
Polyphyllia galeriformis Dana, 1846: 317-318, pl. 21 fig. 3 ("Feejee Islands").
Polyphyllia substellata Milne Edwards & Haime, 1851: 100; 1860: 27 ["Habite l'île Waigiou (Moluques)"]. (New synonymy).
Lithactinia novaehiberniae Milne Edwards & Haime, 1851: 101; 1860: 28-29; Lamberts, 1983: 9; 1984: 20-22, figs. 8-15. (Valid emendation).
Lithactinia pileiformis — Milne Edwards & Haime, 1860: 29; Quelch, 1886: 142; Ortmann, 1888: 179.
Lithactinia galeriformis — Milne Edwards & Haime, 1860: 29; Quelch, 1886: 142-143.
Polyphyllia novae-hiberniae — Folkeson, 1919: pl. 1 fig. 27; Matthai, 1924: 50; Pillai, 1972: 204.
Polyphyllia talpina — Ditlev, 1980: 58 (partim), fig. 245.

Type material examined. — MNHN Fun231 (holotype of *Lithactinia novaehiberniae*; type loc. Port Praslin, New Ireland, BISMARCK IS.); MNHN Fun261 (paralectotype of *Polyphyllia pelvis*; Vanikoro, Santa Cruz Is., VANUATU [NEW HEBRIDES]); USNM 158, 980, MCZ 553, YPM 1963-1964 (syntypes of *Polyphyllia pileiformis*; type loc. FIJI); USNM 155-156, MCZ, YPM 4300, 5570 (syntypes of *Polyphyllia galeriformis*; type loc. FIJI); MNHN Fun262 (holotype of *Polyphyllia substellata*; type loc. Waigeu, INDONESIA).

Other material. — PAPUA NEW GUINEA. Bismarck Sea: ULB, USNM 78074. SOLOMON IS.: USNM 71752. Bougainville I.: AMNH (6). NEW CALEDONIA: MNHN Fun225, RMNH 14098, USNM 73965-73967. VANUATU (NEW HEBRIDES): AIMS (3). FIJI IS.: BMNH 1886.12.9.211-214, 1889.2.16.1-2, 1937.5.16.1-6, QMB GL3640. TONGA IS.: USNM 61072. SAMOA IS.: BMNH 1928.7.5.2-3, 1931.10.10.1, 1948.9.1.1-2, QMT, USNM 77830.

Characters. — Adult animals are free-living. They are polystomatous by intra- and circumstomadaeal (including peripheral) budding. In unbroken condition the corals have a distinct axial furrow and their outline is elongate with ends varying from tapering to rounded (figs. 463-464). Although fragmentation clefts are not formed in the corallum wall, broken specimens are common due to the thinness of the coralla. Specimens regenerated from fragments are usually irregularly circular in outline (figs. 461-462). The coralla vary from slightly to strongly arched. The length of the specimens ranges from 5.0 to 38.0 cm.

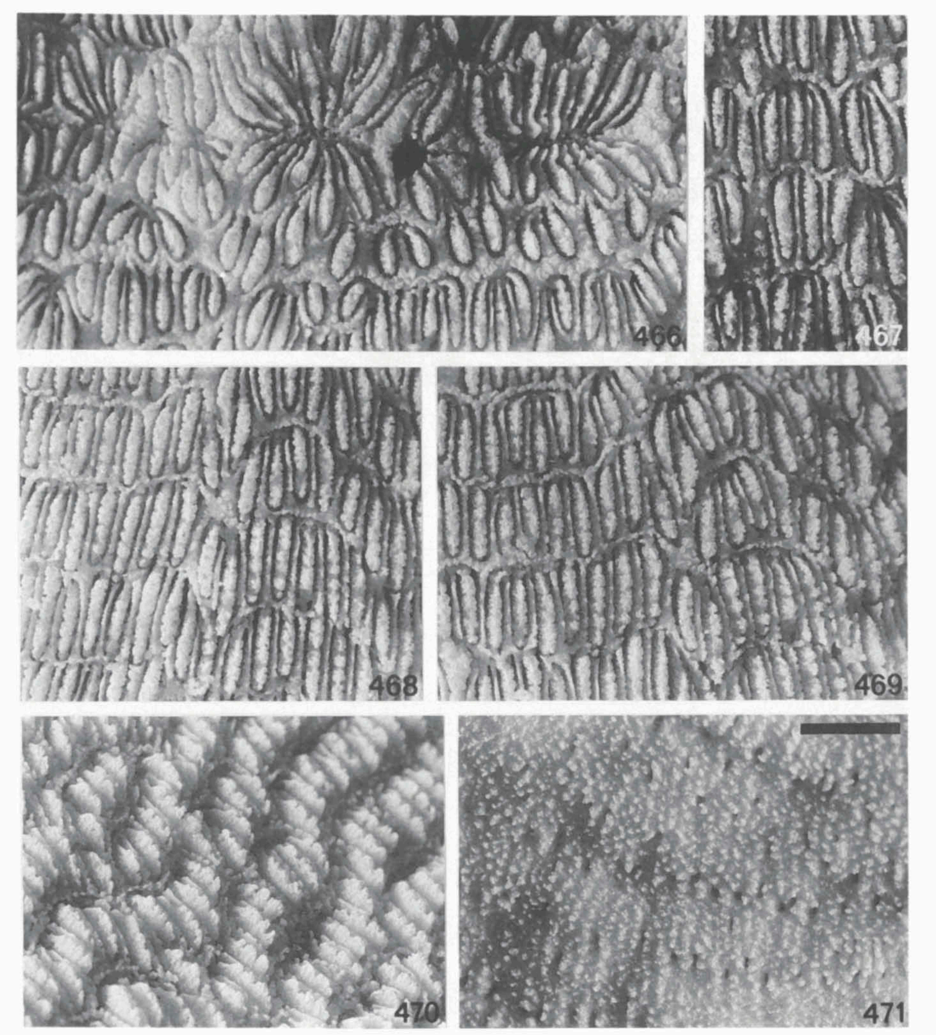
The septa are relatively short because they are interrupted by stomata formed by circumstomadaeal budding. Near the stomata, the ends of the interstomatous septa may be fused with adjacent septa (figs. 466-469). Adjacent septa are oriented in rows parallel to the central axis (figs. 463-464). When, due to fragmentation, there is no axial furrow, the septa are arranged in a concentric pattern (fig. 461). The septa are densely packed and straight. The septa of lower orders are thick, exsert and solid, while those of higher orders are thin, low and perforated. Tentacular lobes are absent. The septal margins are finely ornamented with irregularly angular or lobed dentations (fig. 470). Their number varies from 15 to 25 per cm. The septal sides are densely granulated. The granulations are distributed in indistinct rows perpendicular to the septal margin or in no distinct pattern. The compound synapticulae



Figs. 461-465. Corals (anthocyathi) of *Polyphyllia novaehiberniae*. Scale bars: 1 cm. Figs. 461-462. Upper and lower surface of the holotype of *P. novaehiberniae* (MNHN Fun231; New Ireland, Bismarck Archipelago); the central axis with stomata is lost due to fragmentation. Fig. 463. Upper surface of the paralectotype of *Polyphyllia pelvis* (MNHN Fun261; Vanikoro, New Hebrides); the axial furrow displays many fossae. Figs. 464-465. Upper and lower surface of a complete coral (RMNH 14098; New Caledonia) with a distinct row of fossae.

connecting the septa laterally cannot easily be distinguished because of the tight arrangement of the septa.

The stomata inside the axial furrow, which are formed by intrastomadaeal budding, are more distinct than those alongside it, which are formed by circumstomadaeal budding. The columellae remain either undeveloped and



Figs. 466-471. Close-ups of a *Polyphyllia novaehiberniae* coral (RMNH 14098; New Caledonia). Scale bar: 0.5 cm. Fig. 466. Part of the upper surface showing the founder calix and secondary stomata in the central axis, and those besides it. Figs. 467-470. Septa from above and from aside to show septal arrangement and granulation patterns. Fig. 471. Costae and perforations in the corallum wall.

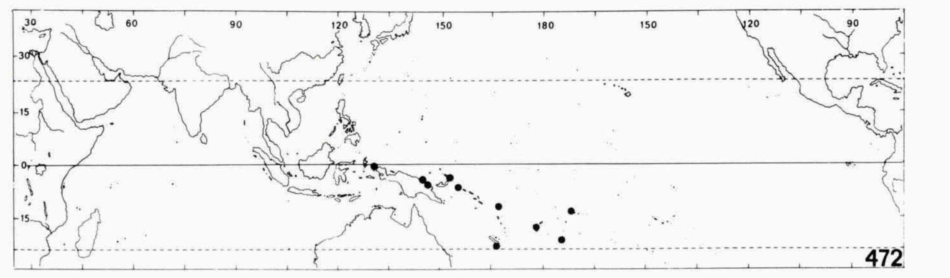


Fig. 472. The range of *Polyphyllia novaehiberniae*. Records are from examined material (●).

rudimentary, especially in the lateral stomata, or they are formed by some indistinct paliform lobes and trabeculae.

The corallum wall is perforated. It is not covered by granulations. A detachment scar may be present at the aboral side of specimens in anthocyathus phase (fig. 465). The costae are indistinct and finely ornamented. The costal spines are either short and granulated or spinose (fig. 471). Their number varies from 20 to 30 per cm costa.

The living animal is brown; it is densely covered by many tentacles which usually remain extended during day and night.

Geographical distribution (fig. 472). — *P. novaehiberniae* occurs in an area limited to the West Pacific Ocean, from Waigeu (or Waigeo) off Vogelkop Peninsula at western New Guinea, towards the Samoan Islands.

Remarks. — According to Lamberts (1984), the species belongs in a separate genus, *Lithactinia*, because it lacks an axial row of stomata. Most specimens observed during the present study are in broken condition and therefore lack the axial row of stomata. The unbroken specimen (RMNH 14098) figured by Lamberts (1984: fig. 10) shows several distinct mouths inside the axial furrow (compare figs. 464, 466), although Lamberts denies their presence.

Lamberts (1984) reported the holotype of *Lithactinia novaehiberniae* as lost. He designated two (!) neotypes of the species, an undamaged coral from Tonga (USNM 61072) and a broken and regenerated specimen from the Solomon Islands (USNM 71752). This neotype designation is invalid as Art. 75a of the International Code on Zoological Nomenclature requires a single specimen to be the neotype. Furthermore, Lamberts gave no reasons for believing the holotype to be lost and the illustrations originally published by Lesson (1831: pl. 6) are clear enough to reveal the diagnostic characters of the species. However, examination of the MNHN-collection revealed that the holotype was still there (figs. 461-462).

Corals of *Polyphyllia novaehiberniae* are in general thinner and more fragile than specimens of *P. talpina*. Therefore, *P. novaehiberniae* is more frequently found in a broken and eventually regenerated condition. Opposite to Lamberts' (1984) statements, the distribution ranges of the two taxa show a distinct overlap, from western Irian Jaya (Indonesia) towards New Caledonia, which suggests that they should be considered separate species indeed.

Polyphyllia talpina (Lamarck, 1801)
(figs. 29, 473-483, 654-655)

Madrepora pileus — Pallas, 1766: 286 (partim); Boddaert, 1768: 353-356 (partim); Wilkens, 1787: 26-30 (partim); Esper, 1791: 87-92, 287 (partim).
Madrepora talpa Houttuyn, 1772: 116-117 (partim). Not: Müller, 1775.
Madrepora limax Houttuyn, 1772: 119-121 (partim; no locality given).
Not *Madrepora limax* Esper, 1797.
Fungia talpina Lamarck, 1801: 370 ("l'Océan des Indes orientales").
Fungia talpa — Lamarck, 1815: 237; Oken, 1815: 74; Lamarck, 1816: 237; Lamouroux, 1824: 419; Lamarck, 1836: 373.
Fongia talpa — Blainville, 1820: 216-217.
Agaricia talpa — Schweigger, 1820: 415 (partim).
Herpolitha talpa — Eschscholtz, 1825: 746.
Polyphyllia talpa — Blainville, 1830: 305; 1834: 339-340, pl. 52 fig. 1-1b; Ehrenberg, 1834: 52; Dana, 1846: 313-314, pl. 21 fig. 5-5d; Ortmann, 1888: 179; 1889: pl. 18 fig. 12b; Milne Edwards & Haime, 1851: 100; 1860: 27.
Polyphyllia pelvis Quoy & Gaimard, 1833: 185-187 (partim), pl. 20 figs. 8-10 ("Carteret, à la Nouvelle-Hollande"); Blainville, 1834: 339, pl. 52 fig. 1; Dana, 1846: 315-316; Milne Edwards & Haime, 1851: 99-100; 1860: 26-27, pl. D11 fig. 1.
Polyphyllia sigmoides Ehrenberg, 1834: 52 (Red Sea); Dana, 1846: 314-315.
Polyphyllia leptophylla Ehrenberg, 1834: 52 (Red Sea); Dana, 1846: 314, pl. 20 fig. 6a-6c.
Polyphyllia fungia Dana, 1846: 316 (locality unknown). (New synonymy).
Cryptabacia talpina — Milne Edwards & Haime, 1851: 95-96; 1860: 22-23; Verrill, 1864: 52; Studer, 1880: 46; Duncan, 1886: 15-16; Quelch, 1886: 141; Bedot, 1907: 226-229, pl. 34, pl. 35 figs. 177-179.
Cryptobacia leptophylla — Milne Edwards & Haime, 1851: 96; 1860: 23.
Herpetolitha talpina — Saville-Kent, 1893: 176, chromo pl. 6 fig. 17.
Polyphyllia talpina — Gardiner, 1909: 287-288, pl. 36 fig. 13, pl. 38 figs. 18-19, pl. 39 fig. 26; Vaughan, 1918: 130-131, pl. 54 fig. 2; Van der Horst, 1921: 16-17; Matthai, 1923: 78; 1924: 49; Boschma, 1925: 232-233, pl. figs. 86-92, pl. 9 figs. 109-110; Faustino, 1927: 197-198, pl. 64 fig. 3; Thiel, 1932: 89-90, pl. 12 fig. 2; Boschma, 1934: 4204-4206, fig. 6; Ma, 1937: 148, pl. 75 figs. 1-2; Eguchi, 1938: 363-364; Umbgrove, 1939: 45; Yabe & Sugiyama, 1941: 81-82, pl. 86 figs. 1-2c, pl. 87 fig. 3; Vaughan & Wells, 1943: pl. 19 fig. 1; Crossland, 1952: 155; Nemenzo: 1955: 77-78, pl. 14 fig. 7; Purchon, 1956: 157; Searle, 1956: 17, pl. 18; Wells & Davies, 1966: 48; Pillai, 1972: 204; Pichon, 1974: 176, fig. 2; Sukarno, 1974: 14; Scheer & Pillai, 1974: 40, pl. 18 fig. 3; Zou, Song & Ma, 1975: 31, pl. 15 fig. 2; Ditlev, 1976: 7; Pillai & Scheer, 1976: 45; Zou, 1978: 101; Veron & Pichon, 1979: 183-186, figs. 305-310; Ditlev, 1980: 58 (partim), figs. 45, 242-244; Shirai, 1980: 534; Betterton, 1981: 205, pl. 89; Pillai, 1983: 86; Randall & Myers, 1983: 20, figs. 99, 360-361; Wood, 1983: 122-123, 144; Lamberts, 1984: 18-20, figs. 3-6; Johnston, 1986: 159; Nemenzo, 1986: 156, fig. 182; Veron, 1986a: 32; 1986b: 352-353; Sakai & Yamazato, 1987: 46; Wood & Tan, 1987: 197; Veron & Kelley, 1988: 29; Veron & Marsh, 1988: 85-86.
Polyphyllia producta Folkeson, 1919: 17-18, pl. 1 figs. 25-26 ("45 miles W.S.W. off Cape Jaubert", Western Australia).

Polyphyllia sp. — Phillipps, 1978: 101, pl. 7B; Green, Harris, Robertson & Santavy, 1979: 299, fig.18.

Polyphyllia talpinna — Nemenzo, 1981: 202, fig. 228. (Incorrect spelling).

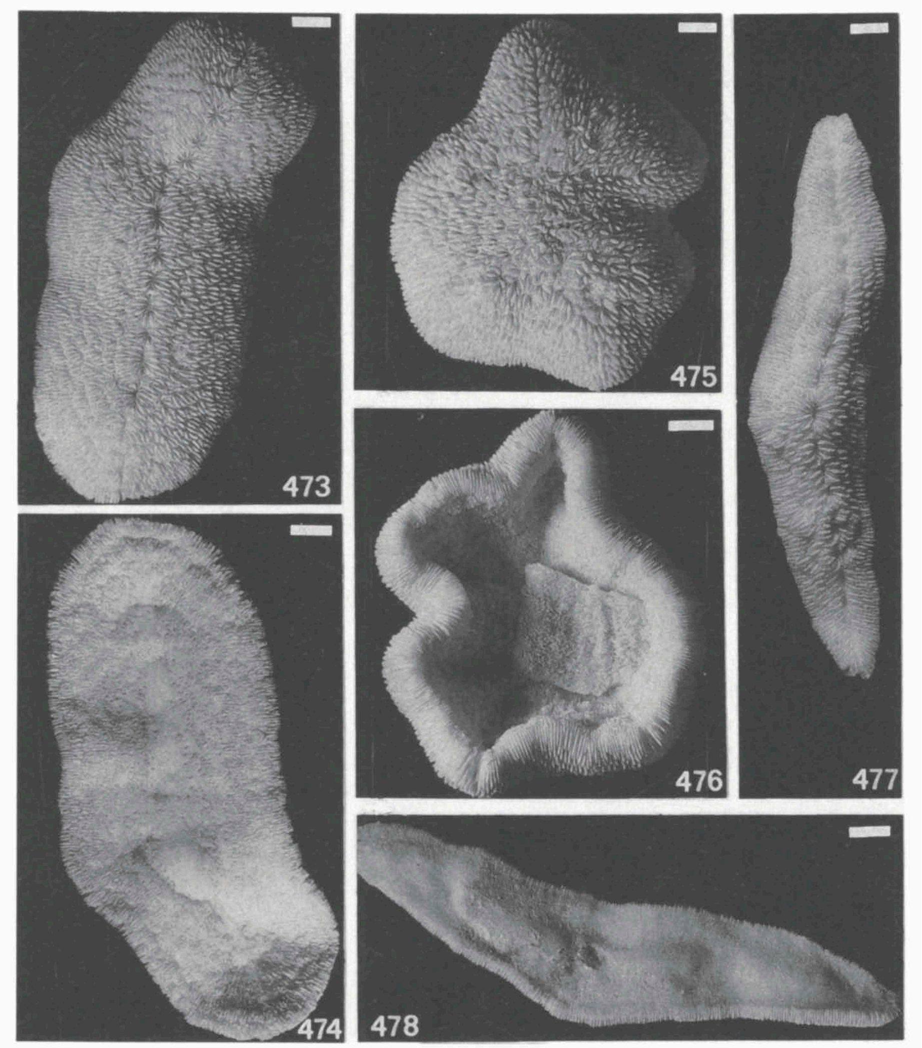
Type material examined. — MNHN 77 (2 syntypes of *Polyphyllia talpina*; type loc. unknown); MNHN Fun260 (lectotype [present designation] of *Polyphyllia pelvis*; Carteret, Bismarck Archipelago).

Other material. — N MADAGASCAR: ZMA 1738. MALDIVES: RMNH 22173. N SRI LANKA: YPM 1849. MALAYSIA. Malacca Str.: BMNH 1883.10.8.33, MCZ 384a. Sabah: USNM 47962. SINGAPORE: AMNH 1748, BMNH 1898.12.1.7, MCZ 520 (7), USNM 73986, YPM 65, 1435. S VIETNAM: USNM 45691. JAPAN: ZMA 1006. PHILIPPINES: USNM 45398, 73987-73994. SW Luzon: USNM 77938. Cebu: UPZD: 56, 210, 568. Cuyo Is.: USNM 80452. Palawan: USNM 78004. INDONESIA. Sumatra: RMNH 10142. Riau Is.: ZMA 6774. Belitung (Billiton): ZMA 988-991. NW Java: RMNH 16037-16040, ZMA 998. Java Sea: RMNH 10137. SW Sulawesi: RMNH 10130, 15223, 15224, 16143 (7), 16146-16147 (4), 20753, 20834, 20986 (2), ZMA 994-996. Tanah Jampea: RMNH 10129. Tiger Is.: RMNH 20541, 20542. NE Sumba: RMNH 20268. N Sumbawa: RMNH 21339, 21621. Flores: RMNH 10132. Kera: RMNH 13878. Moluccas: RMNH 10131, ZMA 6773. Ambon: BMNH 1886.12.9.110, 1946.1.1.25, RMNH 8420 (5), 10136, 10141. Obi Latu: RMNH 15741. Banda: RMNH 8414-8419 (17). Tanimber Is.: RMNH 15742. Kei Is.: RMNH 8421, 10139-10140, ZMA 992. Aru Is.: ZMA 993, 1002. PAPUA NEW GUINEA. Bismarck Sea: ULB. AUSTRALIA. Kimberley: BMNH 1974.6.28.1, WAM 583.87. Pilbara: WAM 381.79. Northern Territory: BMNH 1959.2.18.4, NTM 1826, 6160. Torres Str.: MCZ 5281, 7511 (4), QMB G845, ZMA 6629. N Great Barrier Reef: QMB G7595, G8063-8065, GL3643. C Great Barrier Reef: BMNH 1958.11.20.1, QMB G7628, GBR280, GL3634, USNM 45543. S Great Barrier Reef: G6776, GL3642. CAROLINE IS.: USNM 77793. NEW CALEDONIA: MNHN 1841, ZMA 6314-6315.

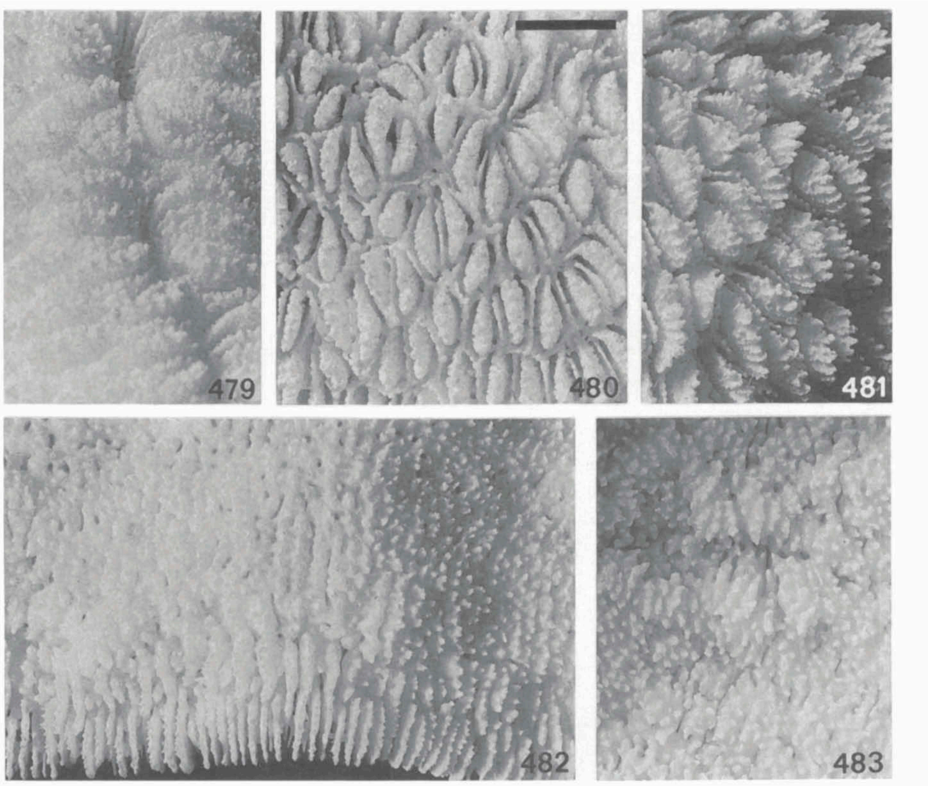
Characters. — Adult animals are free-living. They are polystomatous by intra- and circumstomadaeal budding. The latter includes peripheral budding. The corals are usually elongate with ends varying from tapering to rounded. There are no fragmentation clefts in the corallum wall. Corals may break by external causes; their outline eventually becomes irregularly circular or star-shaped (figs. 475-476). The coralla are relatively thick and vary from flat to highly arched. The length of the specimens varies between 1.5 and 53.0 cm.

The interstomatous septa are short because of the high density of the stomata. At their ends, they may be partly fused with neighbouring septa. At the coral periphery they are oriented parallel to each other, while closer to the central axis they radiate from the stomata (figs. 473, 477). The septa are densely packed, straight and of unequal thickness and height. The septa of lower orders are thick and solid, those of higher orders are thin and usually perforated. The septa of lower orders are more exsert than those of higher orders. Tentacular lobes are absent. The septal margins are finely ornamented with irregularly angular dentations (figs. 479-481, 654). Their number varies from 12 to 20 per cm. The septal sides are thinly and irregularly covered by granulations (fig. 654). The compound synapticulae connecting the septa laterally cannot always easily be distinguished, due to the dense arrangement of the septa. The lateral secondary stomata are usually indistinct compared to the stomata in the axial furrow. The columellae are poorly developed; they are either rudimentary or formed by some partly fused indistinct paliform lobes and trabeculae.

The corallum wall is perforated. It is not covered by granulations. A



Figs. 473-478. Corals (anthocyathi) of *Polyphyllia talpina* from Indonesia. Scale bars: 1 cm. Figs. 473-474. Upper and lower surface of a broad coral (RMNH 16038; NW Java). Figs. 475-476. Upper and lower surface of a regenerated fragment (RMNH 15224; SW Sulawesi); the central axis of stomata is lacking due to the earlier fragmentation. Figs. 477-478. Upper surface of an elongate coral (RMNH 16040; NW Java) with a detachment scar.



Figs. 479-483. Close-ups of *Polyphyllia talpina* corals. Scale bar: 0.5 cm. Fig. 479. Part of the central axis of the coral in fig. 477. Figs. 480-481. Septa of the coral in fig. 475 from above and from aside to show septal arrangement and granulation pattern. Fig. 482. Costae of the coral in fig. 474. Fig. 483. Costae of the coral in fig. 476.

detachment scar is distinct at the aboral side of small specimens in anthocyathus-phase. At the coral periphery, the costae are distinct and straight (fig. 482); closer to the centre, however, they become difficult to distinguish because here they become laterally fused (fig. 483). They are coarsely ornamented with spines which are either elongate and granular at the tips or blunt and spinose (fig. 655). Their number varies from 15 to 30 per cm.

The living animal is usually greyish-brown (fig. 29). It is densely covered by many tentacles, which usually remain extended both day and night. They are usually translucent and colourless, although their tips may be white.

Geographical distribution (fig. 484). — In the Indian Ocean, the species has been collected from the southwestern part (Madagascar) towards the eastern part (Andaman Sea to Western Australia). From the Indo-Malayan region the area extends further in the Pacific, towards southern Japan, Guam, the

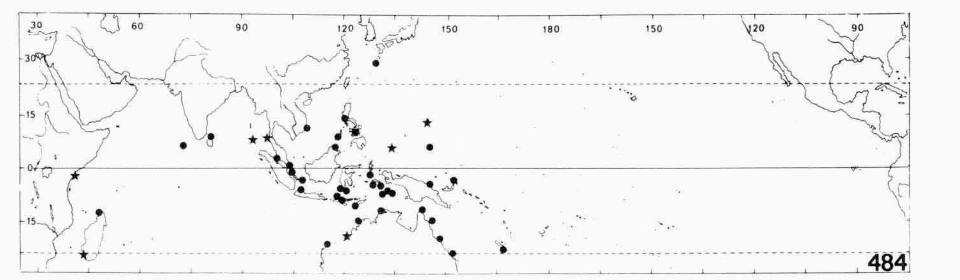


Fig. 484. The range of *Polyphyllia talpina*. Records are from examined material (●) and published illustrations (★).

Solomon Islands and New Caledonia.

Remarks. — Although the epithet *talpina*, currently in use for the species, is not the senior synonym, it is proposed for conservation (Hoeksema, 1988). Otherwise, the species would have to be named *Polyphyllia limax* (Houttuyn), which would be confusing because the epithet *limax* is better known in *Herpolitha limax* (Esper). The specific name *talpa* Houttuyn, 1772, as published in the binomen *Madrepora talpa,* is proposed for suppression since it caused much confusion (Hoeksema, 1988). Houttuyn (1772) used the name for both a specimen of *Herpolitha limax* (Esper), illustrated by Boddaert (1768: pl. 14), and a coral of *Polyphyllia talpina* (Lamarck), which was figured by Rumphius (1750: pl. 88 fig. 2) and later selected as lectotype (Hoeksema, 1988: 14, third line: read *talpa* instead of *limax*).

The species has been described under many different names, due to its variable form. Not all of the type specimens could be studied, but some of the illustrations leave no doubt about the identity of the taxon to which they refer. Most of the nominal taxa were already synonymized by previous authors.

The species differs from its closest relative, *P. novaehiberniae*, by a thicker and heavier corallum and by septa which are shorter and arranged in a more or less radiating pattern instead of being parallel to each other. Because its coralla are much thicker and more fragile, it is less frequently found in a broken or regenerated condition.

Compared to *Herpolitha limax*, *Polyphyllia talpina* has shorter septa; it has a relatively greater number of stomata, which are more evenly distributed; it also has a denser coverage of tentacles.

Sandalolitha Quelch, 1884

Type species: *Sandalolitha dentata* Quelch, 1884. By monotypy.

Sandalolitha Quelch, 1884: 294; Duncan, 1885: 144; 1886: 143-144; Veron & Pichon, 1979: 189-190; Veron, 1986b: 356.
Döderleinia Gardiner, 1909: 281-282. (Type species: *Halomitra irregularis* Gardiner, 1898 [= *Sandalolitha robusta* (Quelch, 1886)]. Designated by Wells, 1937).
Not *Döderleinia* Mayer, 1872; Steindachner, 1883.
Doederleinia — Van der Horst, 1921: 17. (Valid emendation).
Parahalomitra Wells, 1937: 74, figs. 4-6; Vaughan & Wells, 1943: 142; Wells, 1956: 389; 1966: 242; Ditlev, 1980: 58; Nemenzo, 1981: 203; 1986: 157; Chevalier & Beauvais, 1987: 710 (as subgenus of *Halomitra*). (Type species: *Halomitra irregularis* Gardiner, 1898 [= *Sandaloltha robusta* (Quelch, 1886)]. By original designation).

Characters. — Adult animals are free-living. The detachment scar is large. The polyps become polystomatous by circumstomadaeal budding. The corallum wall is perforate. The septal and costal ornamentations are coarse. The granulations on the septal sides are irregularly dispersed.

Remarks. — In the literature, *Sandalolitha* remained ignored for a long time because its type species, *S. dentata* Quelch, 1884, was hardly known. The more common *S. robusta* (Quelch, 1886), was originally not classified as a *Sandalolitha*, but as a *Podabacia*. New genera, *Doederleinia* and *Parahalomitra*, were established for the reason that *S. robusta* has an anthocyathus-stage in its life cycle, whereas *Podabacia* lacks this. The generic name *Parahalomitra* is still used by some authors, like Chevalier & Beauvais (1987), who considered it a subgenus of *Halomitra*. However, since Pillai & Scheer (1976) classified both of Quelch' species in *Sandalolitha*, the latter name is more commonly accepted.

Sandalolitha and *Podabacia* have almost similar septa and costae, except that those in *Sandalolitha* are slightly coarser in ornamentation. The septal ornamentations of *Sandalolitha* also resemble those of *Zoopilus*, although the latter has much coarser septal and costal ornamentations than *Sandalolitha*. The septal dentations of *Sandalolitha* cannot be found in *Fungia*, as suggested by Wells (1966: 242), who considers them equal to those of *F. (Verrillofungia)*. The rows and ridges of granulations parallel to the septal margins, typical for *F. (Verrillofungia)*, are absent in *Sandalolitha*.

In overall shape, corals of *Sandalolitha* somewhat resemble those of *Halomitra* and therefore may be confused with them. They differ in shape and, particularly, in the ornamentations of the septa and costae.

Sandalolitha dentata Quelch, 1884
(figs. 485-495, 658-659)

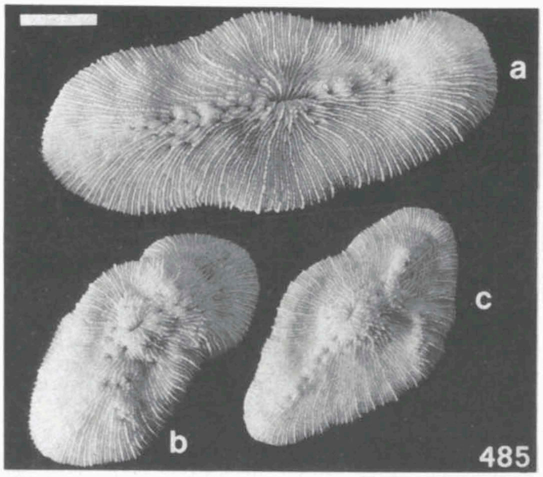
Sandalolitha dentata Quelch, 1884: 295 (Tahiti, Society Islands); Quelch, 1886: 144-145, pl. 7 fig. 1-1d; Pillai & Scheer, 1976: 46, pl. 18 fig. 2; Hoeksema & Moka, 1989: figs. 9a-b.
Podabacia dentata — Studer, 1901: 413-414.
Doederleinia sluiteri Van der Horst, 1921: 71, pl. 3 figs. 3-4 ("Banda-anchorage"); Van Soest, 1979: 107. (New synonymy).
Halomitra robusta — Boschma, 1925: 242-249 (partim), pl. 8 figs. 99-103 pl. 9 figs. 108, 113-115, 122, pl. 10 figs. 132-133.
Halomitra sluiteri — not: Ma, 1937.
Parahalomitra dentata — Wells, 1954: 450; Chevalier, 1979: 132.
Parahalomitra sluiteri — Nemenzo & Ferraris, 1982: 120-121, fig. 9.
Sandalolitha robusta — Veron & Pichon, 1979: 190-193 (partim), figs. 319-320; Randall & Myers, 1983: 20 (partim), figs. 364-365; Veron & Kelley, 1988: 29, 34, fig. 10f; Veron & Marsh, 1988: 86 (partim).
Parahalomitra robusta — Shirai, 1980: 532.

Type material examined. — BMNH 1886.12.9.109 (holotype of *Sandalolitha dentata*; type loc. Tahiti, SOCIETY IS.).

Other material. — MALDIVES: RMNH 22154 (2), YPM 7840. PHILIPPINES: USNM 77976. Cebu: UPMSI 353. INDONESIA. NW Java: RMNH 16041, 16044-16045 (3). SW Sulawesi: RMNH 16211 (2), 16213 (2), 16215, 16217-16222 (13), 21027, 22101-22105 (34). Tiger Is.: RMNH 21121, 21214. Tukang Besi Is.: RMNH 20112. N Sumbawa: RMNH 21340, 21676. Banda: RMNH 8393, 8400, 8403-8407 (13), 8432 (4), 8453. AUSTRALIA. Christmas I.: WAM 222.87, 276.87. Pilbara: WAM 528.81. N Great Barrier Reef: QMB GL3631. S Great Barrier Reef: QMB G6771. PAPUA NEW GUINEA. Bismarck Sea: ULB. PALAU IS.: USNM 78418. MARIANA IS. Guam: USNM 80095. CAROLINE IS.: USNM 77791 (2). MARSHALL IS.: USNM 77867-77868. FIJI IS.: USNM 78421 (2). LINE IS.: USNM 78419. COOK IS.: GPC. SOCIETY IS.: MNHN. TUAMOTU IS.: MNHN.

Characters. — Adult animals are not attached. The polyps are polystomatous by circumstomadaeal budding. They are irregularly oval with their ends varying from tapering to rounded. There are no fragmentation clefts in the corallum wall. The coralla vary from thin to thick and from flat to highly arched. The length of the specimens varies between 4.0 and 34.0 cm.

The septa are densely packed and usually straight, except around the stomata and near the corallum margin, where they may bend slightly. The septa are of unequal thickness and height. The septa of lower orders are thicker and distinctly more exsert than those of higher orders. The septa are perforated and may be fenestrate as well (fig. 658). The presence of tentacular lobes is restricted to young anthocauli. The septal margins are coarsely ornamented with irregularly serrate, long dentations (figs. 490-493, 658). Their number varies from 8 to 25 per cm. The septal sides are thinly to densely granulated. The granulations are unevenly dispersed or arranged in irregular rows perpendicular to the septal margin (fig. 658). The compound synapticulae connecting the septa laterally cannot always be easily distinguished,



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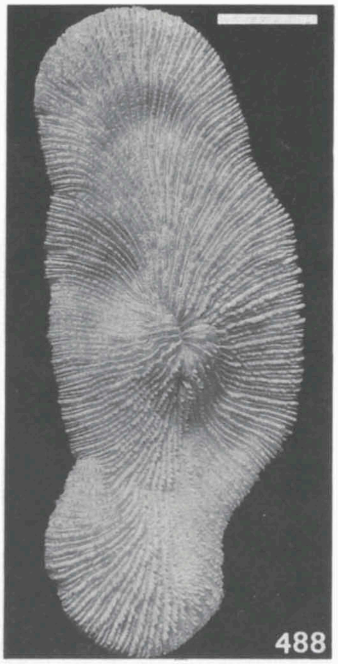

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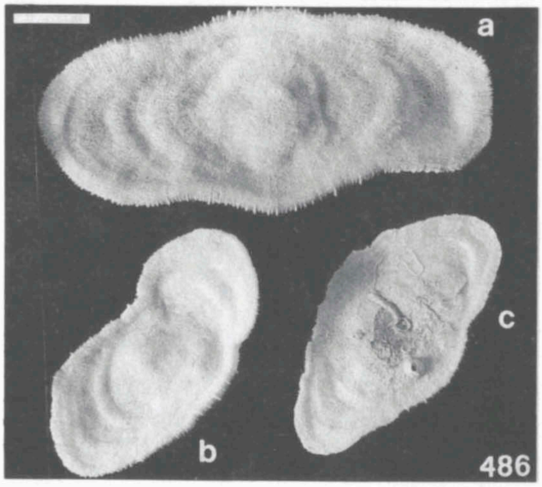

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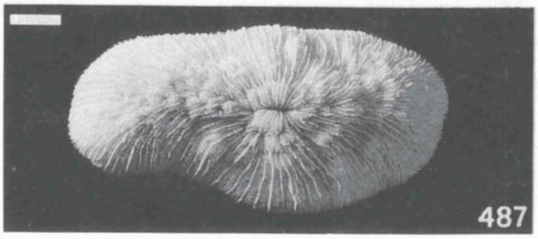

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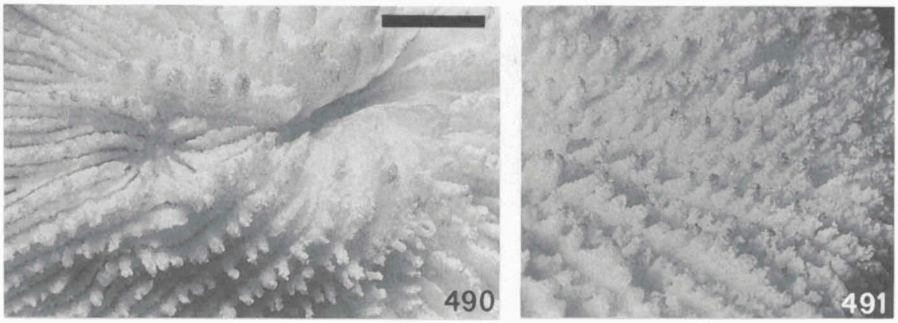
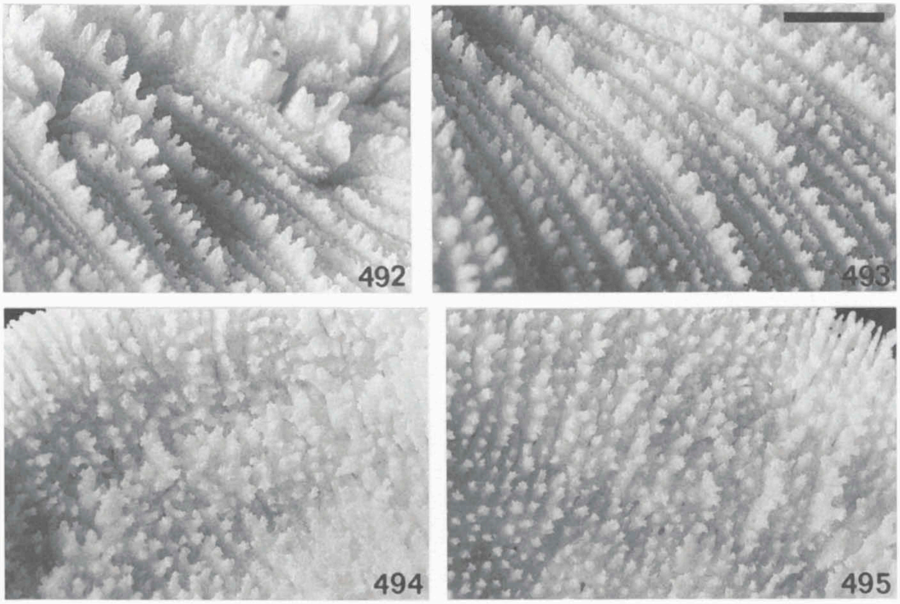
Figs. 485-489. Corals (anthocyathi) of *Sandalolitha dentata*. Scale bars: 2.5 cm. Figs. 485-486. Upper and lower surface of three medium-sized corals with the fossae in a axis-like orientation (RMNH 22105; SW Sulawesi, Indon.). Fig. 487. Upper surface of a large coral (RMNH 22105). Fig. 488. Upper surface of the holotype with two fossae, the primary of which is the largest (BMNH 1886.12.9.216; Tahiti, Society Is.). Fig. 489. As fig. 487.

because of the tight septal arrangement.

In specimens not yet fullgrown, the secondary stomata are usually concentrated around the distinctly larger, centrally located primary stoma (fig. 488). At first secondary stomata become arranged in a row along the central axis (fig. 485). In large specimens new stomata become distributed more evenly over the whole corallum surface (figs. 487, 489). The columellae are poorly developed; they are formed by some loosely packed trabeculae and paliform



Figs. 490-491. Close-ups of the holotype of *Sandalolitha dentata* showing the two unequally sized fossae and the septal dentations. Scale bar: 0.5 cm.



Figs. 492-495. Close-ups of *Sandalolitha dentata* corals (RMNH 22105; SW Sulawesi, Indon.). Scale bar: 0.5 cm. Figs. 492-493. Stomata and septa of the coral in fig. 485a. Fig. 494. Costae of the coral in fig. 486b. Fig. 495. Costae of the coral in fig. 486a.

lobes with the tips pointing in various directions.

The corallum wall is perforated and covered by granulations (fig. 659). A detachment scar (diameter > 1 cm) is usually distinct at the aboral side of small specimens in anthocyathus-stage, and less frequently in specimens of intermediate size (fig. 486c). The costae are unequal; they are straight and distinct near the corallum margin, less distinct near the centre. All costae are coarsely ornamented (figs. 494-495). The costal spines are either short and covered by some granulations or long and echinose. The number of the spines varies from 10 to 25 per cm.

The living animal is usually brown. Specimens are observed which have alternating, radiating zones of green and brown. The small and inconspicuous tentacles are transparent and colourless.

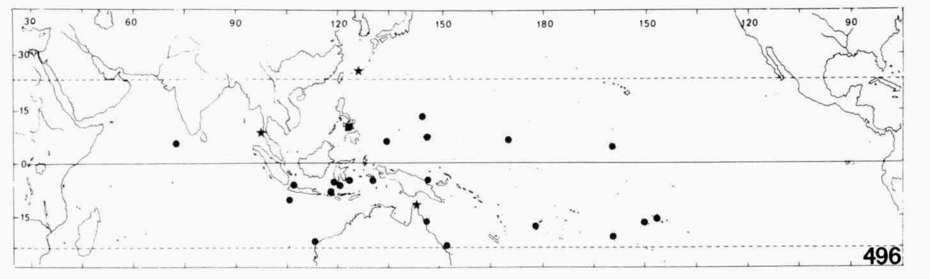


Fig. 496. The range of *Sandalolitha dentata*. Records are from examined material (●) and published illustrations (★).

Geographical distribution (fig. 496). — The range extends from the Maldives, in the Indian Ocean, through the Malayan Archipelago, towards southern Japan, the Line Islands and the Tuamotu Archipelago in the Pacific.

Remarks. — The holotype of *Doederleinia sluiteri* (ZMA 275) could not be traced. However, Van der Horst's (1921: pl. 3 figs. 3-4) illustrations show clearly that it belongs to *S. dentata*: the corallum is elongate, the stomata are mainly clustered at the centre and the dentations are long and slim.

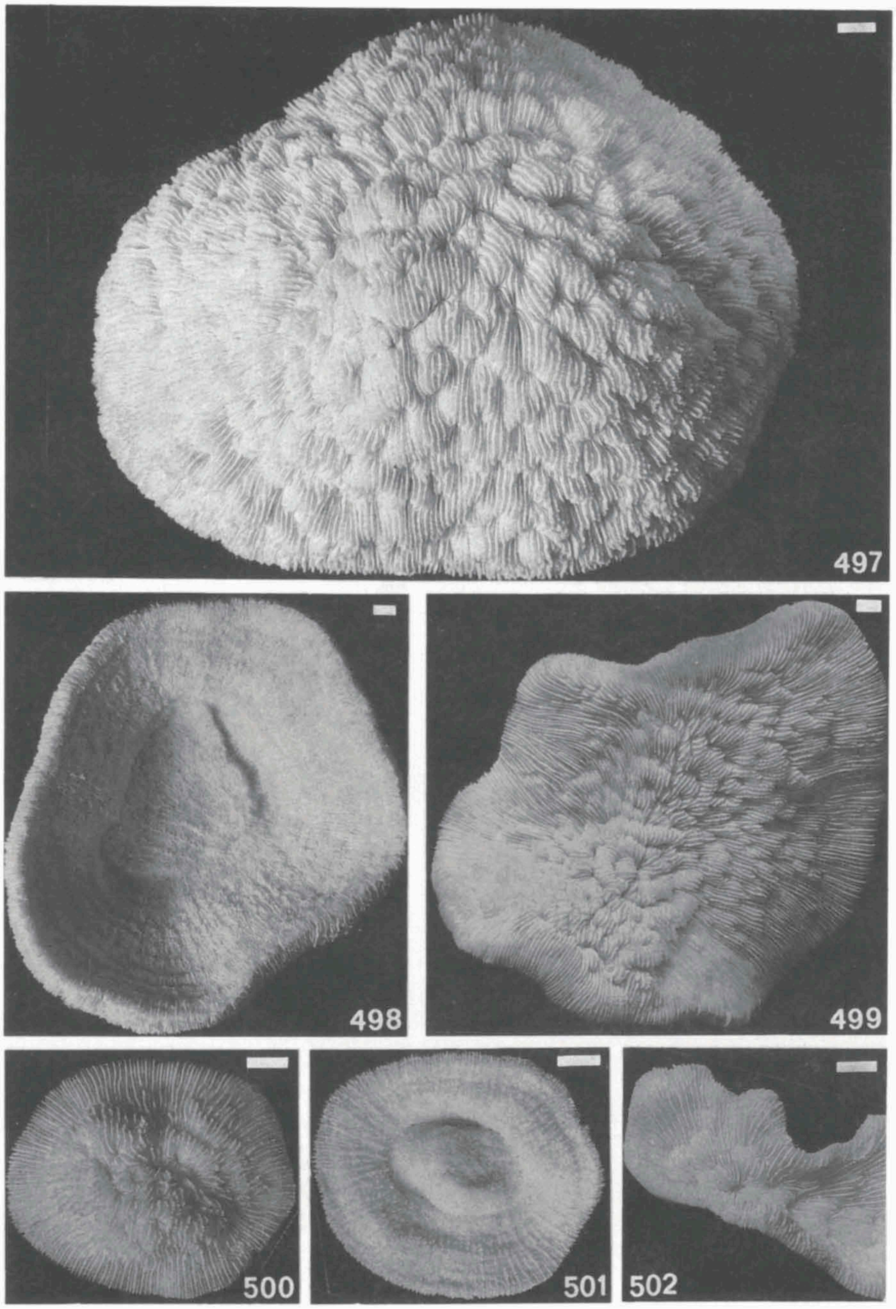
In skeleton morphology, *S. dentata* differs clearly from its closest relative, *S. robusta* by (1) its longer and sharper septal ornamentations, (2) more protruding lower order septa, (3) secondary stomata which are not produced by peripheral budding, resulting in a more clustered distribution, especially in juvenile specimens, and (4) a more elongate outline. The coloration of the two species may also be different; in Indonesia, animals of *S. robusta* are in general more evenly coloured than those of *S. dentata*.

Sandalolitha robusta (Quelch, 1886)
(figs. 30, 497-506, 656-657)

Fungia pileus — Lamarck, 1815: 236-237 (partim; including: ? var. *oblonga* Lamarck, 1815 ["l'Océan des Grandes Indes"]).
Podabacia robusta Quelch, 1886: 140-141, pl. 6 fig. 5-5b ("Amboina", Moluccas); Studer, 1901: 415-416; Bedot, 1907: 221-222, pl. 32 figs. 165-168; Matthai, 1923: 78.
Halomitra irregularis Gardiner, 1898: 528-529, pl. 63 figs. 1-2 (Funafuti); Ma, 1937: 146, pl. 40 figs. 5-6.
Podabacia irregularis — Studer, 1901: 415.
Halomitra robusta — Boschma, 1925: 242-249 (partim), pl. 8 fig. 104, pl. 9 figs. 107, 112, 116, 120, pl. 10 figs. 130-131; Boschma, 1929: 46; Thiel, 1932: 84-87, pl. 11 figs. 1-2; Yabe & Sugiyama, 1935: 396-397; Ma, 1937: 145-146, pl. 70 figs. 1-2; Abe, 1938: 484-488, figs. 8-10; Eguchi, 1938: 364; Umbgrove, 1939: 45, pl. 14 figs. 1-2; 1940: 295-296, pl. 27 fig. 2; Yabe & Sugiyama, 1941: 82, pl. 81 fig. 3-3a, pls. 84-85, pl. 86 fig. 3; Crossland, 1952: 155; Sukarno, 1974: 14; Chevalier, 1979: 132.
Döderleinia irregularis — Gardiner, 1909: 282, pl. 39 figs. 27-28; Yonge, 1930: 38-39.
Doederleinia irregularis — Van der Horst, 1921: 70-71, pl. 4 fig. 2.
Doederleinia robusta — Van der Horst, 1921: 69-70, pl. 4 fig. 1.
Halomitra sluiteri — Ma, 1937: 146, pl. 72 figs. 1-2
Parahalomitra irregularis — Wells, 1937: 74; Nemenzo, 1955: 79-80, pl. 13 figs. 4-5; Shirai, 1980: 532; Nemenzo, 1981: 203, figs. 230a-b; 1986: 157, figs. 184-185.
Parahalomitra robusta — Vaughan & Wells, 1943: pl. 19 fig. 3; Wells, 1954: 449-450, pl. 161 figs. 4-5, pl. 162 figs. 1-2; Nemenzo, 1955: 80-81, pl. 1 fig. 4; Stephenson & Wells, 1955: 27; Wells, 1966: 242; Zou, Song & Ma, 1975: 31-32, pl. 8 fig. 2; Ditlev, 1976: 7; Maragos & Jokiel, 1978: 62; Zou, 1978: 101-102, pl. 7 figs. 1-2; Phillipps, 1979: 335, pl. 7; Ditlev, 1980: 58, fig. 246; Betterton, 1981: 206, pl. 90; Nemenzo, 1981: 205, fig. 231; 1986: 158, fig. 186. Not: Shirai, 1980.
Sandalolitha robusta — Pillai & Scheer, 1976: 46-47, pl. 18 figs. 3-4; Veron & Pichon, 1979: 190-193 (partim), figs. 315-318; Randall & Myers, 1983: 20 (partim); Wood, 1983: 126-127, 145 (partim); Wallace, 1984: 38, fig. 22.4; Johnston, 1986: 159; Nakamori, 1986: pl. 14 figs. 4a-b, pl. 24 fig. 3; Veron, 1986a: 32 (partim); 1986b: 356-357; Nishihira, Yanagiya & Sakai, 1987: 56; Sakai & Yamazato, 1987: 46; Veron & Marsh, 1988: 86 (partim). Not: Wood & Tan, 1987; Veron & Kelley, 1988.
Parahalomitra sp. — Phillips, 1978: 101, pl. 8A; Green, Harris, Robertson & Santavy, 1979: 299, fig. 19.

Type material examined. — BMNH 1886.12.9.216 (holotype of *Podabacia robusta*; type loc. Ambon, INDONESIA); UMZC (holotype of *Halomitra irregularis*; type loc. Funafuti, ELLICE IS.)

Other material. — JAPAN: ZMA 273. PHILIPPINES. SW Luzon: USNM 77932. E Mindoro: UPZD 453. Basilan I.: USNM 77982. MALAYSIA. Sabah: USNM 47965. INDONESIA. NW Java: RMNH 9328, 16042-16043, 16046-16047. SW Sulawesi: RMNH 15231-15232, 15745, 16172 (2), 16207-16209 (14), 20671. Tiger Is.: RMNH 21079. Togian Is.: RMNH 9606-9614. NE Sumba: RMNH 20240. W Timor: ZMA 274. Tukang Besi Is.: RMNH 15748, 20056, 20148. Moluccas: ZMA 268-269, 271-272. Ambon: BMNH 1946.1.1.14. Halmahera: RMNH 15747. Lucipara Is.: ZMA 267. Banda: RMNH 8401-8402, 8433. Tanimber Is.: RMNH 15749 (2). Kei Is.: RMNH 15770. AUSTRALIA. Kimberley: WAM 1608.88. Northern territory: BMNH 1892.12.1.624, 1931.11.7.31. AUSTRALIA. Torres Str.: AMNH 3159. N Great Barrier Reef: QMB G3079, G8053-8055, GBR337. C Great Barrier Reef: BMNH 1892.12.1.429/437, 1897.3.9.151, 1934.5.14.153/155-156/208, QMB G3078, G6717, G7044, GBR281, RMNH 9605. S Great Barrier Reef: QMB G6773, QMT. PAPUA NEW GUINEA. Bismarck Sea: ULB. PALAU IS.: USNM

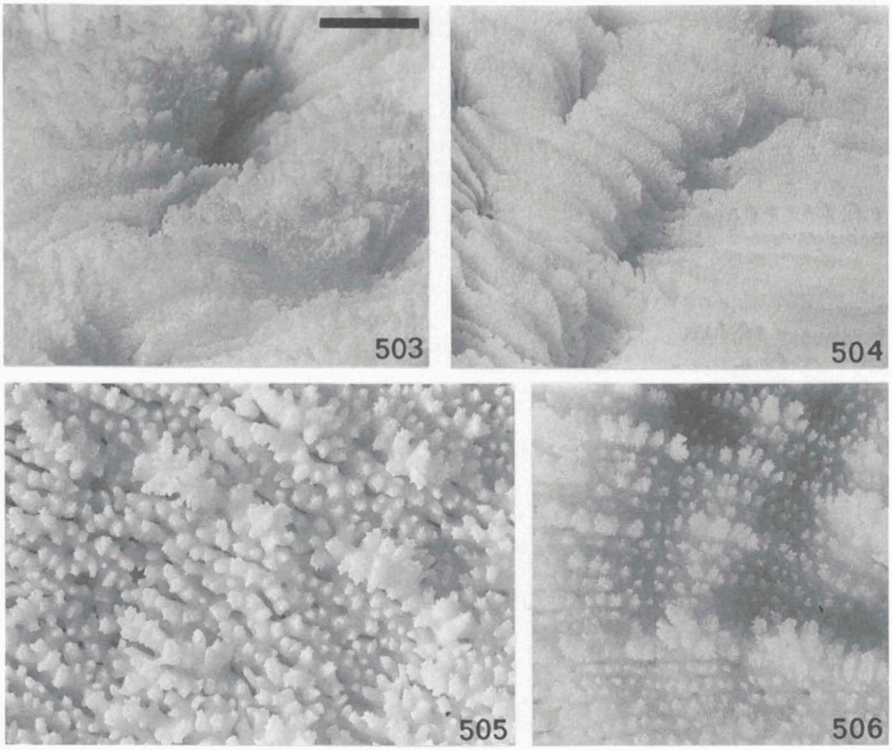


Figs. 497-502. Corals (anthocyathi) of *Sandalolitha robusta*. Scale bars: 1 cm. Figs. 497-498. Upper and lower surface of the holotype of *Podabacia robusta*, a regenerated fragment (BMNH 1886.12.9.109; Ambon, Indon.). Fig. 499. A flat coral (RMNH 16046; NW Java, Indon.). Figs. 500-501. A small coral (RMNH 16045; NW Java). Fig. 502. A small anthocyathus (RMNH 16044; NW Java).

78016-78019 (5), 78037, 78041 (3). SOLOMON IS.: BMNH 1884.12.11.6, 1938.3.17.13. NEW CALEDONIA: MNHN 1840, USNM 78068, ZMA 6291-6292, 6378. COOK IS.: GPC.

Characters. — Adult animals are free-living. The polyps are polystomatous by circumstomadaeal (especially peripheral) budding. Their outline varies from irregularly circular to oval. There are no fragmentation clefts in the corallum wall. The coralla are thick and vary from highly arched to a slightly cup-shaped, with a concave upper surface. The length of the coralla varies between 2.5 and 44.5 cm.

The septa are densely packed and straight, except around the stomata, where they bend. The septa of lower orders are thicker and more protruding than those of higher orders. The septa are fenestrate; especially higher order septa, which are much perforated (fig. 656). Tentacular lobes are absent. The septal margins are coarsely ornamented with irregularly lobate dentations (figs. 503-504, 656). Their number varies from 14 to 25 per cm. The septal sides are thinly to densely granulated. The granulations are almost evenly dis-



Figs. 503-506. Close-ups of *Sandalolitha robusta* corals. Scale bar: 0.5 cm. Fig. 503. Septa of the holotype (see fig. 497). Fig. 504. Septa of the coral in fig. 499. Fig. 505. Costae of the holotype (see fig. 498). Fig. 506. Costae of the coral in fig. 499.

tributed or arranged in indistinct rows perpendicular to the septal margin (fig. 656). The compound synapticulae connecting the septa laterally cannot always easily be distinguished, because of the tight septal arrangement.

The stomata are distributed almost evenly over the coral surface. There is a narrow margin without any stomata. The columellae are poorly developed; they are formed by loosely packed trabeculae and paliform lobes with the tips pointing in various directions.

The corallum wall is perforated and covered by granulations. A large detachment scar (diameter more than 1 cm) is only distinct at the aboral side of small specimens in anthocyathus-stage. The costae are unequal in thickness and height; they are straight and distinct near the corallum margin, but less distinct near the centre. All costae are coarsely ornamented with short echinous spines (figs. 505-506, 657). The number of the costal spines varies from 11 to 26 per cm.

The living animal is usually brown (fig. 30), but may alternatively be green or ochre coloured. The small tentacles are usually colourless and translucent; they are inconspicuous because of their small size.

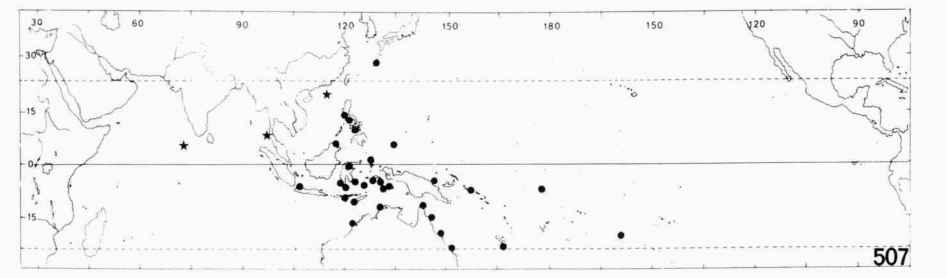


Fig. 507. The range of *Sandalolitha robusta*. Records are from examined material (●) and published illustrations (★).

Geographical distribution (fig. 507). — *S. robusta* has its most western location at the Maldives, in the Indian Ocean. In the Pacific its area reaches towards southern Japan, eastern Australia, New Caledonia and the Ellice Islands.

Remarks. — The holotype of *Podabacia robusta* lacks a central, primary fossa because it regenerated from a fragment (figs. 497-498). In septal and costal ornamentations it is equal to the holotype of *Halomitra irregularis*.

The differences between *S. robusta* and *S. dentata* are discussed in the remarks on the other species. *S. robusta* can be confused with free-living, regenerated fragments of *Podabacia crustacea*, but the latter species has finer septal dentations.

Zoopilus Dana, 1846

Type species: *Zoopilus echinatus* Dana, 1846. By monotypy.

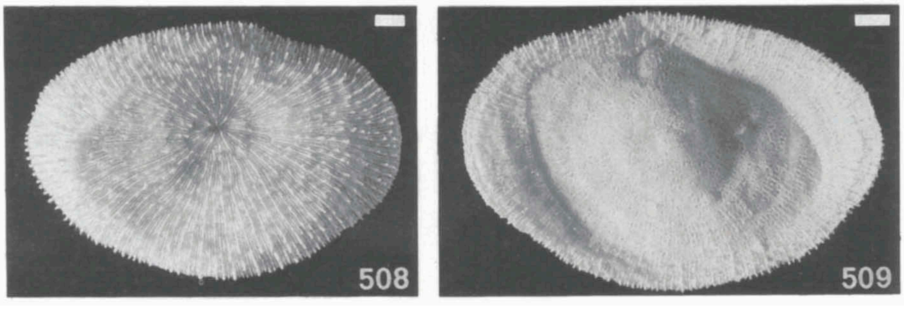
Zoopilus Dana, 1846: 318-319; Milne Edwards & Haime, 1849: 72; 1850: xlviii; Duncan, 1885: 146; Vaughan & Wells, 1943: 144; Wells, 1956: 390; 1966: 241; Nemenzo, 1976: 244; 1981: 205; 1986: 158; Chevalier & Beauvais, 1987: 710.
Zoophilus — Ditlev, 1980: 57. (Incorrect spelling).

Characters. — Adult animals are free-living. The polyps are polystomatous by circumstomadaeal budding. Their outline is irregularly oval. The corallum wall is perforated. The coralla vary from flat to highly arched; they are thin and very fragile. The septal and costal ornamentations are relatively coarse. The granulations on the septal sides are irregularly distributed.

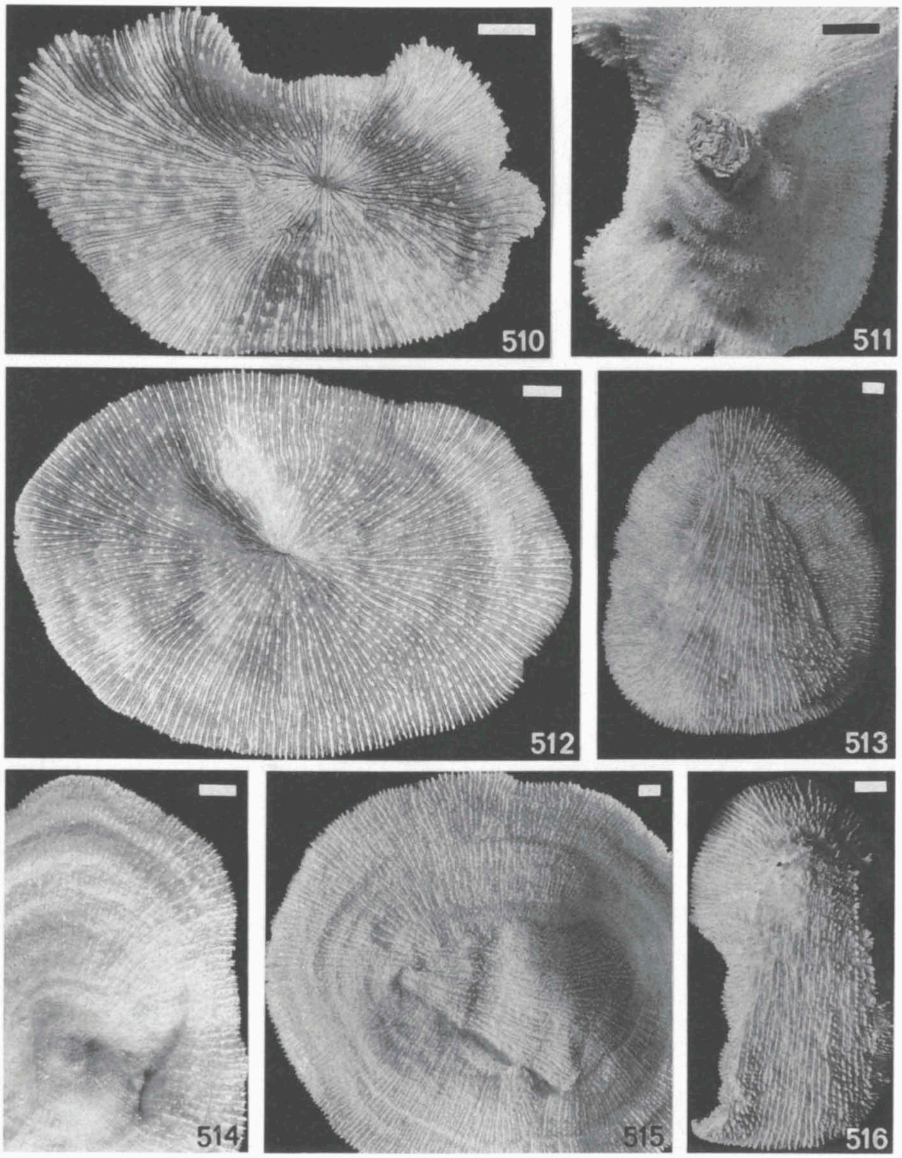
Remarks. — In overall corallum shape, this monospecific genus resembles *Halomitra* and *Sandalolitha*, the latter of which it has an oval corallum outline in common. The septal and costal ornamentations of *Zoopilus* are almost identical to those of *Ctenactis*. They also resemble those of *Sandalolitha* and *Podabacia*, although in the species of the latter genus the septo-costal ornamentations are finer.

Zoopilus echinatus Dana, 1846
(figs. 31, 508-523, 660-661)

Zoopilus echinatus Dana, 1846: 319, pl. 21 fig. 6-6a ("Feejee Islands"); Verrill, 1864: 53; Giebel, 1879: 322-324; Vaughan & Wells, 1943: pl. 19 fig. 2; Wells, 1966: 241; Wood, 1983: 130-131, 145 (partim); Johnston, 1986: 159; Veron, 1986b: 588, 591; Wood & Tan, 1987: 198. Not: Nemenzo, 1976; 1981; 1986.
Halomitra echinata — Boschma, 1925: 235-237, pl. 10 figs. 123-125, pl. 11 figs. 134-135.
Zoophilus echinatus — Ditlev, 1980: 57, fig. 238. (Incorrect spelling).



Figs. 508-509. Upper and lower surface of a small anthocyathus of *Zoopilus echinatus* (RMNH 22113; SW Sulawesi, Indon.). Scale bar: 1 cm.



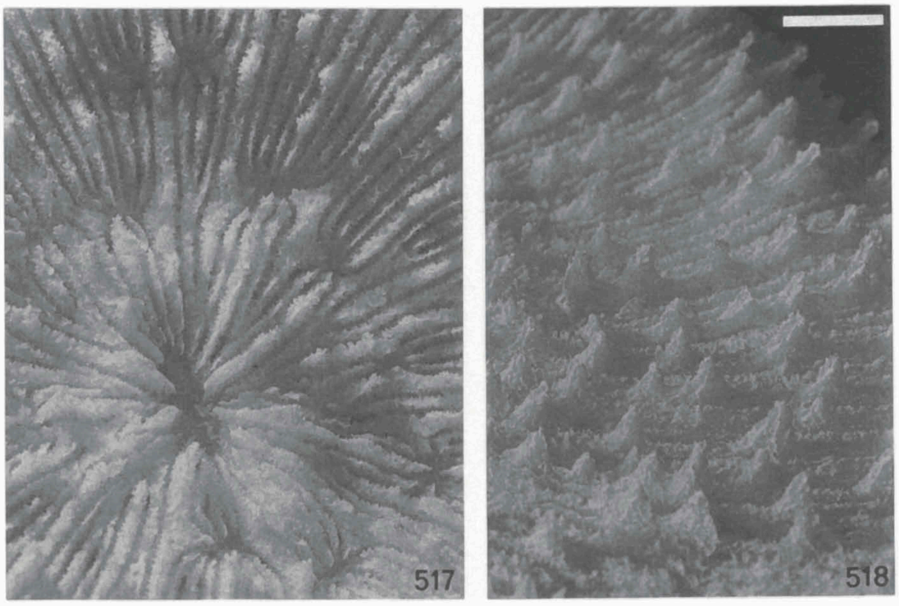
Figs. 510-516. Corals of *Zoopilus echinatus* (Indonesia). Scale bars: 1 cm. Figs. 510-511. Upper and part of lower surface of an anthocaulus broken-off from the substratum with the stalk (RMNH 22112; SW Sulawesi). Fig. 512. Upper surface of a medium-sized coral (RMNH 20880; Komodo). Fig. 513. Upper surface of a regenerated fragment (RMNH 15772; Halmahera). Fig. 514. Aboral surface of the coral in fig. 512. Fig. 515. Aboral surface of a regenerated fragment (RMNH 20880; Komodo). Fig. 516. As fig. 515 (RMNH 8413; Banda).

Type material examined. — USNM 154, MCZ 5420 (3), 5651, MNHN Fun243, YPM 1944, 4299 (syntypes of *Zoopilus echinatus*; type loc. FIJI).

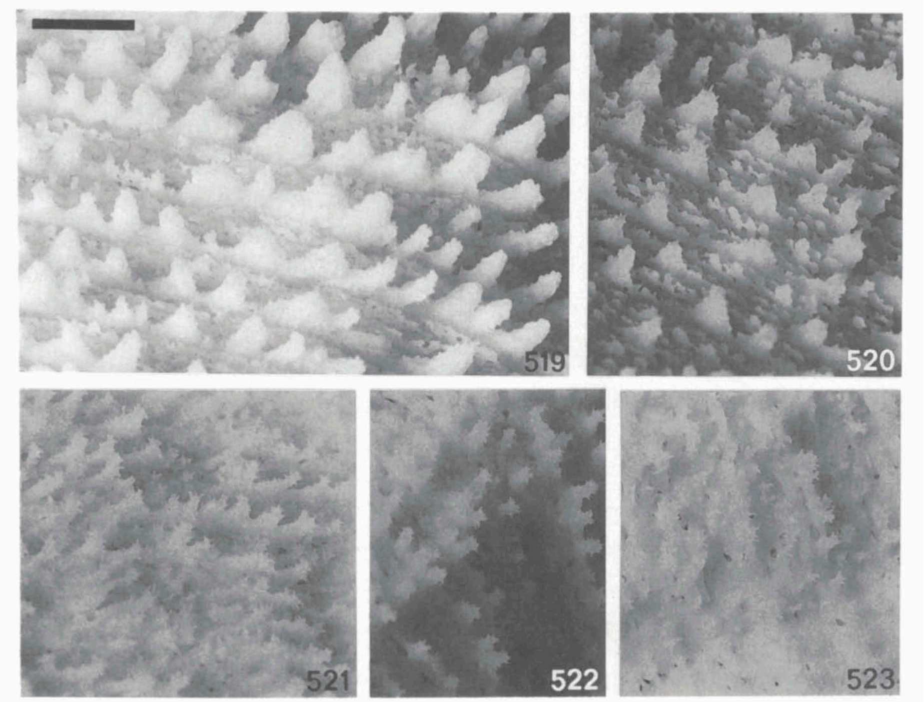
Other material. — MALAYSIA. Sabah: BMNH. INDONESIA. SW Sulawesi: RMNH 21026 (2), 22112-22116 (16). Komodo: RMNH 20416 (20), 21469. N Sumbawa: RMNH 21318, 21654 (2). Banda: RMNH 8412-8413 (3). Halmahera: RMNH 15772. PAPUA NEW GUINEA. Bismarck Sea: ULB. FIJI IS.: WAM 345.78. MARSHALL IS.: RMNH 14623, USNM 77848-77849.

Characters. — Adult animals are not attached. Polystomatism is achieved by circumstomadaeal budding. The outline of unbroken coralla is irregularly oval; the outline of regenerated fragments is very variable. The animals do not form fragmentation clefts in the corallum wall, but they may break vary easily due to their thinness and fragility. The coralla usually vary from flat to highly arched, although anthocauli and young anthocyathi may be slightly cup-shaped. The length of the specimens varies between 8.5 and 93.0 cm.

The septa are loosely packed and straight. The septa of lower order cycles are thicker and more exsert than those of higher orders. The septa are not just perforated, but they may be fenestrate as well (fig. 660). Tentacular lobes are absent. The septal margins are very coarsely ornamented with irregularly angular (or lobate), elongate and sharp dentations (figs. 518-520). Their number varies from 2 to 7 per cm. The septal sides are thinly granulated. The



Figs. 517-518. Close-ups of the oral surface of the *Zoopilus echinatus* coral in fig. 508 showing septa and the large primary fossa with small secondary ones around it. Scale bar: 0.5 cm.



Figs. 519-523. Close-ups of *Zoopilus echinatus* corals. Scale bar: 0.5 cm. Fig. 519. Septa of a coral (RMNH 146231 Enewetok, Marshall Is.). Figs. 520-523. Septa and costae of the coral in fig. 513.

granulations are either almost evenly distributed or arranged in indistinct rows perpendicular to the septal margin (fig. 660). The compound synapticulae connecting the septa laterally are not well developed but can easily be detected, because of the loose septal arrangement.

The primary stoma is relatively large and clear, whereas secondary stomata remain almost rudimentary and inconspicuous (fig. 517). In broken coralla the primary stoma is usually missing, making it appear as if the animals have no stomata at all. The columellae are either rudimentary and massive or consist of fused trabeculae and paliform lobes with the tips pointing in various directions.

The corallum wall is perforated with its lower surface covered by granulations. A detachment scar is distinct in corals in early anthocyathus-phase (fig. 509). It usually remains detectable in larger specimens (fig. 514) when these are unbroken. (The scar shown in fig. 511 is an artefact; it concerns an anthocaulus intentionally broken off its substratum). The costae differ in thickness and height. They are straight and distinct over their whole length. They are coarsely ornamented with elongate, echinose spines from which

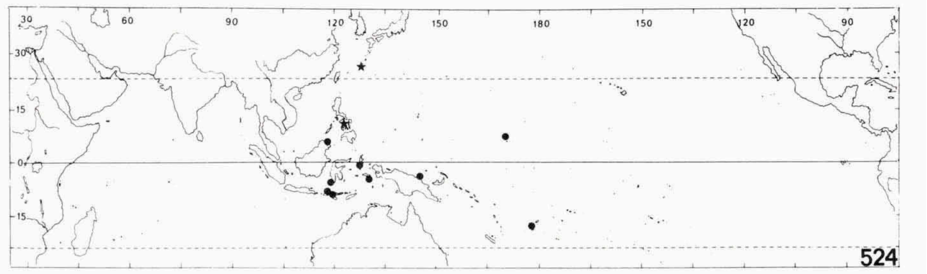


Fig. 524. The range of *Zoopilus echinatus*. Records are from examined material (●) and published illustrations (★).

many granulations or thin branches point in various directions (figs. 521-523, 661). The number of spines varies from 4 to 12 per cm costa.

The living animals are dark brown (fig. 31). The tentacles are transparent and colourless; they are inconspicuous because of their small size.

Geographical distribution (fig. 524). — The range extends from eastern Indonesia towards southern Japan, the Marshall Islands and the Fiji Islands. The locality closest to the Indian Ocean is Komodo Island (Indonesia).

Remarks. — Boschma (1925) classified the species with *Halomitra*, ignoring the differences in corallum outline and in septo-costal ornamentations. Boschma (1925) could not be aware of the oval corallum outline in *Zoopilus* because only broken coralla were available to him. A specimen which was identified as *Zoopilus echinatus* by Nemenzo (1976; 1981; 1986) actually belongs to *Halomitra clavator* spec. nov. It has a circular outline and shows club-shaped septal dentations.

Halomitra Dana, 1846

Type species: *Fungia pileus* Lamarck, 1801 [= *Halomitra pileus* (Linnaeus, 1758)]. By monotypy.

Halomitra Dana, 1846: 311; Milne Edwards & Haime, 1849: 71; 1850: xlviii; 1851: 96-97; 1860: 20-21; Duncan, 1885, 144; Quelch, 1886: 138-140; Studer, 1901: 405-408; Gardiner, 1909: 280; Van der Horst, 1921: 19; Boschma, 1925: 233-235; Vaughan & Wells, 1943: 142; Wells, 1956: 389; 1966: 243; Veron & Pichon, 1979: 186-187; Ditlev, 1980: 58; Nemenzo, 1981: 203; 1986: 156; Veron, 1986b: 354; Chevalier & Beauvais, 1987: 710.

Characters. — Adult animals are free-living. The polyps are mostly polystomatous by circumstomadaeal budding, in lesser degree by intra-stomadaeal budding of the secondary stomata. They are discoidal and vary from flat to highly arched. The corallum wall is perforated and its lower surface is granulated. The septal and costal ornamentations are coarse. The granulations on the septal sides are either arranged in rows or fused in ridges perpendicular to the septal margin.

Remarks. — The septal dentations and costal spines of *Halomitra* resemble those of *Fungia (Fungia)*. *Halomitra* differs mainly from the latter in the formation of secondary mouths around the centrally located primary mouth. This enables the corals to become much larger than those of *F. (Fungia)*. In overall shape *Halomitra* resembles *Zoopilus* and (in lesser degree) *Sandalolitha*, which both differ from *Halomitra* in the septo-costal structures.

In the present study two species are recognized, *H. pileus* and *H. clavator* spec. nov.

Halomitra pileus (Linnaeus, 1758)
(figs. 32, 525-538, 662-663)

Madrepora pileus Linnaeus, 1758: 794 ("O. Asiatico"); Pallas, 1766: 285-286 (partim); Boddaert, 1768: 353-356 (partim); Houttuyn, 1772: 118-119; Müller, 1775: 678; Wilkens, 1787: 26-30 (partim); Esper, 1791: 87-92, 287 (partim); Gmelin, 1791: 3758 (partim). Not: Ellis & Solander, 1786; Esper, 1797.

Fungia pileus — Lamarck, 1801: 370; 1815, 1816: 237-238 (partim); Lamouroux, 1824: 420; Blainville, 1830: 303; 1834: 337; Lamarck, 1836: 374.

Fongia pileus — Blainville, 1820: 217.

Halomitra pileus — Dana, 1846: 311-312, pl. 21 fig. 2-2b; Milne Edwards & Haime, 1851: 97; 1860: 21-22; Ortmann, 1888: 179; Studer, 1901: 409-411, pl. 23; Van der Horst, 1921: 72; Boschma, 1934: 4206, fig. 7; Boschma, 1959: 268-271, photo 27 fig. 1; Veron & Pichon, 1979: 187-189, figs. 311-314; Ditlev, 1980: 58, fig. 248; Wijsman-Best, Faure & Pichon, 1980: 612, pl. 10 fig. 5; Randall & Myers, 1983: 20, figs. 362-363; Wood, 1983: 123, 126, 144; Johnston, 1986: 159; Veron, 1986b: 354-355; Wood & Tan, 1987: 198; Veron & Kelley, 1988: 29; Hoeksema & Moka, 1989: figs. 10a-b.

Halomitra clypeus Verrill, 1864: 52 ("Feejee Islands").

Halomitra tiara Verrill, 1864: 53 ("Kingsmills Islands"); Quelch, 1886: 140; Studer, 1901: 411-412, pl. 25; Felix, 1920: 13-14; Van der Horst, 1921: 72-73; Faustino, 1927: 189-190.

Halomitra fungia — Studer, 1877: 646-647.

Halomitra concentrica Studer, 1901: 412-413, pl. 26 (Palau Islands); Faustino, 1927: 190-191, pl. 61.

Podabacia philippinensis Studer, 1901: 414-415, pl. 28 fig. 7 (Philippines).

Halomitra philippinensis — Gardiner, 1905: 942; 1909: 280-281; Boschma, 1925: 237-242, pl. 8 figs. 93-98, pl. 9 figs. 105-106, 111, 118-119, 121, pl. 11 figs. 127, 129; Faustino, 1927: 192-194, pls. 62-63; Thiel, 1932: 84, pl. 12 fig. 1; Ma, 1937: 145, pl. 71 fig. 1, pl. 96 fig. 4; Eguchi, 1938: 364-365; Yabe & Sugiyama, 1941: 82, pl. 81 fig. 1-1c, pls. 82-83; Vaughan & Wells, 1943: pl. 19 fig. 4; Matthai, 1948: pl. 3 fig. 1; Wells, 1954: 449; Nemenzo, 1955: 78-79, pl. 14 figs. 5-6; Talbot, 1965: 463; Wells & Davies, 1966: 48; Rosen, 1971a: 76; Pillai, 1972: 203; Pichon, 1974: 176, fig. 10; Pillai & Scheer, 1976: 45; Maragos & Jokiel, 1978: 61; Zou, 1978: 102; Nemenzo, 1981: 203, fig. 229; Hamilton & Brakel, 1984: 252; Nemenzo, 1986: 157, fig. 183.

Halomitra louwinae Van der Horst, 1921: 73, pl. 3 figs. 1-2 (Banda); Van Soest, 1979: 107.

Doederleinia vetusta Gerth, 1925: 39-40, pl. 6 figs. 3-3a (Miocene, "Linggapdang bei Margasari", Java). (New synonymy).

Halomitra vetusta — Umbgrove, 1946b: 535-536, pl. 80 fig. 4.

Zoopilus gomezi Nemenzo, 1980: 295-296, 298, fig. 6 (Pangangan I., Bohol). (New synonymy).
Sandalolitha robusta — Wood, 1983: 126-127, 145 (partim); Wood & Tan, 1987: 197-198, pl. 8a.

Type material examined. — MCZ 548, 7513, MNHN Fun226, USNM 159, YPM 1962 (syntypes of *Halomitra clypeus*; type loc. FIJI); MCZ (holotype of *Halomitra tiara*; type loc. KINGSMILL IS.); ZMA 518, 521 (syntypes of *Halomitra louwinae*; type loc. Banda, INDONESIA); RGM 3892 (holotype of *Doederleinia vetusta*; type loc. Java, INDONESIA); UPMSI 4 (holotype of *Zoopilus gomezi*; type loc. Pangangan I., Bohol, Philippines); UPSMI 70-71, 185, 187 (paratypes of *Zoopilus gomezi*; Pangangan I., Bohol, PHILIPPINES).

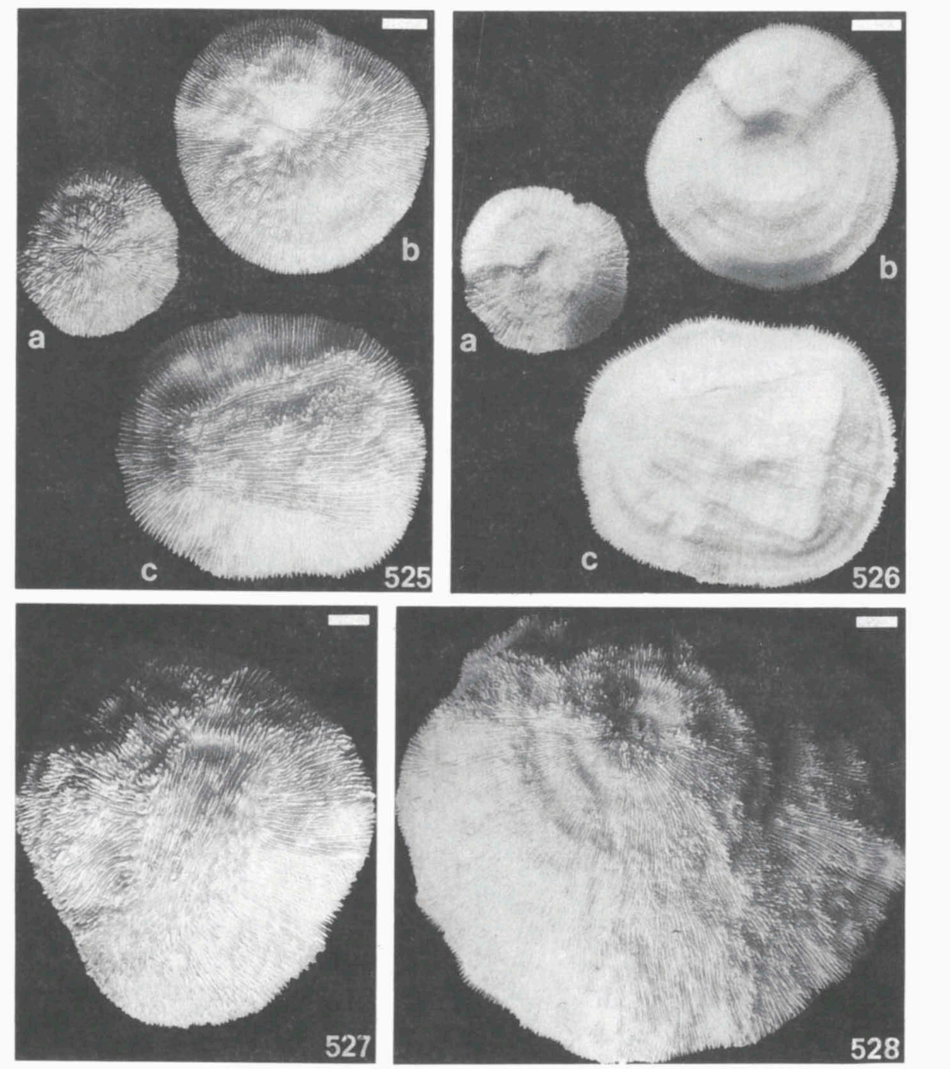
Other material. — TANZANIA: USNM 78430. ZANZIBAR: BMNH 1955.10.11.21. N MADAGASCAR: USNM 77730 (2). SEYCHELLES: BMNH 1950.1.11.693. CHAGOS IS.: BMNH 1891.4.9.21/23-24., 1970.7.30.36-37, USNM 77767 (2). MALDIVES: RMNH 14202, 14218. PHILIPPINES. Cebu: BMNH 1886.12.9.208. Malaysia. Malaya: BMNH 1979.9.25.1. INDONESIA. NW Java: RGM 77664 (fossil), RMNH 16125-16128. SW Sulawesi: RMNH 15233-15234, 20835 (4), 21025, 22106-22110 (13). Tiger Is.: RMNH 21078 (2), 21120, 21173 (3). Komodo: RMNH 21467 (5), 21516 (3). N Sumbawa: RMNH 21675. Timor: RMNH 13896. Moluccas: ZMA 270, 515, 6901 (2). Ambon: RMNH 8388. Obi Latu: RMNH 15743-15744 (3). Banda: RMNH 8399, 8408 (14), 8410-8411 (33), 9409 (9), 9598 (2), USNM 78426-78427, ZMA 508. PALAU IS.: USNM 47092. CAROLINE IS.: USNM 77774, 77790 (4). PAPUA NEW GUINEA. Bismarck Sea: QMB G1069, ULB. AUSTRALIA. Torres Str.: MCZ 7512. C Great Barrier Reef: BMNH 1897.3.9.149/155/157/167, 1934.5.14.154, QMB G2932. SOLOMON IS.: BMNH 1884.12.11.7, 1938.3.17.6-8/10-12. MARSHALL IS.: USNM 77819 (2), 78429. GILBERT IS.: USNM 77773 (2), 77916 (3). FIJI IS.: ANSP 1498. TONGA IS.: BMNH 1891..3.6.111/116. SAMOA IS.: AMNH 629. PHOENIX. IS.: USNM 78422, 78428.

Characters. — Adult animals are not attached. The polyps are polystomatous by circumstomadaeal budding and by intrastomadaeal budding in some of the secondary stomata. The outline of the coralla varies from irregularly circular to slightly oval. The coralla are usually thin, but sometimes thick; they vary from flat to highly arched. There are no fragmentation clefts in the corallum wall. The diameter of the specimens varies between 2.0 and 63.0 cm.

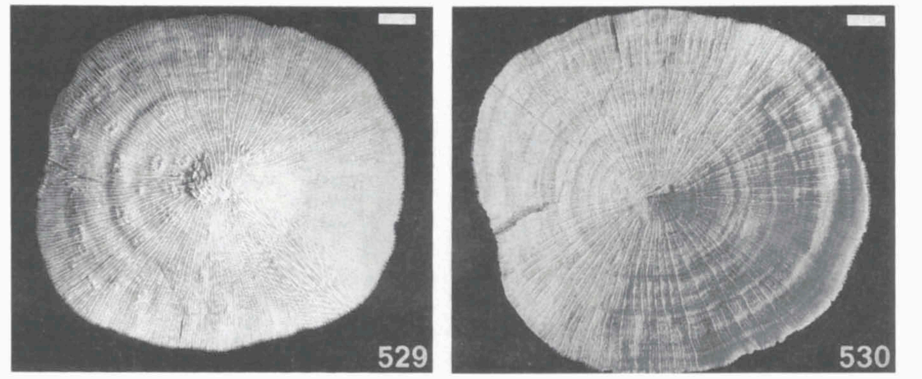
The septa are loosely packed and straight. The septa of lower orders are thicker and more exsert than those of higher orders. Septa of low orders are solid, whereas those of higher orders may be perforated. All septa are highest near a mouth, where they support a tentacle. Tentacular lobes, when present, are not always distinct. The septal margins are coarsely ornamented with irregularly angular and sharp dentations (figs. 531, 533, 535, 537). Their number varies from 5 to 15 per cm. The septal sides are thinly granulated. The granulations are fine. At the septal base they are evenly distributed, whereas at the septal fringe they are either arranged in rows or fused in ridges perpendicular to the septal margin (fig. 662). The compound synapticulae connecting the septa laterally can easily be distinguished, because of the loose septal arrangement.

All stomata are distinct. They are unevenly distributed, some of them in pairs as a result of intrastomadaeal budding. The primary stoma is usually located at the centre, with the secondary stomata around it, but when a corallum regenerates from a fragment the primary stoma is usually lacking. The columellae are either massive and rudimentary or formed by partly fused trabeculae and paliform lobes with the tips pointing in various directions.

The corallum wall is perforated and its lower surface is covered with



Figs. 525-528. Corals (anthocyathi) of *Halomitra pileus* (Indonesia). Scale bars: 2 cm. Figs. 525-526. Upper and lower surface of three small corals: (a) RMNH 15233 (SW Sulawesi), (b-c) RMNH 16127, 16125 (both NW Java) of which the latter a regenerated fragment lacking the central fossa. Fig. 527. Upper surface of a syntype of *Halomitra louwinae* (ZMA 518; Banda), a regenerated fragment. Fig. 528. Upper surface of a coral (RMNH 16128, NW Java).



Figs. 529-530. Upper and lower surface of the holotype of *Zoopilus gomezi* (= *Halomitra pileus* UPMSI 4; Bohol, Philipp.) Scale bars: 2 cm.

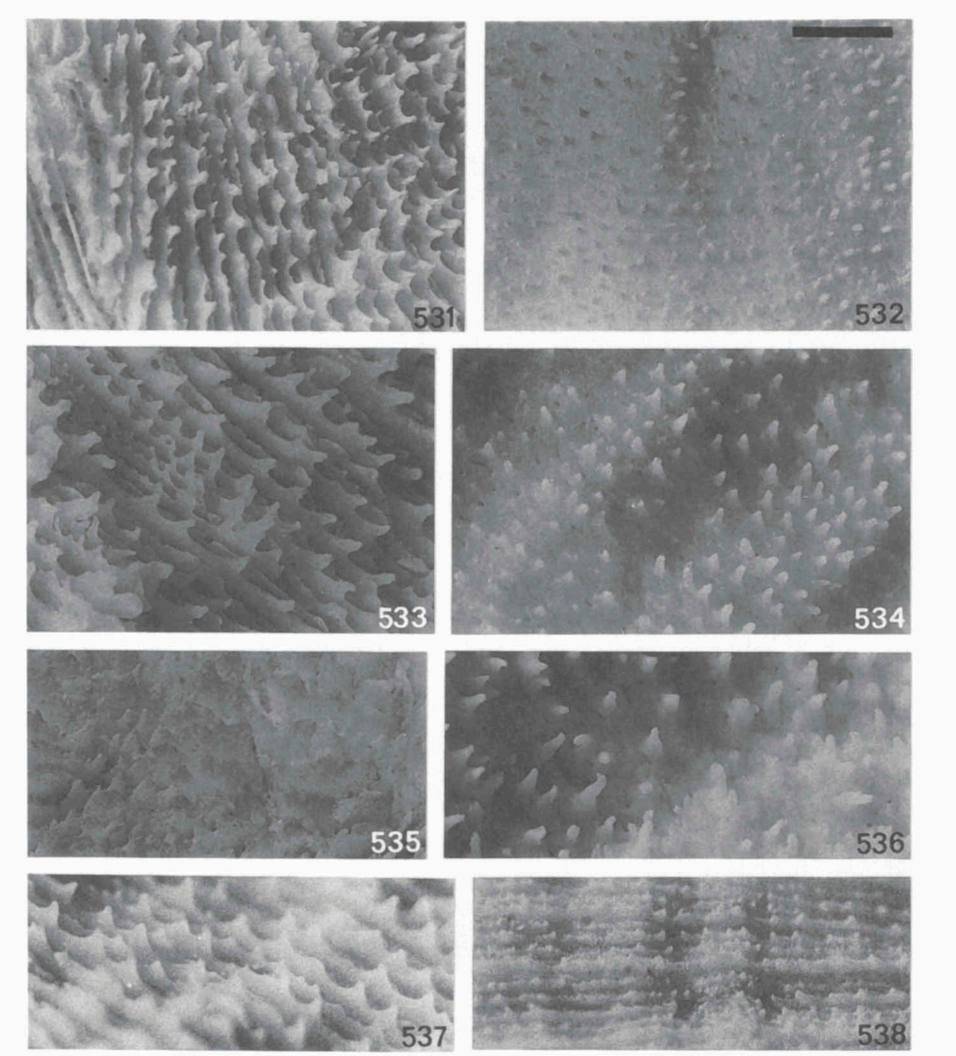
granulations (fig. 663). A detachment scar may be detected at the aboral side of small specimens in anthocythus-stage. The costae may differ in thickness and height. They are straight and distinct near the corallum margin, but become less prominent near the centre. All costae are coarsely ornamented with cone-shaped spines which are granulated at the tips (figs. 532, 534, 536, 538, 663). Their number varies from 8 to 12 per cm.

The animals are usually ochre-like brown with a violet margin (fig. 32). The mouths are white. The small tentacles are translucent and colourless.

Geographical distribution (fig. 539). — The species occurs in an area which extends from the southwestern part of the Indian Ocean towards the Central Pacific (Guam, the Marshall Islands, Phoenix Islands, Samoan and Tonga Islands).

Remarks. — Not all type specimens of nominal taxa mentioned in the synonymy could be traced. Concerning *Madrepora pileus*, Linneaus (1758: 794) referred to a coral illustrated by Rumphius (1750: pl. 88 fig. 3), who named it *Mitra polonica*. This coral, the holotype of *H. pileus*, was curated in Florence, but was reported as lost by Martelli (1903). The illustration of the holotype is clear enough to reveal its identity and therefore it is not necessary to designate a neotype of *H. pileus*.

The holotypes of *Halomitra concentrica* and *Podabacia philippinensis* are lost. However, the photographs published with the original descriptions are sharp enough to show that these specimens belong to *H. pileus*. The holotype of *H. tiara* and the syntypes of *H. clypeus* and *H. louwinae* have anomalous growth-forms (see e.g. fig. 527), which "distinguishes" them from regularly formed specimens of *H. pileus*. The holotype of *Doederleinia vetusta* is a fossil specimen of *H. pileus* which does not show any distinctive characters. The holotype and paratypes of *Zoopilus gomezi* (figs. 529-530) have a thin shape, like some of the *H. pileus* specimens from Banda (see material) which were originally described by Boschma (1925). These thin coralla are more fragile than usual and may break easily. However, they fit in a range of shapes, varying in thickness and their septal dentations and costal spines (figs. 537-



Figs. 531-538. Close-ups of *Halomitra pileus* corals. Scale bar: 0.5 cm. Figs. 531-532. Septa and costae of the coral in figs. 525b and 526b. Figs. 533-534. Septa and costae of the coral in figs. 525c and 526c. Figs. 535-536. Septa and costae of the coral in figs. 525a and 526a. Figs. 537-538. Septa and costae of the holotype of *Zoopilus gomezi* (see figs. 529-530).

538) do not differ from those observed in specimens of *H. pileus*. Therefore the type specimens of *Zoopilus gomezi* are considered examples of an extremely thin variety of *H. pileus*.

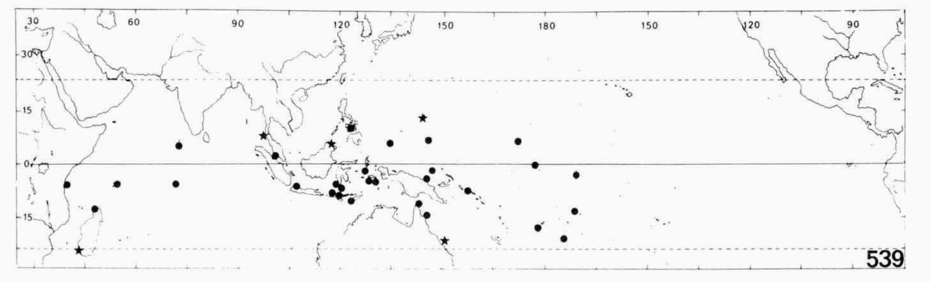


Fig. 539. The range of *Halomitra pileus*. Records are from examined material (●) and published illustrations (★).

Halomitra clavator spec. nov.
(figs. 33, 540-552)

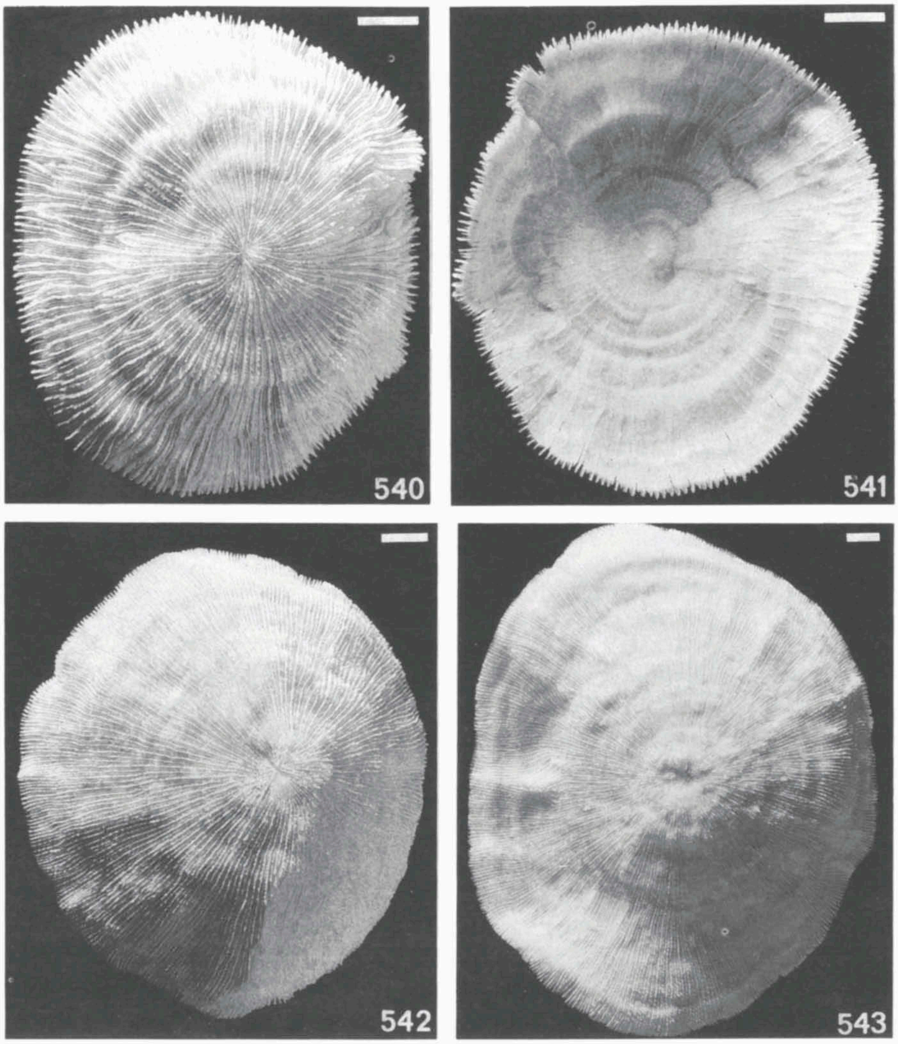
Zoopilus echinatus — Nemenzo, 1976: 244-245, pl. 7 fig. 1; 1981: 205, fig. 232; 1986: 159, fig. 187.

Type material. — RMNH 21468 (holotype of *Halomitra clavator*; type loc. Snellius-II Exped. Sta. 4.253, S coast of islet Gili Lawa Laut, NE Komodo, INDONESIA); RMNH 21457 (paratype of *H. clavator*; same loc.); RMNH 22111 (paratype of *H. clavator*; W side of Pulau Badi, Spermonde Archipelago, SW Sulawesi, INDONESIA).

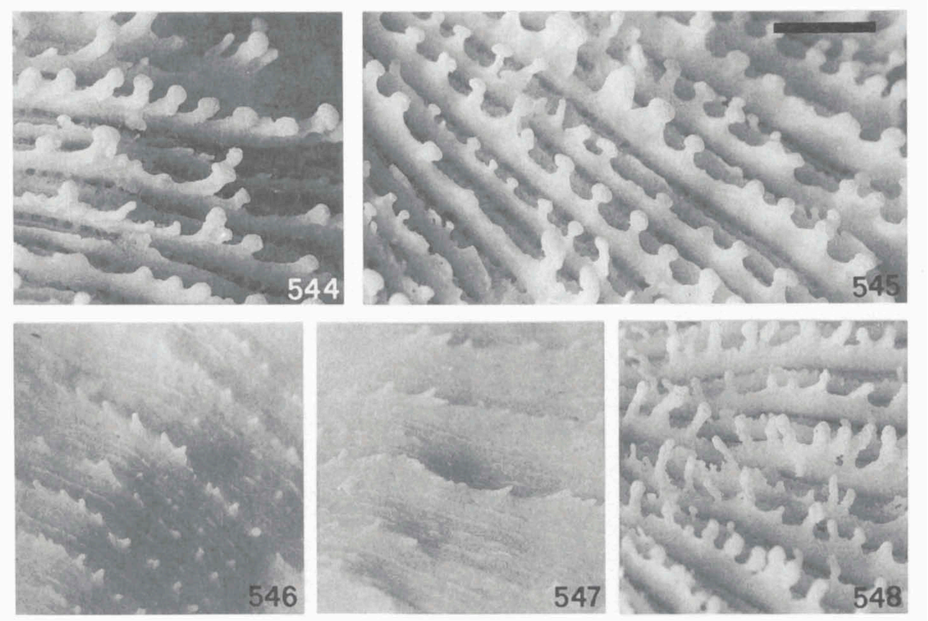
Characters. — Adults animals are free-living. The polyps are polystomatous by polystomadaeal budding. Their outline is irregularly circular. At the periphery there are clefts in the corallum wall which may facilitate fragmentation (fig. 541). All specimens are unbroken and arched. Their diameter varies between 25.0 and 38.0 cm.

The septa are loosely packed and straight. The septa of lower orders are thicker and more protruding than those of higher orders. The septa are rarely perforated. Tentacular lobes are absent. The septal margins are coarsely ornamented with long, club-shaped dentations with thickened, granulated tips (figs. 544-545, 548-550). Their number varies from 5 to 11 per cm. The septal sides are thinly granulated. The granulations are fine and unevenly distributed, although at the sides of the dentations they may fuse into indistinct ridges perpendicular to the septal margin. The compound synapticulae connecting the septa laterally can easily be distinguished, because of the loose septal arrangement. The stomata are not clear; usually they can only be seen as small interruptions of the septa. The columellae are poorly developed and massive. In the youngest stomata the columella may not yet be developed.

The corallum wall is perforated and covered by fine granulations. A detachment scar is distinct at the aboral side of all specimens in anthocyathus phase. The costae differ in thickness and height. They are straight and distinct near the corallum margin, whereas they are less distinct near the centre. The lower order costae are coarsely ornamentated with cone-shaped spines which are



Figs. 540-543. Holotype and paratypes of *Halomitra clavator* from Indonesia. Scale bars: 2.5 cm. Figs. 540-541. Upper and lower surface of the holotype (RMNH 21468; Komodo) with distinct clefts in the corallum wall. Fig. 542. Upper surface of a paratype (RMNH 21457; Komodo). Fig. 543. Upper surface of a paratype (RMNH 22111; Badi I., Spermonde Archipelago, SW Sulawesi).



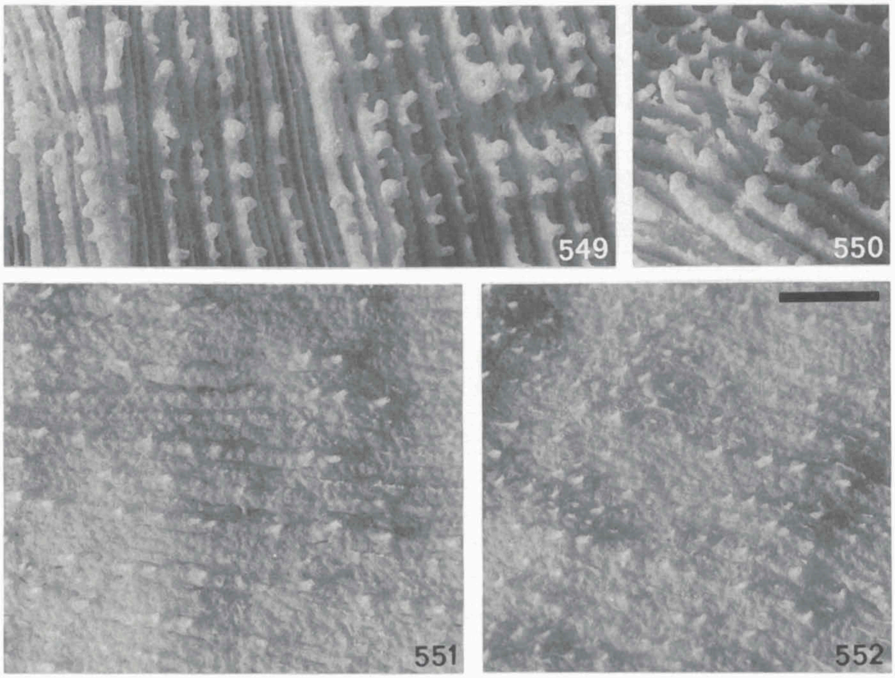
Figs. 544-548. Close-ups of the holo- and a paratype of *Halomitra clavator*. Scale bar: 0.5 cm. Figs. 544-545. Septa of the holotype showing club-shaped dentations. Figs. 546-547. Costae of the holotype. Fig. 548. Septa of the paratype from Komodo (see fig. 542).

granular at the tips (figs. 546-547, 551-552). The spines of the higher order costae are undeveloped or remain rudimentary. Their number varies from 5 to 15 per cm.

In the field the species can easily be recognized by its colouration: an ochre-like brown with a slightly lighter margin (fig. 33). The small tentacles are translucent and colourless.

Geographical distribution (fig. 553). — The species was discovered off Komodo Island, Indonesia, where two specimens were found in a sheltered bay. Another specimen was found in the Spermonde Archipelago, SW Sulawesi, just above a reef base, were little wave action is expected to occur (fig. 33). A specimen from Cebu (Philippines) originally described as *Zoopilus echinatus* by Nemenzo (1976) actually belongs to the same species

Remarks. — All specimens from Indonesia are in unbroken condition, but they are so thin that it is very likely that the species also exists in broken and regenerated shape. The specimen illustrated by Nemenzo (1976; 1981; 1986) is broken, but not regenerated. It is round with the central fossa still present; and was probably damaged after collecting. Its discoidal shape distinguishes it from *Zoopilus echinatus*, which has an oval outline. Its septal dentations are club-shaped ("blunt pointed"), which is clearly visible in Nemenzo's figures.



Figs. 549-552. Close-ups of the paratype of *Halomitra clavator* from SW Sulawesi (see fig. 543). Figs. 549-550. Septa and stomata from above and from aside. Figs. 551-552. Costae and perforations in the wall.

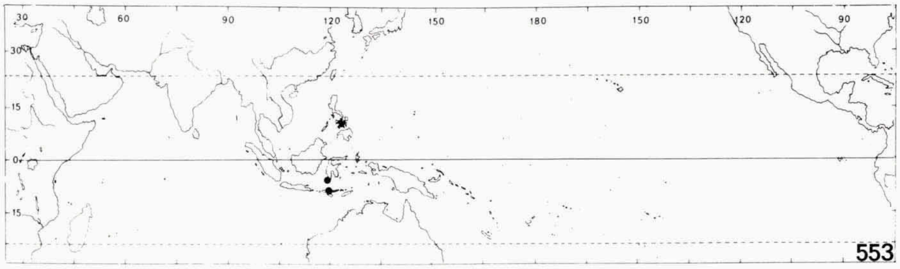


Fig. 553. The range of *Halomitra clavator*. Records are from examined material (●) and published illustrations (★).

The species differs from its closest relative, *H. pileus*, because (1) it is thinner and more fragile, (2) the stomata are less clear, (3) the height of the septa from the centre towards the margin, is more constant, (4) the septal dentations are club-shaped instead of angular, (5) the costae are less equal, (6) the coloration is more even and the mouths are not white. The fact that the species has not been recognized before, may be because it requires a very restricted habitat, which causes it to be rare (Hoeksema & Moka, 1989). All specimens were collected in sheltered, stable habitats, together with specimens of *H. pileus* and *Zoopilus echinatus*. Superficially, it looks like *Z. echinatus*, but it has different septal and costal ornamentations and a much lighter colour.

Etymology. — "Clavator" is Latin for "club-bearer".

Cantharellus Hoeksema & Best, 1984

Type species *Cantharellus noumeae* Hoeksema & Best, 1984. By monotypy.

Characters. — Adult animals are monostomatous and remain attached in adult stage. They are cup-shaped. The corallum wall is imperforate and without fragmentation clefts. The septa and costae are simply ornamented; their projections are fine and granular. The septal margins may be frayed.

Remarks. — Apart from the attached mode of life, *Cantharellus* has many characters in common with *Fungia (Cycloseris)*. With *Lithophyllon*, it shares the sedentary shape and solid corallum wall, but not in the number of stomata and the form of the septal and costal ornamentations. Morphologically, *Cantharellus* is situated in between these groups. In overall shape the corallum of *Cantharellus* resembles that of *Trochoseris* Milne Edwards & Haime, 1849, an extinct genus in the Agariciidae (Middle Cretaceous — Oligocene) from Eurasia and the West Indies (see Wells, 1956).

In the present revision, two species are recognized, which both have a very restricted geographical distribution. When the original description of the genus was published (Hoeksema & Best, 1984), *Fungia doederleinia* was not classified with *Cantharellus* because it was not yet known well enough to be recognized as such. The habitat of the two species is restricted to hard substrata in the neighbourhood of silt. Specimens may be collected detached from the substratum, but in that case they still have the stalk (or the upper part of it) connected to the corallum. They show neither a detachment scar nor traces of a detachment process when they are in anthocaulus stage.

Cantharellus doederleini (Von Marenzeller, 1907) comb. nov.
(figs. 554-556)

Fungia döderleini Von Marenzeller, 1907: 88, pl. 21 figs. 71-71a (Dahab, Gulf of Aqaba).
Not *Fungia döderleini* Yabe & Sugiyama, 1941.

Fungia doederleini — Loya & Slobodkin, 1971: 123. (Valid emendation).
Cycloseris doederleini — Schuhmacher, 1979: figs. 19-20; Scheer & Pillai, 1983: 75, pl. 16 figs. 2-4; Schuhmacher & Mergner, 1985: 428.

Type material examined. — NMW 15180 (holotype of *Fungia doederleini*; type loc. Dahab, Gulf of Aqaba, RED SEA).

Other material. — RED SEA. Gulf of Aqaba, Eilat: RMNH 18063 (5), UB (3), USNM 78254-78255 (4), 78257-78258, 78272.

Characters. — The animals are solitary and remain in anthocaulus stage, although they may accidently become loosened from the substratum. They vary from flat to slightly cup-shaped. There are no fragmentation clefts in the corallum wall. The corallum outline varies from slightly oval to irregularly circular. The diameter of the specimens varies between 1.5 and 5.0 cm.
The length of the central fossa, measured at its bottom, is 1/15 to 1/5 of the corallum length. The septal edges at both sides of the fossa stand upright, whereas they diverge away from it at both of its ends. The columella is formed by a mingled mass of loosely packed and partly fused trabeculae and paliform

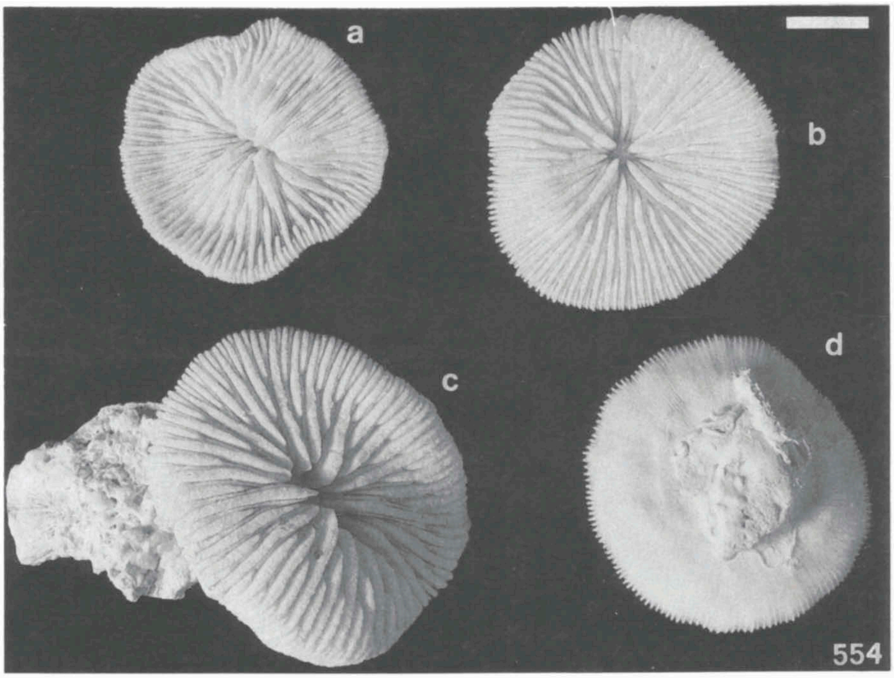
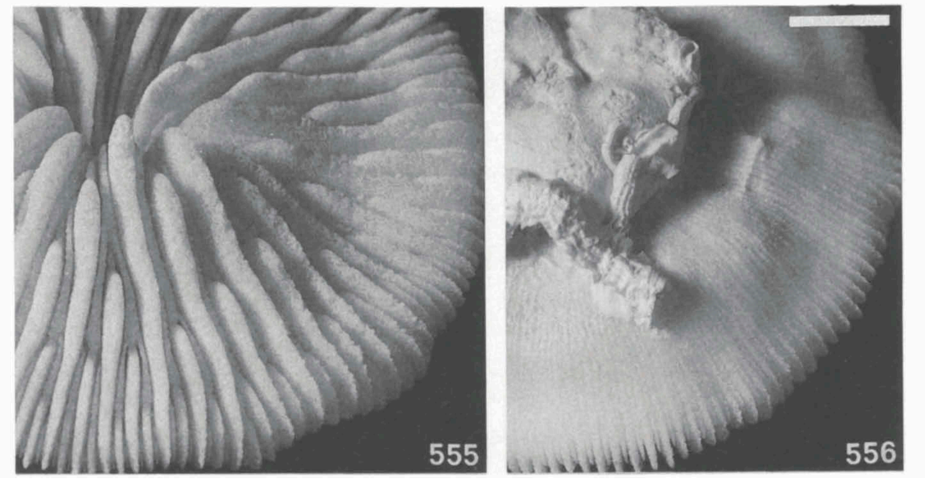


Fig. 554a-d. Corals of *Cantharellus doederleini* (Eilat, Gulf of Aqaba, Red Sea): (a-b) upper surface of two broken-off corals (USNM 78254), (c) upper surface of an attached coral (USNM 78258), (d) aboral surface of a detached coral with the stalk covered by epibionts (USNM 78272). Scale bar: 1 cm.



Figs. 555-556. Septa and costae of the *Cantharellus doederleini* coral in fig. 554d. Scale bar: 0.5 cm.

lobes with their tips pointing in various directions.

The septa are densely packed and straight. The septa of lower orders are thick and solid, those of higher orders thinner and perforated. The septa of lowest orders are more protruding than those of higher orders. Tentacular lobes are absent. The septal margins are indistinctly dentated or almost smooth (fig. 555). The dentations are irregularly granular. Their number varies from 30 to 80 per cm. The septal sides are densely granulated. The granulations vary from fine to coarse and are irregularly distributed or arranged in rows either perpendicular or parallel to the septal margin. The compound synapticulae, which connect the septa laterally, cannot easily be detected because of the tight septal arrangement.

The corallum wall is solid. Apart from the granular spines on the costae, it is not covered by granulations. In some specimens it is inhabited by epibionts (fig. 554d). A detachment scar is not present. Some of the examined specimens

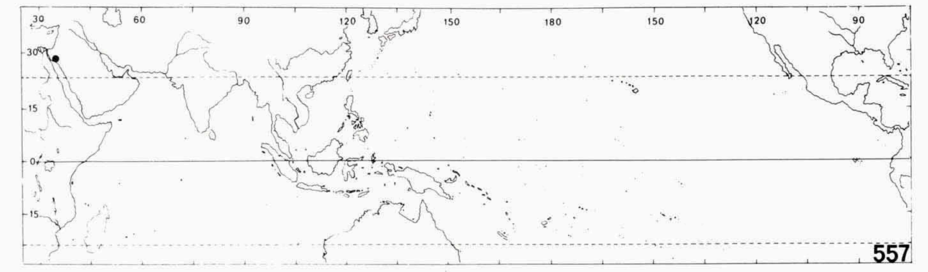


Fig. 557. The location of *Cantharellus doederleini*. Records are from examined material (●).

became detached by an unknown cause but still show the convex lower side that is typical for the attached mode of life. In detached corals the remaining end of the stalk may be covered by lime. The costae are not distinct. They are finely ornamented by granulate and blunt spines (fig. 556), the number of which varies between 50 and 90 per cm.

In the literature the coloration is not recorded.

Geographical distribution (fig. 557). — The species is endemic for the Gulf of Aqaba, northern Red Sea. It has been collected at Dahab and Eilat.

Remarks. — The costae are less distinct than those of *C. noumeae*. It lacks the folded corallum margin shown by large specimens of that species. The septal margins of *C. doederleini* are broader and smoother than in *C. noumeae* and resemble those of *Fungia (Cycloseris) hexagonalis*. The overall shape is more like that of a cup-shaped specimen of *F. (C.) costulata* which is unable to detach and to reach the anthocyathus stage.

Cantharellus noumeae Hoeksema & Best, 1984
(figs. 558-565)

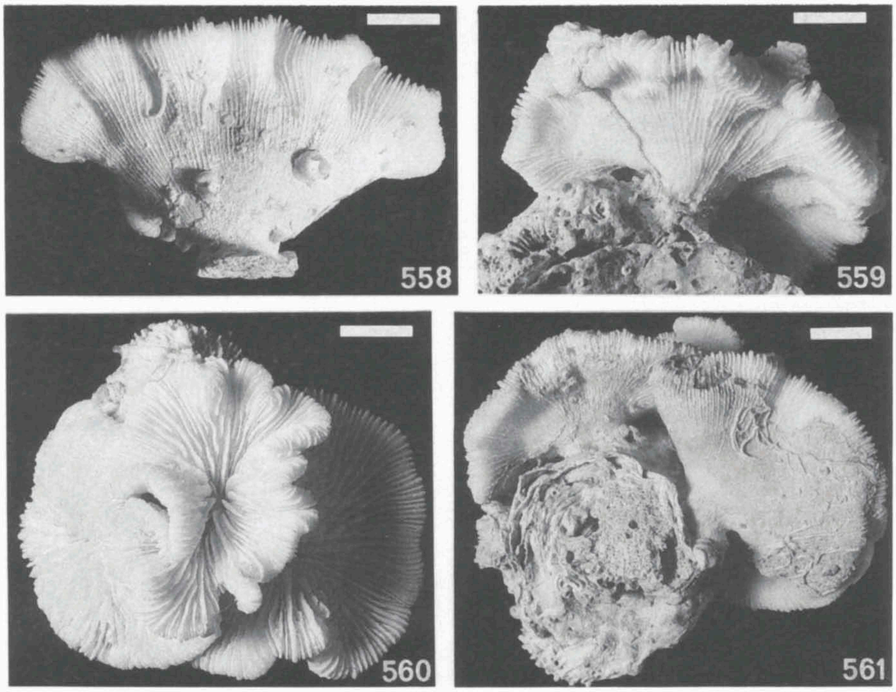
? Trochoseris florescens Felix, 1921: 40-41, pl. 142 figs. 3-4a (Borneo).
Trochoseris florescens — Gerth, 1923: 103-104, pl. 8 fig. 8; 1933: 36-37, pl. 2 figs. 4-4a.
Cantharellus noumeae Hoeksema & Best, 1984: 323-328, figs. 2-9 (Nouméa, New Caledonia).
Cycloseris noumeae — Veron, 1986a: 32; Veron & Marsh, 1988: 81.

Type material examined. — RMNH 16241 (holotype) and RMNH 16264-16268 (8; paratypes of *Cantharellus noumeae*; type loc. Nouméa, NEW CALEDONIA).

Other material. — INDONESIA. E Kalimantan: RGM 17710 (Miocene). NEW CALEDONIA: ZMA 6268.

Characters. — The animals are solitary and remain attached. Juvenile specimens are flat, while mature specimens are cup-shaped. The corallum outline varies from regularly circular to slightly oval. In larger specimens the margin is undulated with folds. There are no fragmentation clefts in the corallum wall. The diameter of the specimens varies between 2.5 and 6.5 cm. The length of the central fossa, measured at its bottom, is 1/13 to 1/7 of the corallum length. The septal edges at both sides of the fossa stand upright, whereas those at its ends diverge away from it. The columella is formed by a mingled mass of loosely packed and partly fused trabeculae and paliform lobes with their tips pointing upwards.

The septa are densely packed and straight at the centre, whereas they may be diverging near the margin. The septa of lower orders are thick and solid, those of higher orders thinner and perforated. The septa of low orders are



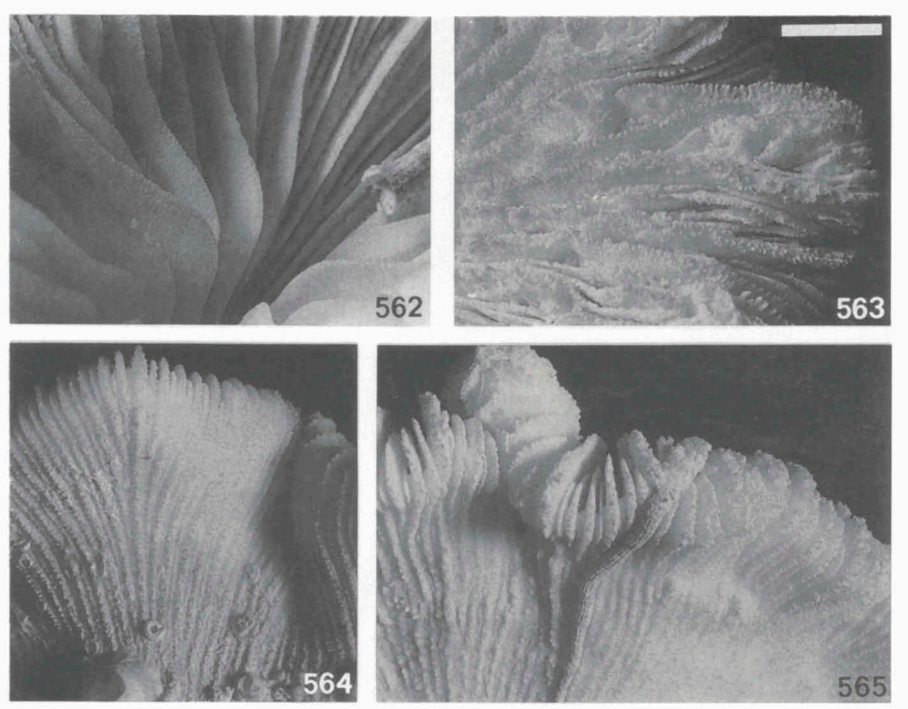
Figs. 558-561. Holotype and paratypes of *Cantharellus noumeae* (Nouméa, New Caledonia). Scale bar: 1 cm. Fig. 558. The holotype from aside (RMNH 16241), the coral has been detached from its substratum by the collector. Fig. 559. Aboral surface of an attached paratype (RMNH 16264). Figs. 560-561. Upper and lower surface of three corals attached to the same substratum (RMNH 16265).

more protruding than those of higher orders. Tentacular lobes are absent. The septal margins are either frayed or finely dentated (figs. 562-563). The dentations are regularly granular and sharp. Their number varies from 40 to 60 per cm. The septal sides are densely granulated. The granulations are fine and either unevenly distributed or arranged in rows perpendicular to the septal margin. The compound synapticulae, which connect the septa laterally, can not easily be detected because of the tight septal arrangement.

The corallum wall is solid and usually inhabited by epibionts. Apart from the granular spines on the costae, it is not covered by granulations. A detachment scar is not present because of the sedentary state of the animals. The costae are distinct over their whole length. They are finely ornamented by granular and blunt spines (figs. 564-565). Their number varies from 30 to 60 per cm.

The living animal is brown. The tentacles are small, transparent and colourless.

Geographical distribution (fig. 566). — The species has been collected alive



Figs. 562-565. Close-ups of *Cantharellus noumeae* corals. Scale bar: 0.5 cm. Fig. 562. Septa of the holotype. Fig. 563. Septa of a paratype (see fig. 559). Fig. 564. Costae of the holotype. Fig. 565. Costae of a paratype (see fig. 559).

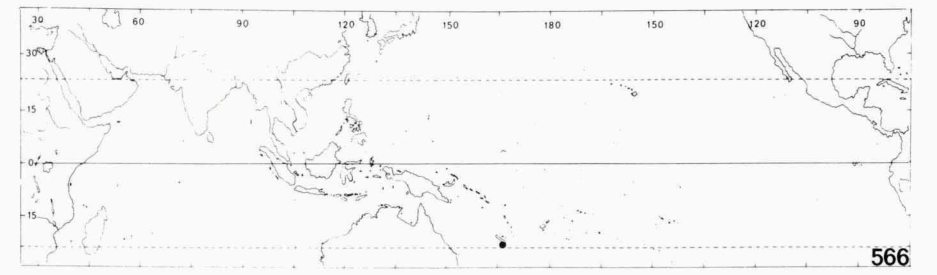


Fig. 566. The present location of *Cantharellus noumeae*. Records are from examined material (●).

from New Caledonia. Further, it is known from the Miocene of E Borneo and Java).

Remarks. — The taxonomic status of *Trochoseris florescens* Felix is not clear because its syntypes, two of which are illustrated by Felix (1921, pl. 142 figs. 3-4a), have not been traced. In overall shape one of the syntypes (Felix, 1921: pl. 142 figs. 4-4a) is almost identical to the holotype of *Cantharellus noumeae*, but the ilustrations given by Felix are not clear enough to show details of the skeleton to discern in which family the coral belongs. *Trochoseris* is a genus of the Agariciidae, a family in which several species superficially resemble attached forms of the Fungiidae. The fragment described by Gerth (1923) is part of a fungiid corallum; it displays distinct compound synapticulae. No secondary stomata can be detected, excluding it from *Lithophyllon*.

Veron (1986a) and Veron & Marsh (1988) classified the species with *Cycloseris*, but they did not give any arguments to support this view. It is therefore unclear whether their records concern specimens of *Cantharellus noumeae* or of some *F. (Cycloseris)* species. The single specimen collected from Western Australia (WAM 172-85), which was supposed to belong to *C. noumeae*, could not be examined for identification because it was lost (Veron, in litt.).

Cantharellus noumeae differs from *C. doederleini* in having a folded corallum margin, thinner septa and more distinct costae. In *C. doederleini* the septal dentations are not distinct, while in *C. noumeae* the dentations are clearly visible. In large specimens of *C. noumeae*, the lower order septum in the middle of a peripheral fold is more exsert than the other ones, which diverge from it. In *C. doederleini* the septa are more equal in size and they are regularly arranged in a radial pattern.

Study of additional material may reveal that the frayed shape of the septal margins observed in some of the specimens turns out to be an anomaly, as in some specimens of *Fungia*. The ravel-shaped projections are elongate and irregularly formed, like the septal dentations characteristic for *Lithophyllon*.

Lithophyllon Rehberg, 1892

Type species: *Lithophyllon undulatum* Rehberg, 1892. By monotypy.

Lithophyllon Rehberg, 1892: pl. 2; Vaughan & Wells, 1943: 140; Wells, 1956: 388; 1966: 236-237; Veron & Pichon, 1979: 193, 195; Ditlev, 1980: 54; Nemenzo, 1981: 199; Veron, 1982: 116; 1986: 358; Nemenzo, 1986: 153; Chevalier & Beauvais, 1987: 711.

Characters. — The animals remain in anthocaulus stage (they do not become detached). The polyps are polystomatous by circumstomadaeal (especially peripheral) budding. They either vary from cup-shaped to foliaceous or they are encrusting. The corallum wall is solid and does not form fragmentation clefts. Its lower surface is covered by granulations. The septal dentations are ravel-shaped. The costae are either simply granular, cylindrical-conical and granulated or arborescent.

Remarks. — Rehberg (1892) did not give a clear description of the genus.

The generic characters can only be recognized from the original illustrations of the type species, *L. undulatum*, and the descriptions given in the captions of the figures. In the present study two species are recognized, one of which is new to science.

According to Wells (1966: 235) the septo-costal structures of *Lithophyllon* are similar to those of *Fungia (Cycloseris)*. In the present study, the septal dentations and especially the costal spines of *Lithophyllon* (figs. 664-668) appear to be more complex than those of *F. (Cycloseris)* (figs. 611-618).

Within the Fungiidae, *Lithophyllon* is most easily confused with the almost isomorphic *Podabacia*, which has a perforated instead of a solid corallum wall. Juvenile corals of *Lithophyllon* that have not yet developed secondary stomata may resemble *Cantharellus* specimens, but they have more complex (arborescent) costal spines.

Specimens of *Lithophyllon* are most easily confused with corals of the agariciid genus *Leptoseris*. Species of the latter genus do not have compound synapticulae. Further, their septa in cross-section show an outline which resembles that of a fir tree, while those of *Lithophyllon* are more or less smooth, apart from the granulations.

Lithophyllon undulatum Rehberg, 1892
(figs. 35-36, 567-581, 590b, 664, 666-667)

Lithophyllon undulatum Rehberg, 1892: pl. 2 figs. 10-12 (locality unknown).

Podabacia dispar Verrill, 1901: 136, pl. 29 fig. 5-5b (Samoa); Van der Horst, 1921: 80, pl. 5 fig. 6. (New synonymy).

Podabacia elegans — Van der Horst, 1921: 80-81, pl. 4 figs. 6-8; Yabe, Sugiyama & Eguchi, 1936: 64-66, pl. 16 fig. 2, pl. 48 figs. 1-2, pl. 49 figs. 1-4, pl. 50 figs. 1-4, pl. 51 figs. 1-5, pl. 52 figs. 3-6, pl. 53 figs. 1-2, pl. 54, pl. 55 figs. 1-6, pl. 56.

Podabacia lobata Van der Horst, 1921: 79-80, pl. 4 fig. 5, pl. 6 fig. 4 (Japan); Yabe & Sugiyama, 1932: 163-164 (including f. *plicata* Yabe & Sugiyama, 1932 ["Tanabe-wan, Honsyû"]; f. *varians* Yabe & Sugiyama, 1932 ["Tanabe-wan, Honsyû"], f. *setoensis* Yabe & Sugiyama, 1932 ["Hukusima, Kyûsyû"], f. *kiiensis* Yabe & Sugiyama, 1932 ["Tanabe-wan, Honsyû"], f. *nomaensis* Yabe & Sugiyama, 1932 ["Hukusima, Kyûsyû"], f. *vanderhorsti* Yabe & Sugiyama, 1932 ["Tanabe-wan, Honsyû"]); Yabe & Sugiyama, 1935a: 202-203; Yabe & Sugiyama, 1935b: 396; Ma, 1958: pl. 16 figs. 1-2; Van Soest, 1979: 107. (New synonymy).

Leptoseris floriformis Gerth, 1923: 107-108, pl. 8 fig. 2 (Miocene, E Borneo). (New synonymy).

Leptoseris fragilis — Matthai, 1924: 51, pl. 10 fig. 1.

Podabacia formosa Yabe & Sugiyama, 1932: 164 ("Syaryô-tô", Taiwan); Yabe & Sugiyama, 1935: 396; Yabe, Sugiyama & Eguchi, 1936: 66, pl. 16 figs. 4-7, pl. 48 figs. 3-4, pl. 53 fig. 3; Phillipps, 1979: 340, pl. 8. (New synonymy).

Podabacia elongata lobata Ma, 1937: 159-161, pl. 76 figs. 1-2 (erroneously named *Podabacia elongata lobata* (Van der Horst), "Pratas Island, Seto-peninsula"). (New synonymy).

Lithophyllon lobata — Vaughan & Wells, 1943: pl. 17 fig. 10; Utinomi, 1965: 249; 1971: 209-210; Ditlev, 1976: 6; 1980: 54, figs. 39, 228-230; Nemenzo, 1980: 294-295, fig. 5.

Lithophyllon levistei Nemenzo, 1971: 157, pl. 5 fig. 3 (Batangas, SW Luzon); 1981: 199, fig. 223; 1986: 153, fig. 177. (New synonymy).
Lithophyllon elegans — Utinomi, 1971: 210, pl. 12 fig. 2; Eguchi & Miyawaki, 1975: 50, pl. 2 fig. 1.
Lithophyllon (c.f.) *edwardsi* — Veron & Pichon, 1979: 195-196 (partim); Veron, 1982: 116; Cope, 1982: 587-588, pls. 1-2; Scott, 1984: 56, pl. 13; Nakamori, 1986: pl. 15 fig. 1; Veron, 1986a: 32; 1986b: 358-359 (partim); Nishihira, Yanagiya & Sakai, 1987: 56; Sakai & Yamazato, 1987: 46; Wood & Tan, 1987: 198; Veron & Kelley, 1988: 29; Veron & Marsh, 1988: 86.
Lithophyllon aiharai — Shirai, 1980: 535.
Lithophyllon elegans lobata — Shirai, 1980: 535.

Type material examined. — YPM 6178 (holotype of *Podabacia dispar*; type loc. SAMOA); ZMA 986, RMNH 10125 (syntypes of *Podabacia lobata*; type loc. JAPAN); RGM 43126 (holotype of *Leptoseris floriformis*; type loc. E Kalimantan, Borneo, INDONESIA); UPZD 1076 (holotype of *Lithophyllon levistei*; type loc. Batangas, SW Luzon, PHILLIPPINES).

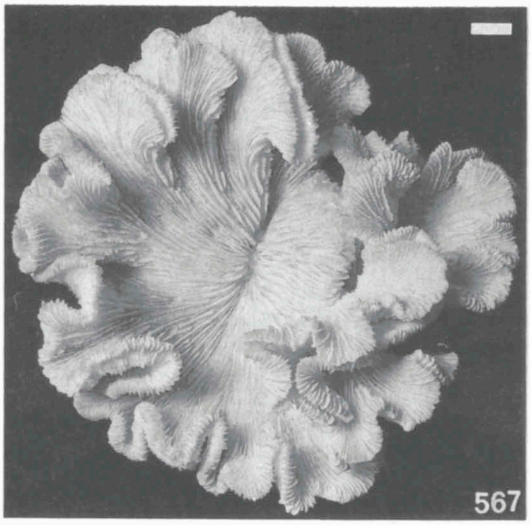
Other material. — JAPAN: ZMA 977, 980. Okinawa: USNM 77776. HONG KONG: USNM 78275. MALAYSIA. Malaya: BMNH 1979.9.25.6/9. Sabah: USNM 47961, 78273. PHILIPPINES: USNM 77985. SW Luzon: USNM 77957. Cebu: UPMSI 311. Pangesinan: UPZD 581, 624, 936-937. INDONESIA. NW Java: RMNH 16186-16188. SW Sulawesi: RMNH 10782, 15225-15226, 20836, 20889, 20939, 22124-22140 (68). Tiger Is.: RMNH 21080, 21193, 21320. Talaud Is.: RMNH 14535 (3). N Sumbawa: RMNH 21347. Timor: RMNH 10128. AUSTRALIA. Kimberley: WAM 183.85. Pilbara: WAM 494.78, 562.78, 485.81, 487.81, 307.84, 831.85. Northern Territory: NTM 6045. N Great Barrier Reef: NTM 6763, 6767, 6770, 6774, 6776-6777, 6779-6780, QMB G7790, GL2604, GL2608. C Great Barrier Reef: NTM 6768-6769. S Great Barrier Reef: NTM 6775.

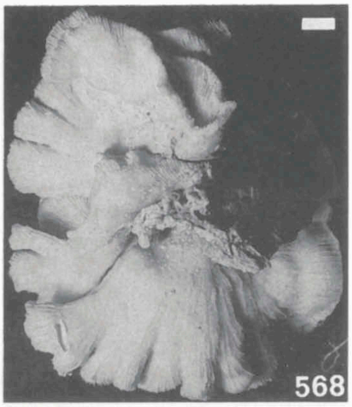
Characters. — The corals are sedentary. They are polystomatous by circumstomadaeal (especially peripheral) budding. Their shape varies from cup-shaped to foliaceous. Their outline is irregularly circular. The animals do not form fragmentation slits in the corallum wall. The corallum margin is either regularly flat or lobed and folded. The diameter of the specimens varies between 1.0 and 81.0 cm.

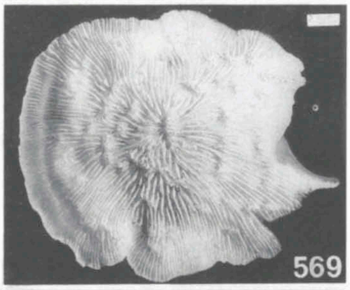
The septa are loosely packed and straight (except in lobed and folded margins). The septa of low order cycles are thick and solid, those of higher orders thin and perforated. The septa of low orders are more protruding than those of higher orders. Tentacular lobes are absent. The septal margins are finely ornamented with ravel-shaped dentations (figs. 576-578, 664). Their number varies from 20 to 50 per cm. The septal sides are thinly granulated. The granulations are irregularly distributed (fig. 664). The compound synapticulae connecting the septa laterally can easily be detected, because of the loose septal arrangement.

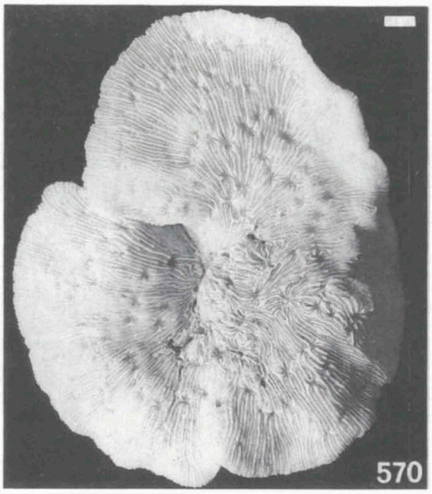
The stomata are usually clearly visible. The primary stoma is the largest; the secondary stomata are evenly distributed around it. Each columella is formed by a mingled mass of loosely packed trabeculae and paliform lobes which have their tips pointing upwards.

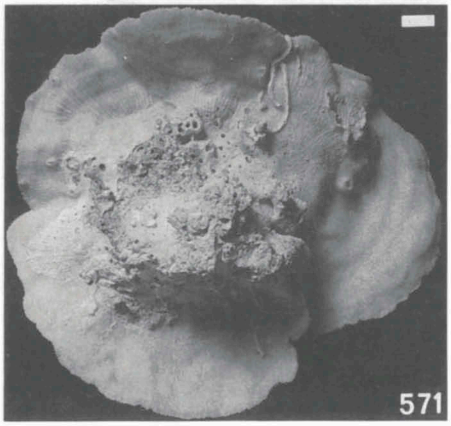
The solid corallum wall is covered by granulations. It may be partly overgrown by epibionts. A detachment scar is not present. The size of the costae varies from equal to subequal; they are straight and usually not distinct. The costae are finely ornamented with conical spines, either blunt or acute, which are covered by sharp granulations giving them an arborescent appearance (figs. 666-667). Their number varies from 70 to 100 per cm.







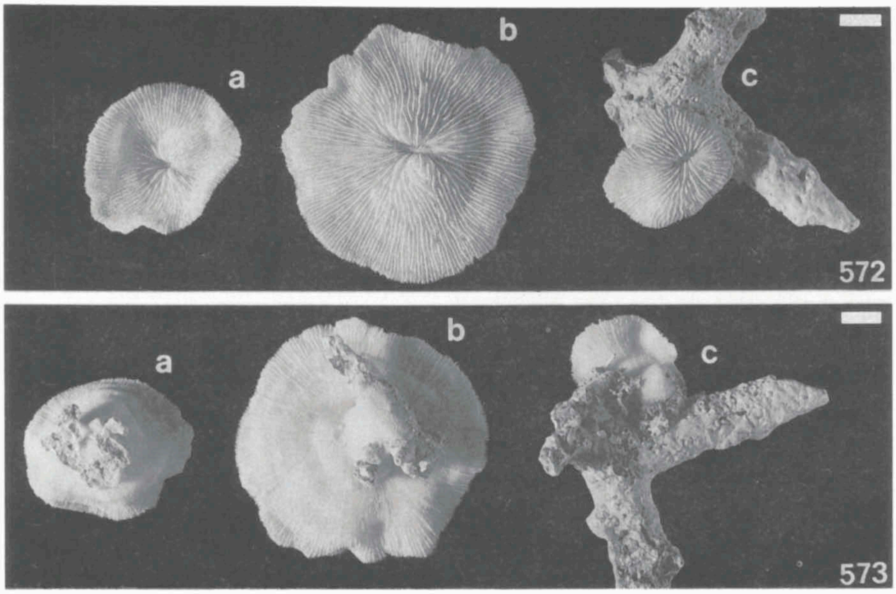




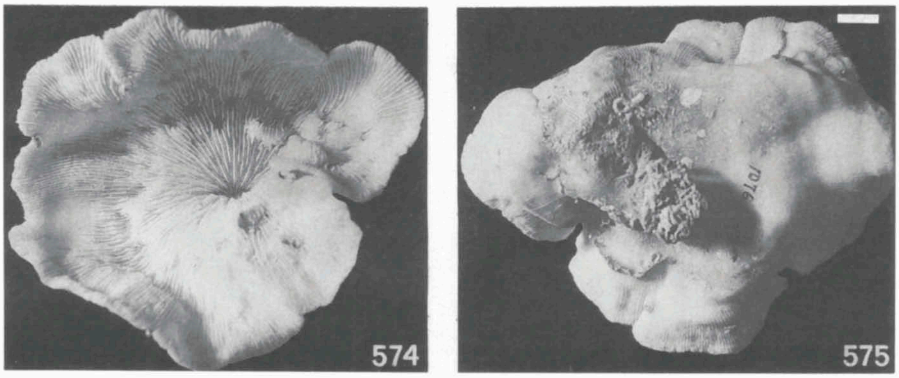
Figs. 567-571. Corals of *Lithopyllon undulatum* from Indonesia. Scale bar: 1 cm. Figs. 567-568. Upper and lower surface of a coral with an undulating margin (RMNH 10128; Timor). Fig. 569. Upper surface of a cup-shaped coral (RMNH 16187; NW Java). Figs. 570-571. Upper and lower surface of an arched coral (RMNH 10782; SW Sulawesi).

The main colour of the living animals varies from a ochre-like yellow to brown (figs. 35-36). The mouths are grey with white lips. The tentacles are small and transparent; they are either colourless or coloured like the rest of the animal.

Geographical distribution (fig. 582). — The range extends from the west



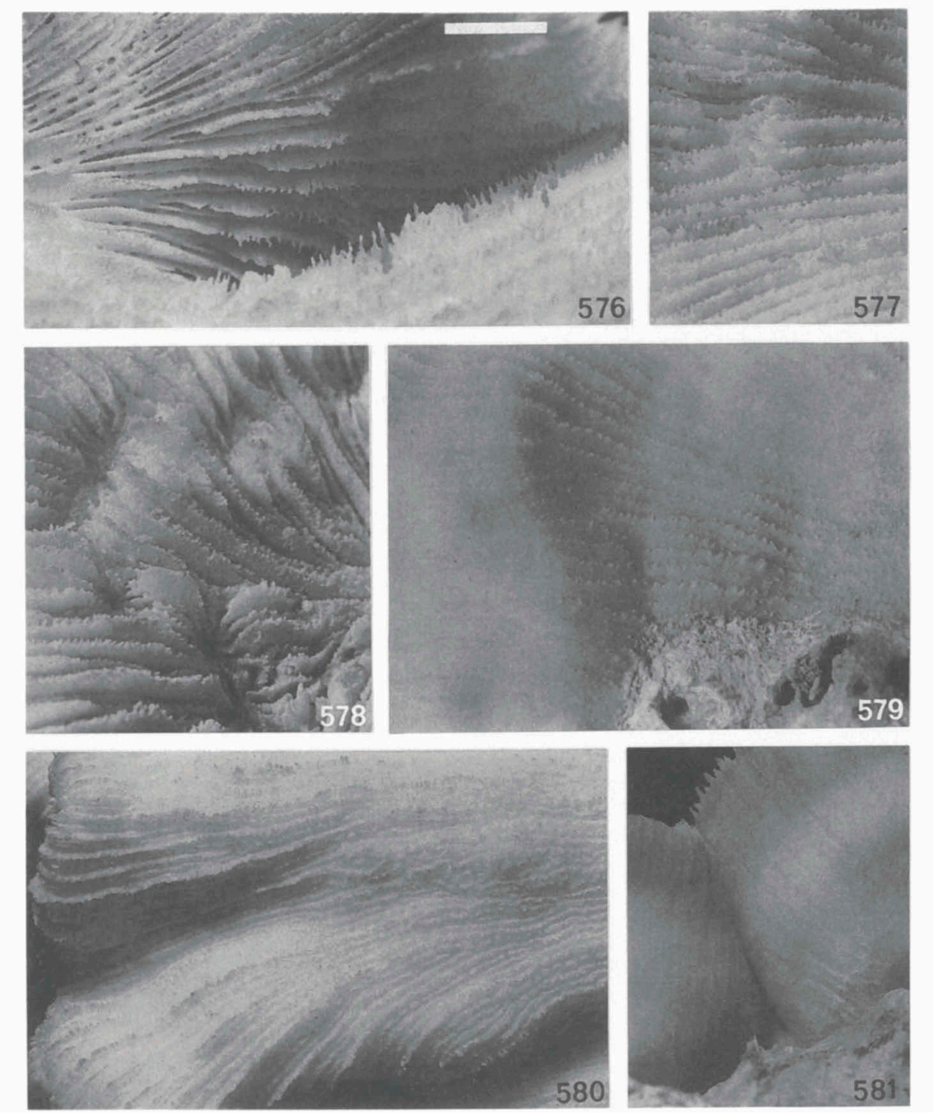
Figs. 572-573. Upper and aboral surface of three juveniles of *Lithophyllon undulatum* (RMNH 22127; SW Sulawesi, Indon.): (a) a coral detached by the collector, (b-c) attached corals. Scale bar: 1 cm.



Figs. 574-575. Upper and lower surface of the holotype of *Lithophyllon levistei* (= *L. undulatum*, UPZD 1076; Batangas, SW Luzon, Philipp.). Scale bar: 1 cm.

side of the Malayan Peninsula northward to China and Japan, and eastward to Samoa.

Remarks. — Rehberg (1892: pl. 2 figs. 10-12) published some accurate illustrations of the holotype; written information was only supplied in the captions (p. 49). This specimen is not in the MGH, where it should be together



Figs. 576-581. Close-ups of *Lithophyllon undulatum* corals. Scale bar: 0.5 cm. Fig. 576. Septa of the coral in fig. 567. Figs. 577-578. Septa and fossae of the coral in fig. 570. Fig. 569. Costae of the coral in fig. 571. Fig. 580. Costae of the coral in fig. 567. Fig. 581. Costae of the coral in fig. 569.

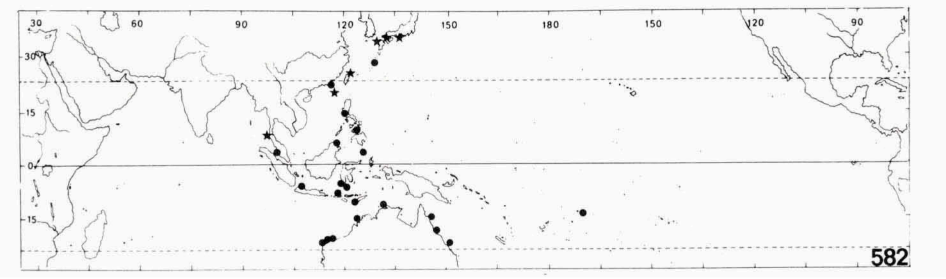


Fig. 582. The range of *Lithophyllon undulatum*. Records are from examined material (●) and published illustrations (★).

with other corals described by Rehberg; it was probably lost during World War II. The type locality is unknown.

Vaughan & Wells (1943: 140) and Wells (1966: 236) believed *Lithophyllon undulatum* to be synonymous with *Leptoseris edwardsi* Rousseau, 1854, the holotype of which could not be traced during the present investigation. However, Rousseau's illustrations (1854: pl. 29 fig. 2-2c) of *Leptoseris edwardsi* clearly reveal that this species does not belong to the Fungiidae and that it originally was classified correctly with *Leptoseris* (Agariciidae). The coral examined by Vaughan & Wells (1943) is probably not the holotype of *L. edwardsi*. According to its accompanying label it came from Tongatabu, while the type locality of *L. edwardsi* was unknown (Rousseau, 1854: 123). During examination of the MNHN material for the present revision, no specimen of *Lithophyllon* could be found from Tongatabu.

In the literature, *L. undulatum* has been described under various names due to the insufficient original description of the species and its variation in overall corallum shape. The septo-costal structures are less variable and can easily be used to identify the species. These structures, and the solid corallum wall, are clearly visible in the illustrations given by Rehberg (1892). Hence it is unnecessary that a neotype is designated.

Whether the holotype of *Podabacia formosa* is still present in the IGPTU coral collection is not known. The specimen is well enough illustrated (Yabe, Sugiyama & Eguchi, 1936) to show its identity as *L. undulatum*. Type specimens of several other nominal taxa mentioned in the synonymy could be examined.

The smallest specimens of *L. undulatum* may be encrusting but during maturation they become cup-shaped and, with increasing diameter, foliaceous. Specimens of *L. mokai* remain small and encrusting. In *L. undulatum* the stomata are more widely spaced and, therefore, specimens of this species have relatively fewer stomata than *L. mokai* corals of about the same size (compare figs. 590b and 590a). Further, the septa of *L. undulatum* are thinner and less densely packed, and in living animals the area around the mouth is grey instead of brown as in *L. mokai.*

Specimens of *L. undulatum* may be confused with corals of *Podabacia crustacea*, another fungiid species with a cup-shaped or foliaceous corallum shape. However, living animals of that species do not show grey mouth areas and their corallum wall is perforated instead of solid. Differences with species of *Cantharellus* and *Leptoseris* (Agariciidae) are discussed in the remarks on the genus *Lithophyllon.*

Lithophyllon mokai spec. nov.
(figs. 37, 583-594, 665, 668)

Lithophyllon (c.f.) *edwardsi* — Veron & Pichon, 1979: 195-196 (partim), figs. 321-323; Wood, 1983: 131, 134; Veron, 1986b: 358-359 (partim).

Type material designated. — RMNH 16189 (holotype of *Lithophyllon mokai*; type loc. N side of Pulau Pari, Kepulauan Seribu [= Thousand Islands], NW Java, INDONESIA); RMNH 16190-16191 (paratypes of *L. mokai*; Pulau Tikus, Kepulauan Seribu, INDONESIA).

Other material. — MALAYSIA. Sabah: USNM 78274. INDONESIA. SW Sulawesi: RMNH 20987, 22141-22152 (59). Tiger Is.: RMNH 21218, 21316. N Sumbawa: RMNH 20810, 21622. MARSHALL IS.: RMNH 14624, USNM 77850, 78244-78246. AUSTRALIA. N Great Barrier Reef: NTM 6764-6765, 6771-6773, 6778, 6789, QMB GL2603, GL2605-2607, GL3611. PAPUA NEW GUINEA. Bismarck Sea: ULB. FIJI IS.: USNM 78346.

Characters. — Adult animals are encrusting. The polyps are polystomatous by circumstomadaeal budding. The corallum outline is irregularly round, depending on the relief and shape of the substratum. The margin is free from the substratum. The upper surface of the corals usually follows the contours of the substratum, which may cause the corallum margin to become lobate (figs. 583-587). There are no fragmentation slits in the corallum wall. The diameter of the specimens varies between 1.5 and 13.0 cm.

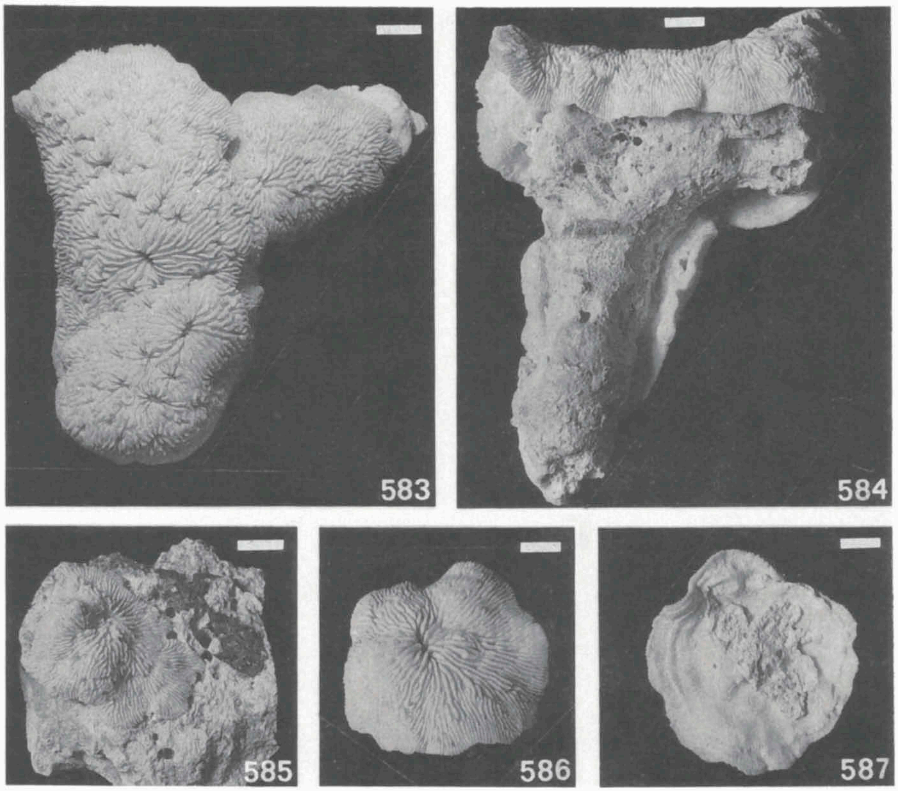
The septa are very densely packed and vary from straight to wrinkled. The septa of low order cycles are thick and solid, whereas those of higher orders are thin and perforated (fig. 665). The septa of lowest orders protrude more than those of other orders. Tentacular lobes may be present, although they are not always distinct. The septal margins are finely ornamented with dentations which are either irregularly granular or ravel-shaped (figs. 591-592, 665). Their number varies from 40 to 50 per cm. The septal sides are densely granulated. The granulations are fine and irregularly distributed. The compound synapticulae connecting the septa laterally cannot easily be detected, because of the tight septal arrangement.

The primary stoma is relatively large. The smaller secondary stomata are densely arranged around it. Each columella is formed by a mingled mass of tightly packed paliform lobes with the tips pointing upwards.

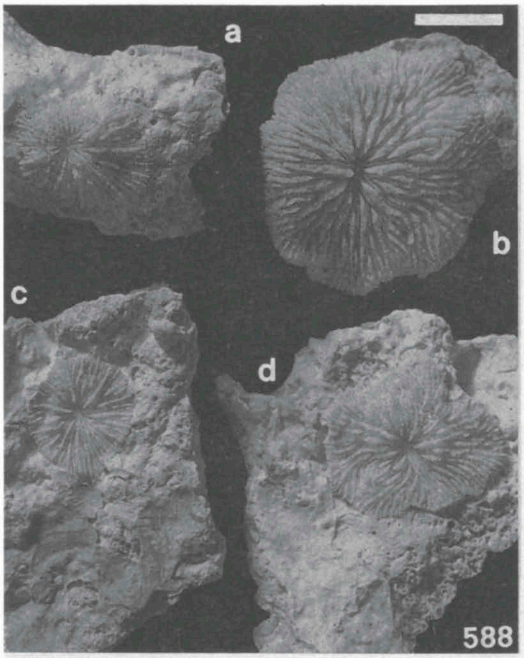
The wall is solid and covered by granulations (fig. 668). The parts which are not in direct contact with the substratum may be overgrown by epibionts. A detachment scar is not present. The indistinct costae are straight and bear numerous fine spines, which are either conical and covered by granulations or rudimentary and granular (figs. 593-594, 668). Their density varies from 70 to 100 per cm.

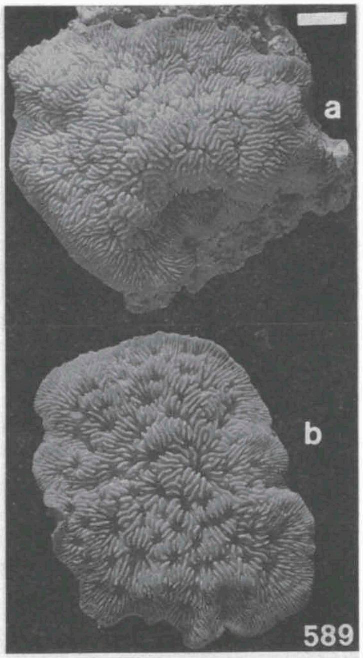
The living animals are brown (fig. 37). The area around the mouths is usually darker than the rest of the polyp. The small tentacles are transparent and colourless.

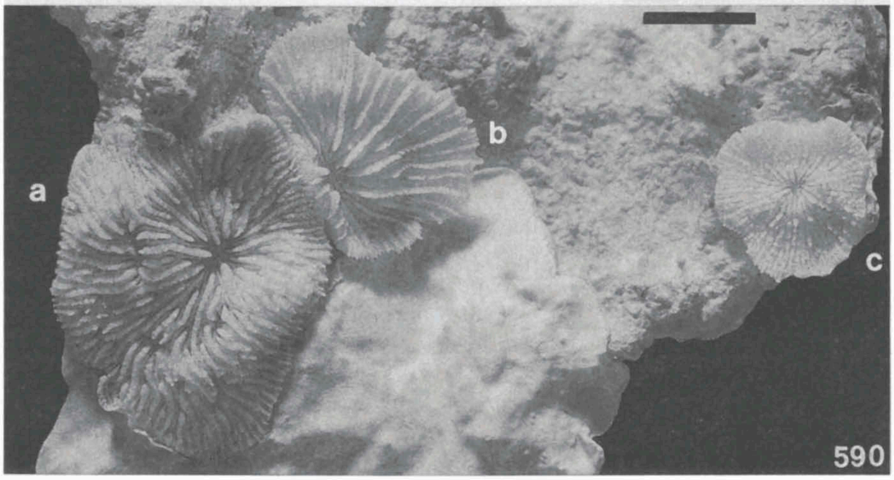
Geographical distribution (fig. 595). — The species occurs mainly in the



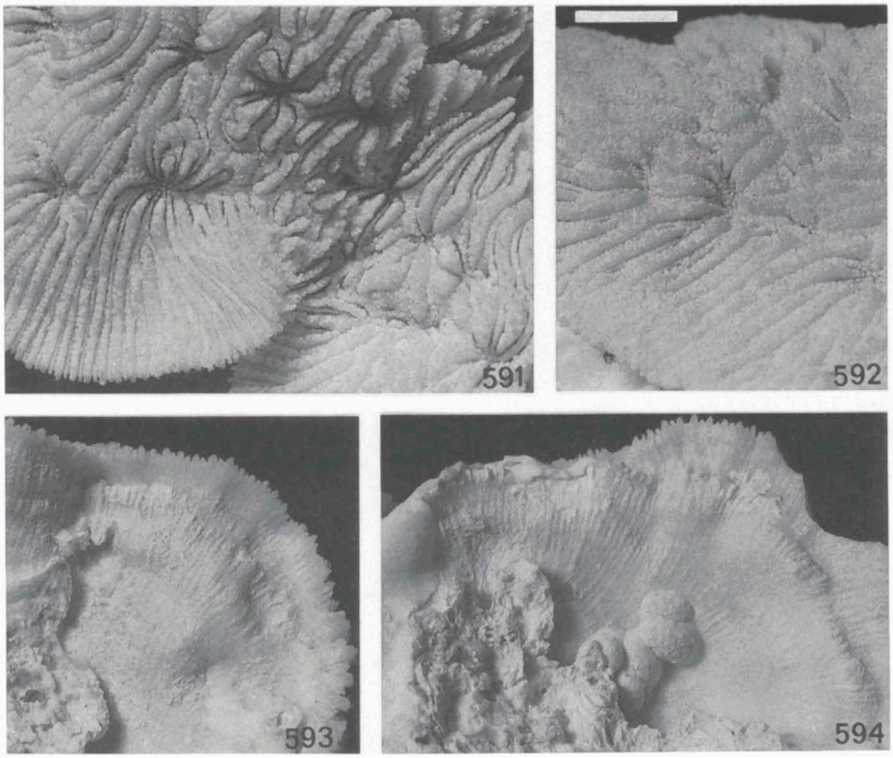
Figs. 583-587. Corals of *Lithopyllon mokai*. Scale bars: 1 cm. Figs. 583-584. Upper and lower surface of the holotype (RMNH 16189; Pulau Tikus, Kepulauan Seribu, NW Java, Indon.). Fig. 585. Upper surface of a paratype (RMNH 16191; Pulau Pari, Kepulauan Seribu, NW Java). Figs. 586-587. Upper surface of a detached coral (RMNH 14624; Enewetok, Marshall Is.).







Figs. 588-590. Corals of *Lithophyllon mokai* (SW Sulawesi, Indon.). Scale bars: 1 cm. Fig. 588a-d. Upper surface of four juveniles (RMNH 22150). Fig. 589a-b. Upper surface of two adults (RMNH 22147). Fig. 590a-c. A piece of dead coral inhabited by three different fungiids competing for space with each other and with an encrusting red coralline alga (RMNH 22151): (a) a small encrusting coral of *Lithophyllon mokai*, (b) a smaller cup-shaped coral of *L. undulatum* and (c) a juvenile of *Podabacia crustacea*.



Figs. 591-594. Close-ups of *Lithophyllon mokai* corals. Scale bar: 0.5 cm. Figs. 591-592. Septa and fossae of the holotype (see fig. 583). Figs. 593-594. Costae and epibionts of the coral in fig. 587.

Pacific. From the Malayan Archipelago its range extends eastward towards the Marshall Islands and the Fiji Islands.

Remarks. — *L. mokai* can easily be distinguished from its closest ally, *L. undulatum*, by its encrusting habit and its higher density of stomata (compare figs. 569-570 with fig. 589). Juvenile specimens of *L. undulatum* may still be

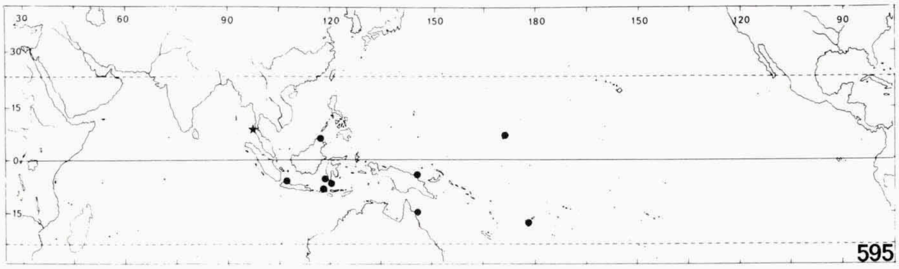


Fig. 595. The range of *Lithophyllon mokai*. Records are from examined material (●) and published illustrations (★).

encrusting, although in a slightly more advanced stage of their life-history they start to become cup-shaped and foliaceous (compare figs. 572-574 and 590b with figs. 588-589 and 590a). *L. mokai* has thicker septa which are more tightly packed than in *L. undulatum*. Because the maximum size of *L. mokai* is smaller and its coloration less bright, it is relatively inconspicuous in the field.

Etymology. — The species is named after Mr. Willem Moka, marine biologist at Hasanuddin University (Ujung Pandang).

Podabacia Milne Edwards & Haime, 1849

Type species: *Agaricia cyathoides* Valenciennes, ms., Milne Edwards & Haime, 1849 [= *Podabacia crustacea* (Pallas, 1766)]. By monotypy.

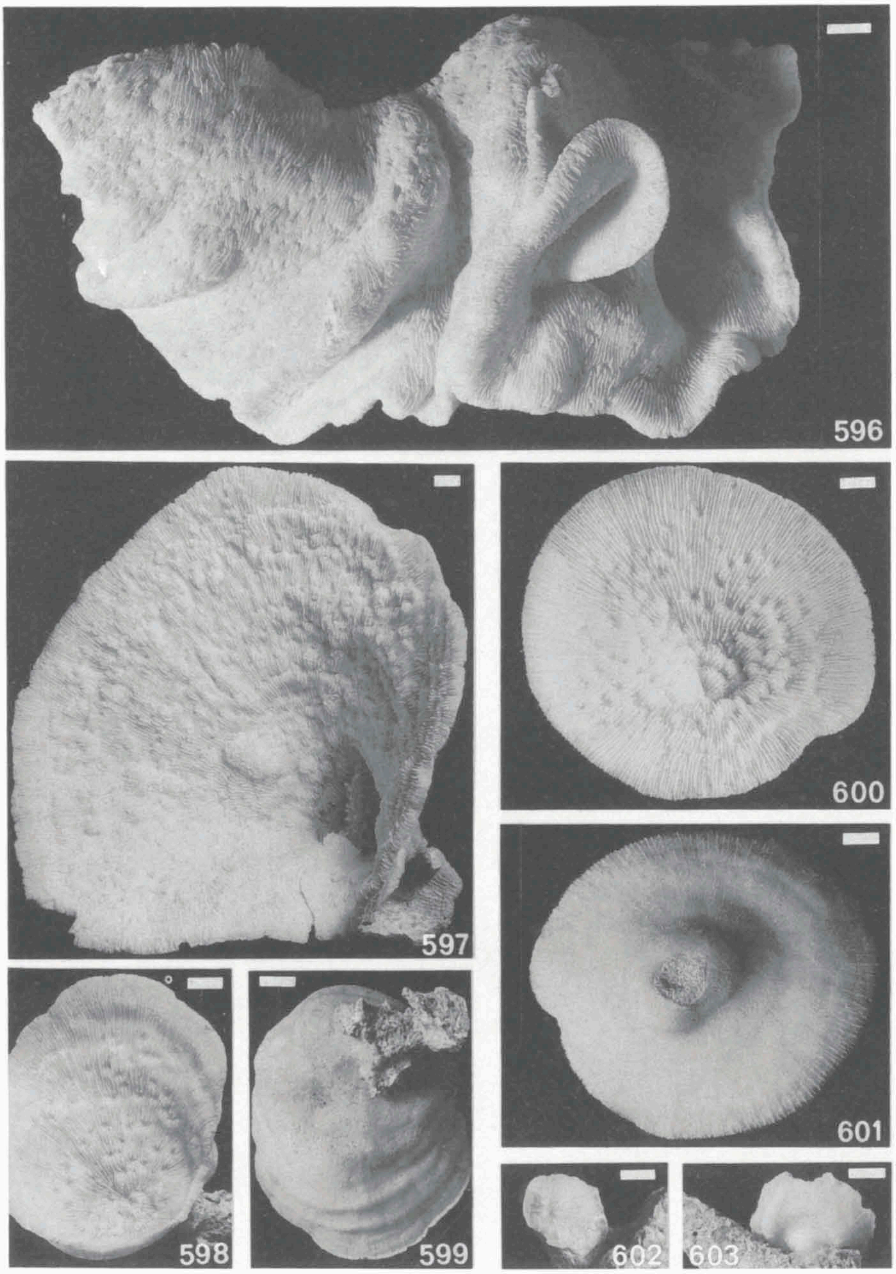
Podabacia Milne Edwards & Haime, 1849: 71; 1850: xlviii; 1851: 98; 1860: 19-20; Quelch, 1886: 140; Ortmann, 1889: 517; Studer, 1901: 413; Gardiner, 1905: 941-942; Vaughan & Wells, 1943: 142; Wells, 1956: 389-390; Wells, 1966: 243; Veron & Pichon, 1979: 197; Ditlev, 1980: 59; Nemenzo, 1981: 199; Scheer & Pillai, 1983: 87; Nemenzo, 1986: 153; Veron, 1986b: 360; Chevalier & Beauvais, 1987: 710.

Characters. — The animals are not free-living; they have no anthocyathus stage. They become polystomatous by circumstomadaeal budding. The corals are either cup-shaped or foliaceous. The corallum wall is perforated and covered by granulations. It is without fragmentation clefts. The septal dentations are fine and lobate with granulations irregularly distributed over their sides. The costal spines are small and slightly echinose.

Remarks. — In overall shape, the coralla of the single species, *Podabacia crustacea*, resemble those of *Lithophyllon undulatum*. The main difference is in the corallum wall, which is perforated instead of solid. The septal dentations of *Podabacia* are more lobate than in *Lithophyllon*. In the structure of the corallum wall, the septa and the costae, the sedentary corals of *Podabacia* are similar to the free-living corals of *Sandalolitha*. In *Podabacia* the septal and costal ornamentations are slightly finer than in *Sandalolitha* and, in contrast to Wells' (1966: 243) opinion, unlike those of *F. (Verrillofungia)*.

Podabacia crustacea (Pallas, 1766)
(figs. 34, 590c, 596-609, 669-670)

Madrepora crustacea Pallas, 1766: 291 ("Mare Americanum"); Boddaert, 1768: 361; Wilkens, 1787: 35-36.
Madrepora pileus — Esper, 1791: 87-92, 287 (partim), pl. 6.
Agaricia explanata — Schweigger, 1829: 415.



Figs. 596-603. Corals of *Podabacia crustacea*. Scale bars: 1 cm. Fig. 596. A large fragment (USNM 78425; Canton I., Phoenix Is). Fig. 597. The neotype, a large cup-shaped coral (RMNH 16129; Kepulauan Seribu, NW Java, Indon.). Figs. 598-599. Upper and lower surface of an attached cup-shaped coral (RMNH 16138; NW Java). Figs. 600-601. Upper and lower surface of a detached coral (RMNH 16131; NW Java). Fig. 602. Upper surface of a small coral (RMNH 16132; NW Java). Fig. 603. Aboral surface of a small coral (RMNH 16135; NW Java).

Pavonia explanulata — Dana, 1846: 322.

Podabacia crustacea — Milne Edwards & Haime, 1851: 98; 1860: 20; Verrill, 1864: 52; Studer, 1877: 647; Studer, 1880: 46; Ortmann, 1888: 180; 1889: 518, pl. 18 fig. 12a; Studer, 1901: 416; Gardiner, 1905: 942; Bedot, 1907: 219-220, pl. 32 figs. 161-164; Van der Horst, 1921: 26; 1922: 421; Matthai, 1924: 50-51, pl. 7 fig. 3, pl. 8 figs. 3-5; Yabe & Sugiyama, 1935: 396; Yabe, Sugiyama & Eguchi, 1936: 64, pl. 47; Ma, 1937: 161 pl. 67 fig. 1, pl. 71 figs. 2-3; Vaughan & Wells, 1943: pl. 19 fig. 5; Matthai, 1948: pl. 3 figs. 2-3, pl. 4 fig. 1; Crossland, 1952: 156-157, pl. 12 fig. 1, pl. 13 fig. 3; Nemenzo, 1955: 73, pl. 1 fig. 5; Purchon, 1956: 157; Searle, 1956: 17, pl. 19B; Scheer, 1964: 618, fig. 8; Loya & Slobodkin, 1971: 123; Pillai, 1971a: 324; 1971b: 9; 1972: 204; Sukarno, 1974: 14; Zou, Song & Ma, 1975: 32-33, pl. 8 fig. 7; Ditlev, 1976: 7; Faure, 1977: 10; Maragos & Jokiel, 1978: 62; Veron & Pichon, 1979: 197-198, figs. 324-327; Ditlev, 1980: 59, figs. 46, 247; Betterton, 1981: 206, pls. 91-92; Boshoff, 1981: 21; Nemenzo, 1981: 199, fig. 224; Faure, 1982: 106; Pillai, 1983: 86; Scheer & Pillai, 1983: 88, pl. 21 figs. 2-3; Randall & Myers, 1983: 40, figs. 366-367; Wood, 1983: 134-135, 145; Hamilton & Brakel, 1984: 252; Johnston, 1986: 159; Nakamori, 1986: pl. 14 figs. 5a-b; Nemenzo, 1986: 153, fig. 178; Veron, 1986a: 32; 1986b: 360-361; Sakai & Yamazato, 1987: 46; Wood & Tan, 1987: 198; Veron & Kelley, 1988: 29, 34; Veron & Marsh, 1988: 86.

Halomitra crustacea — Duncan, 1883: 155-159, pl. 6 figs. 1-5; 1886: 15.

Podabacia involuta Van der Horst, 1921: 26-27, pl. 4 fig. 4, pl. 5 figs. 4-5, pl. 6 fig. 3 (Singapore); Van Soest, 1979: 107.

Lithophyllon sp. — Phillipps, 1978: 101-102, pl. 8B.

Podabacia sp. — Green, Harris, Robertson & Santavy, 1979: 299, fig. 20.

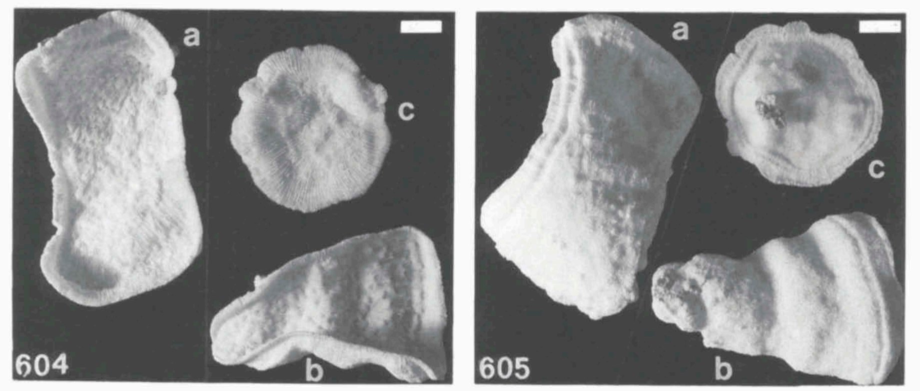
Lithophyllon crustacea — Shirai, 1980: 536.

Sandalolitha robusta — Veron, 1986a: 32 (partim); Veron & Marsh, 1988: 86 (partim).

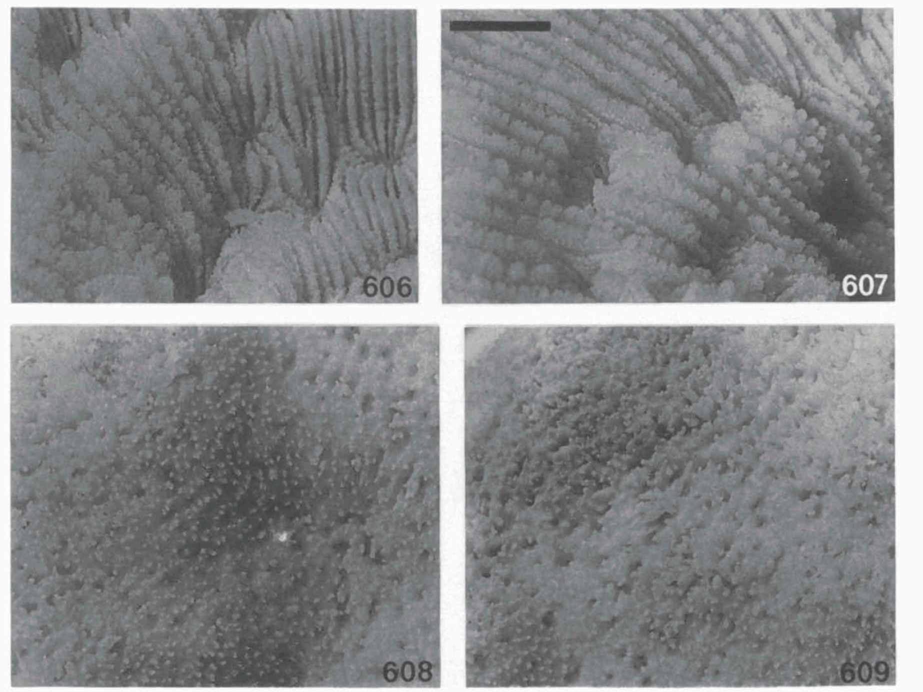
Type material examined. — RMNH 16129 (neotype [present designation] of *Madrepora crustacea*, type loc. Kepulauan Seribu, NW Java, Indonesia); ZMA 955 (holotype of *Podabacia involuta*; type loc. SINGAPORE).

Other material. — RED SEA. Gulf of Aqaba: RMNH 13893. KENYA: RMNH 17095. N MADAGASCAR: ZMA 1693. SEYCHELLES: YPM 7884. LACCADIVE IS.: BMNH 1950.1.11.659/675. SRI LANKA: MNHN FUN 253-254. MALAYSIA: BMNH 1979.9.25.2-5/7-8. Malacca Str.: BMNH 1883.11.8.2-4. MNHN Fun249-251. Sabah: USNM 47951-47952, 47960, 47963-47964, 78423. SINGAPORE: AMNH 1756, BMNH 1954.10.8.4, MCZ 37, 89, 496 (6), 767, 5273, 5277, USNM 77752-77753, YPM 77 (2), 176, ZMA 978. PHILIPPINES: USNM 45397, 77986 (2). SW Luzon: USNM 77932. E Mindoro: UPZD 108. Cebu: MCZ 277. Sulu Is.: RMNH 14522 (3). INDONESIA. Riau Is.: ZMA 6775. Belitung (Billiton): RMNH 10127, ZMA 975, 982. NW Java: RMNH 16130-16140 (16). SW Sulawesi: RMNH 15229-15230 (4), 15673, 15746, 20888, 20902, 22117-22123 (36), ZMA 981. Tiger Is.: RMNH 20664, 21122, 21188 (2), 21241 (2). NE Sumba: RMNH 20243 (2), 20314. Komodo: RMNH 21470. SW Timor: ZMA 6776. Talaud Is.: RMNH 15751 (2). Moluccas: ZMA 507, 974. Ambon: RMNH 10126. Banda: RMNH 8395. AUSTRALIA. Kimberley: WAM 182.85. Pilbara: WAM 41.81 (2). Northern Territory: NTM 6156. N Great Barrier Reef: NTM 6882-6884, 6887, QMB G3630, G8059-8061, GL2648-2651, GL3560, GL3569. C Great Barrier Reef: BMNH 1934.5.14.497, NTM 6885-6886, 6888-6889, MCZ 5274-5275 (3). S Great Barrier Reef: QMB G6933. FIJI IS.: USNM 78424. PHOENIX IS. Canton Is.: USNM 78425.

Characters. — Adult animals remain attached in adult stage. However, pieces may break off accidentally and survive as free-living, regenerating fragments (figs. 604-605). The polyps are polystomatous by circumstomadaeal (especially peripheral) budding. The outline of the corals is irregularly circular. The coral shape varies from cup-shaped to foliaceous. There are no fragmentation clefts in the corallum wall. The diameter of the specimens ranges from 1.5 to 24.5 cm. Field studies in Indonesia revealed that specimens may be observed with a diameter up to 1 m, or even more.



Figs. 604-605. Upper and lower surface of free-living corals of *Podabacia crustacea* (RMNH 22120; SW Sulawesi, Indon.): (a-b) two regenerated fragments and (c) a complete, broken-off coral. Scale bars: 2 cm.



Figs. 606-609. Close-ups of the neotype of *Podabacia crustacea* from NW Java (see fig. 597). Scale bar: 0.5 cm. Figs. 606-607. Septa and some fossae. Figs. 608-609. Costae.

The septa are densely packed. They are straight between the stomata, whereas closer to the stomata, they may be slightly bent (figs. 606-607). The septa of lower order cycles are relatively thicker and more exsert than those of higher orders. The septa of lowest orders are either solid of fenestrate (fig. 669); those of highest orders are more perforated. Tentacular lobes are usually absent, although they may be present in juvenile specimens (fig. 590c). The septal margins are finely ornamented with irregularly granular or slightly lobate dentations (figs. 606-607, 669). Their number varies from 12 to 40 per cm. The septal sides are densely granulated. The granulations are irregularly distributed (fig. 669). The compound synapticulae connecting the septa laterally cannot easily be detected, because of the tight septal arrangement.

The stomata are distinct despite their small size. The secondary stomata are almost evenly distributed around the larger primary stoma. The columella in the primary stoma is formed by some loosely packed trabeculae and paliform lobes with their tips pointing in various directions. In the secondary stomata the columella is usually rudimentary.

The corallum wall is perforated and covered by granulations. A detachment scar is only visible at the aboral side of specimens accidentally broken off from the substratum (fig. 605c). The costae are more distinct in mature specimens than juvenile ones. They are straight; in some specimens they are of about the same size while in others they differ more distinctly in size. They are ornamented with spines which are either blunt and granular or elongate and echinose. The spines are covered by acute granulations pointing in various directions (figs. 608-609, 670). Their number varies from 18 to 40 per cm.

The living animals are usually light brown or slightly greyish brown (fig. 34). The small tentacles are translucent and colourless.

Geographical distribution (fig. 610). — *Podabacia crustacea* lives in an area which extends from the western Indian Ocean (including the Red Sea) to southern Japan and the Tuamotus.

Remarks. — The original description of the species is not very clear. The

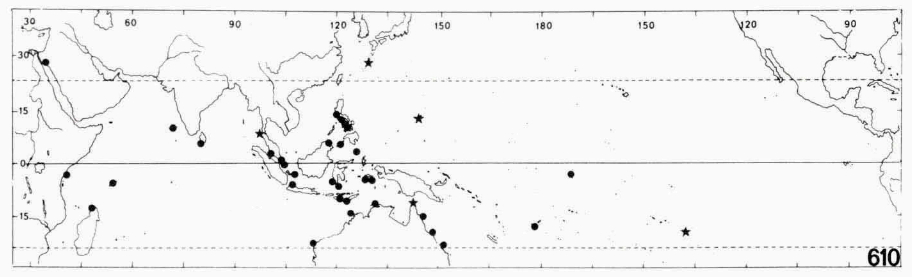


Fig. 610. The range of *Podabacia crustacea*. Records are from examined material (●) and published illustrations (★).

location of the holotype of *Podabacia crustacea* is at present unknown and it is also unclear where it came from, because several of the corals described by Pallas (1766) came from seas or oceans indicated as "Mare Americanum", "Oceanus Indicus" or "Mare Americanum & Indicum". Pallas (1766) did not refer to any illustrations in the literature which might help to recognize the species. In the interests of stability in the nomenclature a neotype has been selected which corresponds as much as possible to the original description. It is a large fragment (fig. 597) with distinct septo-costal structures (figs. 606-609).

Podabacia involuta is a synonym of *P. crustacea*. The holotype of *P. involuta* has a strongly folded corallum margin, which is commonly observed in large specimens of the species. This shape is also frequently encountered in large specimens of *Lithophyllon undulatum*, which have a solid corallum wall instead of a perforated one as in *P. crustacea*. Loosened fragments of *P. crustacea* grow into a similar shape as *Sandalolitha robusta*; they still can be distinguished from *S. robusta* coralla by their finer septal dentations.

FOSSIL RECORD

Most of the available literature on fossil Fungiidae deals with material from the Central Indo-Pacific, especially Indonesia. It is fortunate that the present study could profit much from the earlier review of the fungiid stratigraphic distribution by Wells (1966). Wells' publication has as restriction that it refers mainly to fungiid taxa above the species level. The taxonomic revision preceding this chapter is used to give stratigraphic data concerning the various species (table 1). These are checked against the fossil records compiled by Wells (1966) to adjust the latter with additional information (table 2).

The stratigraphic range of the Fungiidae is restricted to the Cenozoic. The earliest fungiid record concerns a *Fungia (Cycloseris)* from the Paleocene of India (Wells, 1936; see also table 2). Another representative of this subgenus has been collected from the Eocene of Borneo (Fritsch, 1875). Nine species and four subgenera recognized as belonging to *Fungia*, can be traced back to the Miocene. Six *Fungia* species and a single subgenus have been discovered in deposits dating from the Pliocene or later and the single representative of *F. (Lobactis)* is only known from the Quaternary (table 1). Other *Fungia* species are not known in fossil state.

Five genera are known to have occurred since the Miocene, namely *Heliofungia*, *Ctenactis*, *Halomitra*, *Cantharellus* and *Lithophyllon*. Fossils of *Herpolitha* and *Sandalolitha* are not known from epochs earlier than the Pliocene. *Podabacia* has a relatively young stratigraphic history; it has only

Table 1. Fossil records of revised fungiid species based on the following references: (a) Felix, 1915; (b) 1920; (c) 1921; (d) Gerth, 1921; (e) 1923; (f) 1925; (g) 1933; (h) Martin, 1880; (i) Nakamori, 1986; (j) Umbgrove, 1924; (k) 1926; (l) 1938; (m) 1946a; (n) 1946b; (o) 1950; (p) Veron & Kelley, 1988; (q) Yabe & Sugiyama, 1935.

Species	Epoch	Area	References
Fungia (Cycloseris) sinensis	Miocene	Borneo	c
	Pliocene ?	New Guinea	p
Fungia (Cycloseris) cyclolites	Miocene	Borneo	c, e, f
	Miocene ?	Talaud Is.	l
	Early Pliocene	Java	d, n
	Pliocene	New Guinea	p
	Plio-Pleistocene	Borneo	k
	Plio-Pleistocene	Ceram	j
	Plio-Pleistocene	Timor	a
	Pleistocene	Borneo	e
	Pleistocene	Talaud Is.	l
	Pleistocene	Ryukyu Is.	q
Fungia (Cycloseris) somervillei	Late Pliocene	Java	m
	Pliocene ?	New Guinea	p
Fungia (Cycloseris) fragilis	Early Miocene	Java	d
	Miocene	Borneo	e
	Miocene	Java	d, h, g
	Neogene	Nias	f
	Pliocene	New Guinea	p
Fungia (Cycloseris) hexagonalis	Pleistocene	Ryukyu Is.	i
Fungia (Cycloseris) costulata	Miocene	Borneo	c
	Late Pliocene	Java	m
	Plio-Pleistocene	Timor	a
Fungia (Cycloseris) vaughani	Miocene	Borneo	c
Fungia (Verrillofungia) scabra	Miocene	Java	f
	Pliocene	New Guinea	p
Fungia (Verrillofungia) concinna	Pliocene	New Guinea	p
	Late Pliocene	Java	m
	Plio-Pleistocene	Ceram	j
	Plio-Pleistocene	Talaud Is.	l
	Early Pleistocene	Java	o
	Pleistocene	Taiwan	q
Fungia (Verrillofungia) repanda	Late Pliocene	Java	m
	Pliocene ?	New Guinea	p
Fungia (Danafungia) horrida	Miocene	Java	f
	Early Pliocene	Java	n
	Late Pliocene	Java	m
	Early Pleistocene	Java	o
Fungia (Danafungia) scruposa	Early Pliocene	Java	n
	Pleistocene	Ryukyu Is.	q
Fungia (Fungia) fungites	Miocene	Java	d
	Pliocene ?	New Guinea	p
	Plio-Pleistocene	Ceram	j
	Early Pleistocene	Java	o
Fungia (Wellsofungia) granulosa	Early Pliocene	Java	n
	Pliocene	New Guinea	p
	Pleistocene	Ryukyu Is.	q
	Pleistocene	Taiwan	q
Fungia (Lobactis) scutaria	Pleistocene	Ryukyu Is.	i

Table 1 (continued).

Fungia (Pleuractis) moluccensis	Miocene	Java	f
	Early Pliocene	Java	n
Fungia (Pleuractis) paumotensis	Early Pliocene	Java	n
	Pleistocene	Sumatra	k
	Pleistocene	Ryukyu Is.	q
	Pleistocene	Taiwan	q
Heliofungia actiniformis	Miocene	Java	f
	Early Pliocene	Java	n
	Pliocene	Java	d
	Pliocene	New Guinea	p
	Early Pleistocene	Java	o
Ctenactis echinata	Early Pliocene	Java	n
	Pliocene	New Guinea	p
	Late Pliocene	Java	m
	Neogene	Sumatra	f, k
Herpolitha limax	Early Pliocene	Java	n
	Plio-Pleistocene	Ceram	j
	Pleistocene	Ryukyu Is.	i
	Pleistocene	Taiwan	q
Sandalolitha dentata	Pliocene	New Guinea	p
	Pleistocene	Ryukyu Is.	i
Halomitra pileus	Miocene	Java	f
	Early Pliocene	Java	n
	Plio-Pleistocene	Timor	b
Cantharellus noumeae	Miocene	Borneo	e
	Miocene	Java	g
Lithophyllon undulatum	Miocene	Borneo	e
Podabacia crustacea	Pleistocene	Ryukyu Is.	i
	Pleistocene	Taiwan	q

Table 2. Earliest fossil records of the fungiid (sub)genera compiled by Wells (1966), with revised data from table 1.

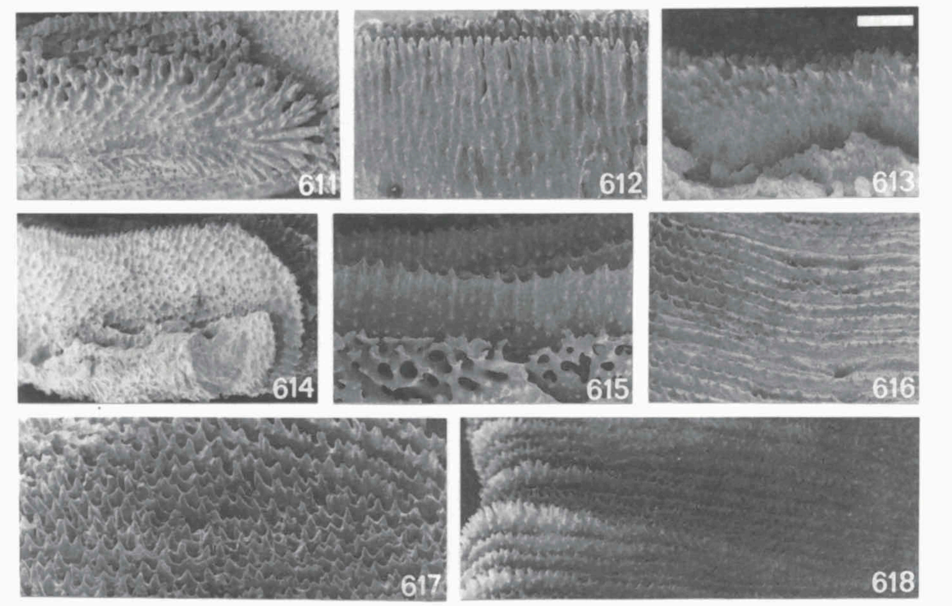
(Sub)genus	Wells (1966)	Table 1
Fungia (Cycloseris)	Paleocene (India)	
Fungia (Verrillofungia)	Miocene (Indon., W Pacif.)	
Fungia (Danafungia)	Recent	Miocene (Indon.)
Fungia (Fungia)	Miocene (Indon.)	
Fungia (Wellsofungia)	-	Pliocene (Indon.)
Fungia (Lobactis)	-	Pleistocene (Japan)
Fungia (Pleuractis)	Pliocene (Indon., W Pacif.)	Miocene (Indon.)
Heliofungia	Miocene (Indon.)	
Ctenactis	Miocene (Indon., W Pacif.)	
Herpolitha	Pliocene ? (Indon., W Pacif.)	Pliocene (Indon.)
Polyphyllia	Recent	
Sandalolitha	Miocene ? (Indon.)	Pliocene (New Guinea)
Zoopilus	Recent	
Halomitra	Miocene (W Pacif.)	
Cantharellus	-	Miocene (Indon.)
Lithophyllon	Oligocene ?	Miocene (Indon.)
Podabacia	Recent	Pleistocene (Japan, Taiwan)

been found from the Quaternary. *Polyphyllia* and *Podabacia* are the only genera without a fossil record (table 2).

Probably several extant fungiid species evolved in the Tertiary. It is difficult to conclude from the stratigraphic record where each species originated because relatively few areas with fossil fungiids are known. In the Central Indo-Pacific many recent species can still be traced back in time until the Miocene. Apparently, since then these species did not show any clearly detectable evolution.

PHYLOGENY

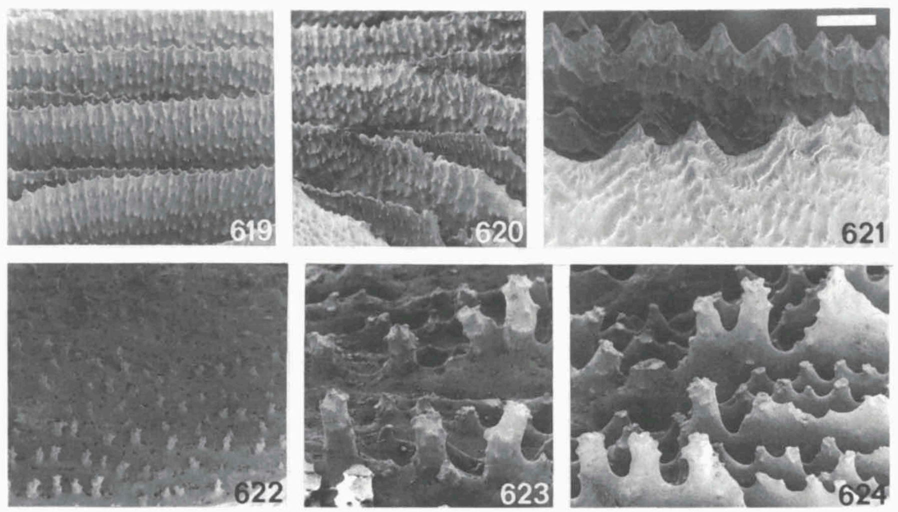
Introduction. — The present study provides a provisional phylogenetic reconstruction of the Fungiidae. In addition it is shown to what extend the (sub)generic classification, as presented in the systematic account, relates to this cladogram.



Figs. 611-618. SEM-photographs of septo-costal ornamentations in *Fungia (Cycloseris)*. Scale bar: 1 mm. Fig. 611. Septa *F. (C). sinensis* (RMNH 21712; SW Sulawesi, Indon.). Fig. 612. Septa *F. (C.) cyclolites* (RMNH 21585; Komodo, Indon.). Fig. 613. Septa *F. (C.). hexagonalis* (RMNH 21418; Komodo). Fig. 614. Septa *F. (C). fragilis* (RMNH 21414; SW Sulawesi). Fig. 615. Septa *F. (C.) vaughani* (RMNH 22071; SW Sulawesi). Fig. 616. Costae *F. (C.). sinensis* (RMNH 21712; SW Sulawesi). Fig. 617. Costae *F. (C.) cyclolites* (RMNH 21585; Komodo). Fig. 618. Costae *F. (C.) vaughani* (RMNH 22071; SW Sulawesi).

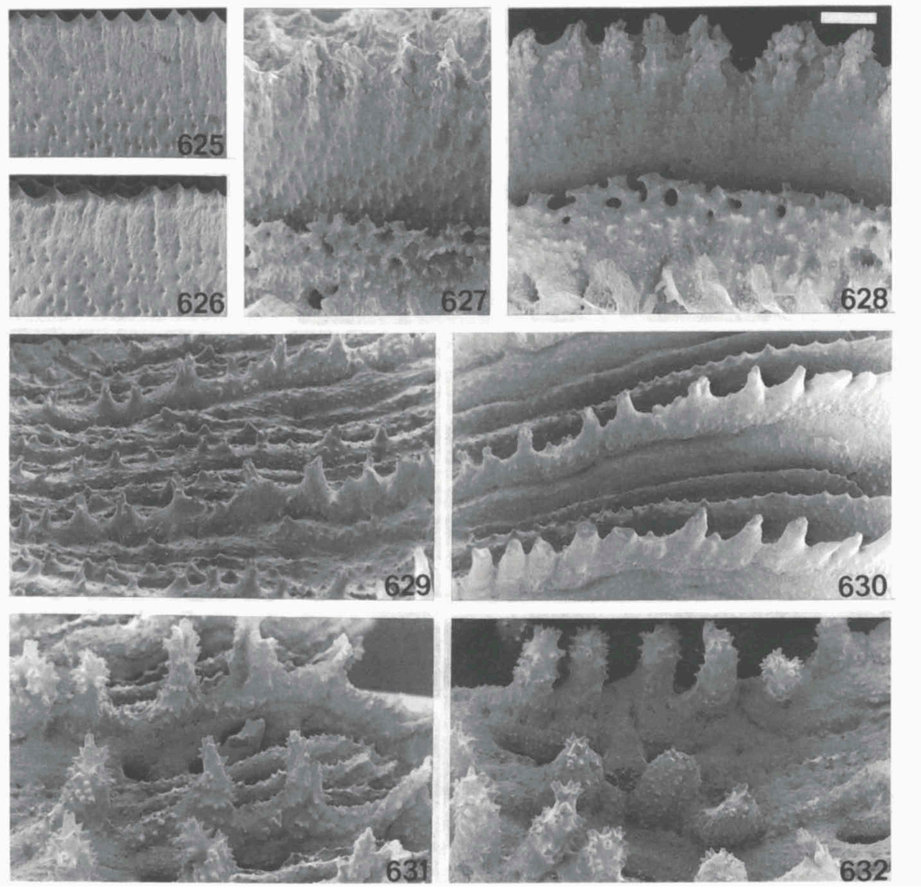
The first comprehensive reconstruction concerning the phylogeny of mushroom corals was published by Döderlein (1902: 53), who produced a dendrogram indicating phylogenetic relationships between the species of *Fungia*. With the help of this phylogenetic reconstruction, he divided *Fungia* into seven species-groups, viz. the "*Patella* -", the "*Actiniformis*-", the "*Scutaria*-", the "*Echinata*-", the "*Repanda*-", the "*Danai*-" and the "*Fungites*"-group (Döderlein, 1901; 1902). The *patella*-group was considered ancestral to all other groups. The affinities between the *actiniformis*- and the *patella*-group, and those between the *scutaria*- and the *patella*-group were not clearly indicated. The *repanda*-group was regarded as directly derived from the *patella*-group, the *echinata*-group from the *scutaria*-group, and the *fungites*- and the *danai*-group were each considered off-spring of the *repanda*-group.

After Döderlein's (1902) revision of *Fungia* the species of the *patella*-group were classified with *Cycloseris*, while the other species-groups were maintained within *Fungia* (see e.g. Vaughan & Wells, 1947). Gardiner (1909: 262) considered *Cycloseris* to contain the "central form from which all the rest originated"; the development of many new groups of species after the commencement of the Quaternary, which included the "colonial genera", might have been related to the requirement of zooxanthellae in the soft tissue of the corals. This view was adopted by Wells (1966: fig. 3), who indicated that *Fungia* and *Lithophyllon* branched off from *Cycloseris*, and each of the other

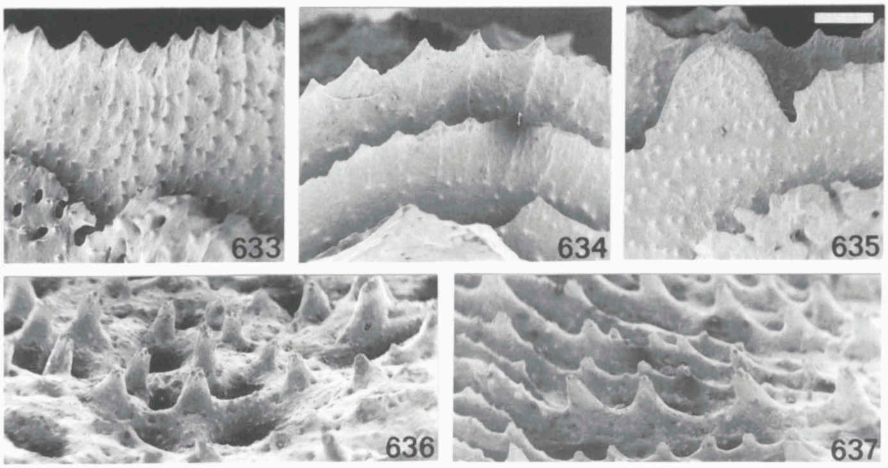


Figs. 619-624. SEM-photographs of septo-costal ornamentations in *Fungia (Verrillofungia)*. Scale bar: 1 mm. Figs. 619-620. Septa *F. (V.) scabra* (RMNH 20187; SW Sulawesi, Indon.). Fig. 621. Septa *F. (V.) repanda* (RMNH 16184; NW Java, Indon.). Fig. 622. Costae *F. (V.) scabra* (RMNH 20187; SW Sulawesi). Figs. 623-624. Costae *F. (V.) repanda* (RMNH 16184; NW Java).

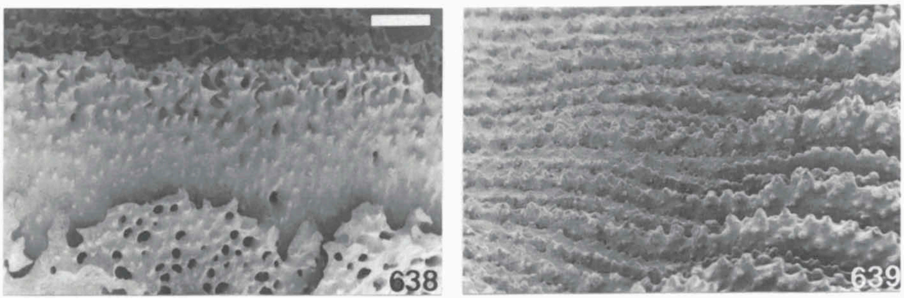
genera from one of the subgenera of *Fungia*. His diagram is a scheme in which possible ancestor-offspring relationships of fungiid taxa are indicated along a geologic time scale. Döderlein's (1902) remaining species-groups became the six subgenera frequently referred to in recent literature: *Fungia (Heliofungia)*, *F. (Pleuractis)*, *F. (Ctenactis)*, *F. (Verrillofungia)*, *F. (Danafungia)* and *F. (Fungia)*. Transformed into a cladogram, Wells' diagram is presented in fig. 671.



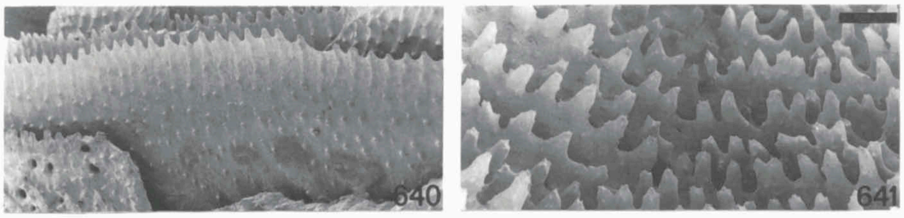
Figs. 625-632. SEM-photographs of septo-costal ornamentations in *Fungia (Danafungia)*. Scale bar: 1 mm. Figs. 625-626. Septa *F. (D.) fralinae* (RMNH 20795; SW Sulawesi, Indon.). Figs. 627-628. Septa *F. (D.) scruposa* (RMNH 20422; SW Sulawesi). Figs. 629-630. Costae *F. (D.) fralinae* (RMNH 20795; SW Sulawesi). Figs. 631-632. Costae *F. (D.) scruposa* (RMNH 20422; SW Sulawesi).



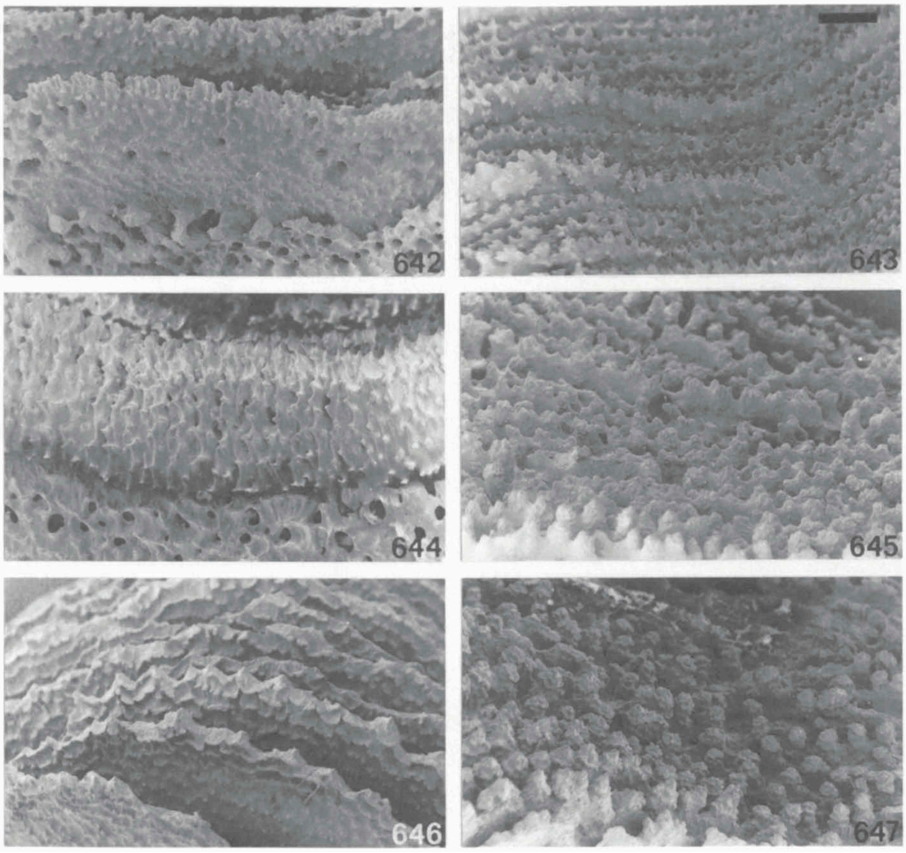
Figs. 633-637. SEM-photographs of septo-costal ornamentations in *Fungia (Fungia)*. Scale bar: 1 mm. Figs. 633-635. Septa *F. (F.) fungites* (RMNH 16121; NW Java, Indon.). Figs. 636-637. Costae of same specimens.



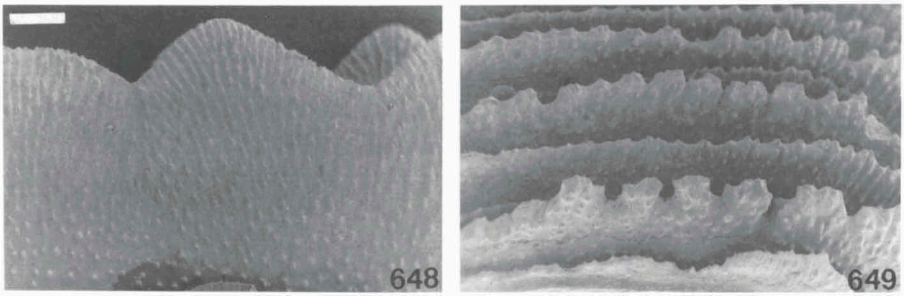
Figs. 638-639. SEM-photographs of septo-costal ornamentations in *Fungia (Wellsofungia)*. Scale bar: 1 mm. Fig. 638. Septa *F. (W.) granulosa* (RMNH 20857; SW Sulawesi, Indon.). Fig. 639. Costae of same specimen.



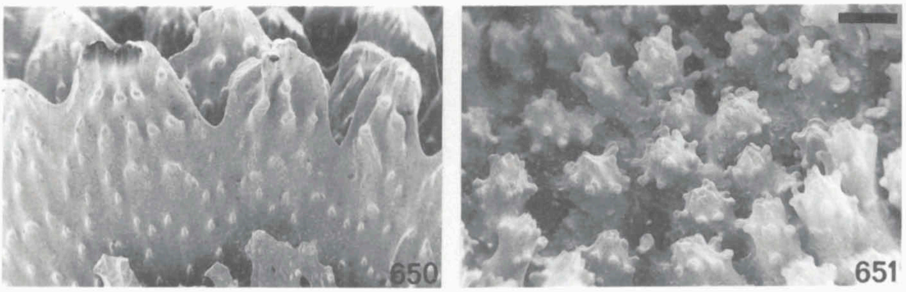
Figs. 640-641. SEM-photographs of septo-costal ornamentations in *Fungia (Lobactis)*. Scale bar: 1 mm. Fig. 640. Septa *F. (L.) scutaria* (RMNH 20143; SW Sulawesi, Indon.). Fig. 641. Costae of same specimen.



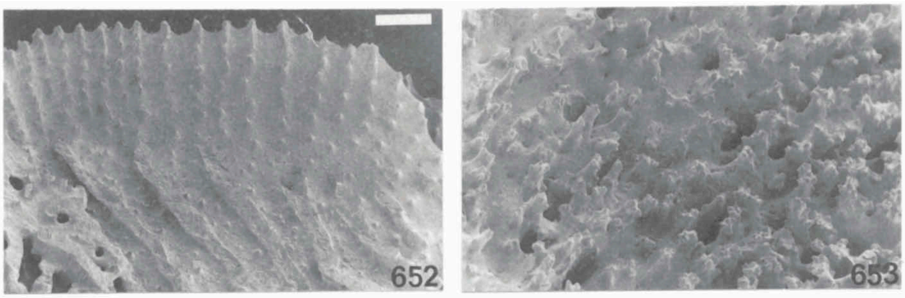
Figs. 642-647. SEM-photographs of septo-costal ornamentations in *Fungia (Pleuractis)*. Scale bar: 1 mm. Figs. 642-643. Septa and costae *F. (P.) moluccensis* (RMNH 20346; SW Sulawesi, Indon.). Figs. 644-645. Septa and costae *F. (P.) gravis* (RMNH 20247; SW Sulawesi). Figs. 646-647. Septa and costae *F. (P.) paumotensis* (RMNH 20266; SW Sulawesi).



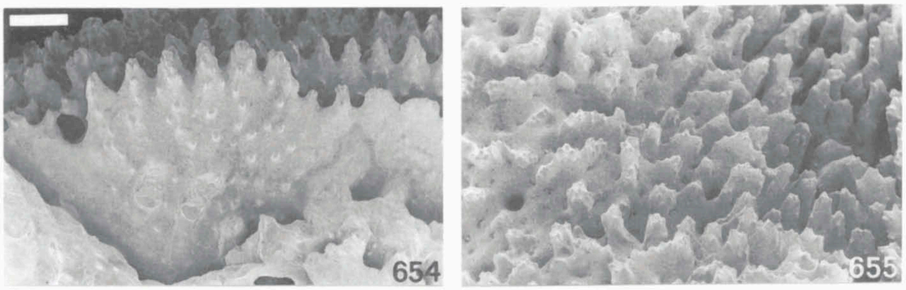
Figs. 648-649. SEM-photographs of septo-costal ornamentations in *Heliofungia*. Scale bar: 1 mm. Fig. 648. Septa *H. actiniformis* (RMNH 20165; SW Sulawesi, Indon.). Fig. 649. Costae of same specimen.



Figs. 650-651. SEM-photographs of septo-costal ornamentations in *Ctenactis*. Scale bar: 1 mm. Fig. 650. Septa *C. echinata* (RMNH 20169; SW Sulawesi, Indon.). Fig. 651. Costae of same specimen.

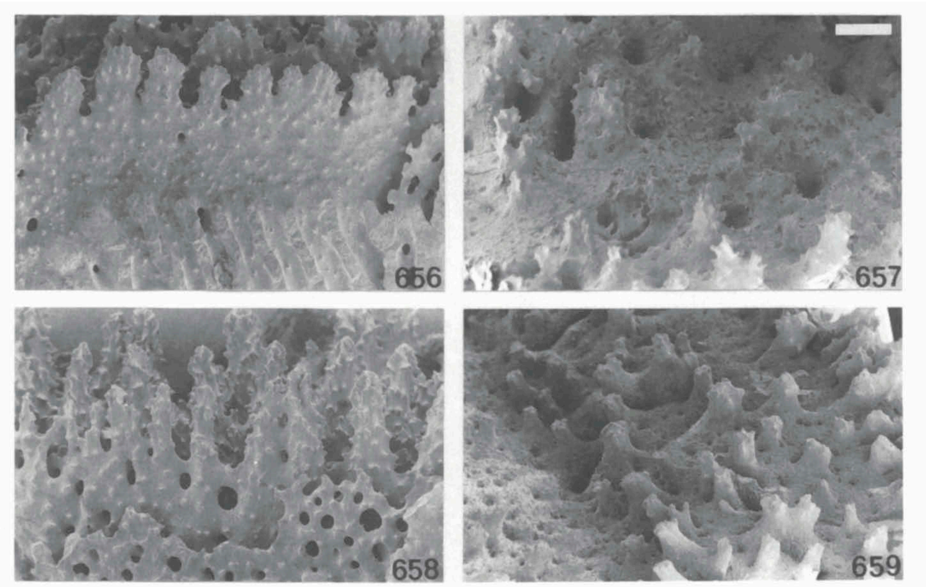


Figs. 652-653. SEM-photographs of septo-costal ornamentations in *Herpolitha*. Scale bar: 1 mm. Fig. 652. Septa *H. limax* (RMNH 16069; SW Sulawesi, Indon.). Fig. 653. Costae of same specimen.

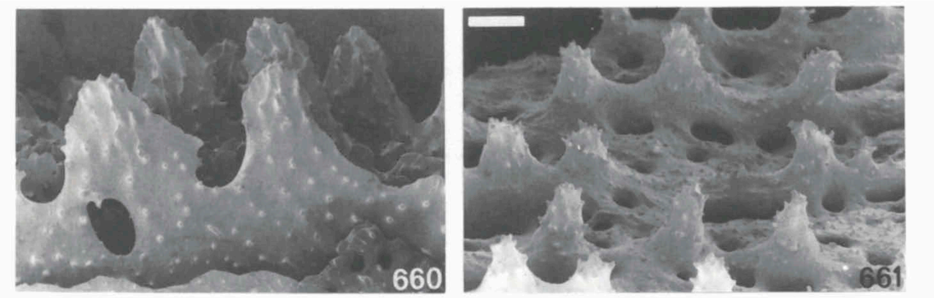


Figs. 654-655. SEM-photographs of septo-costal ornamentations in *Polyphyllia*. Scale bar: 1 mm. Fig. 654. Septa *P. talpina* (RMNH 16146; SW Sulawesi, Indon.). Fig. 655. Costae of same specimen.

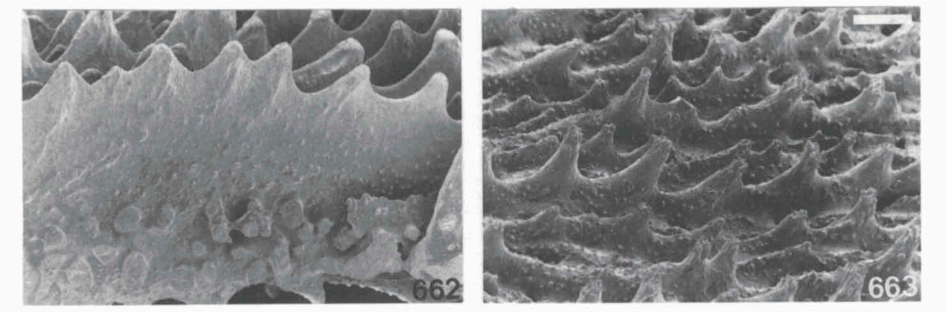
Cairns (1984b) relied on the data published by Wells (1966) and additional information given by Pillai & Scheer (1976) and Veron & Pichon (1979) for the construction of his cladogram of fungiid (sub)genera (Cairns, 1984b: fig. 3). His cladogram is different in several aspects from the one directly derived from Wells' evolutionary scheme (fig. 672). In Cairns' (1984b) cladogram *Cycloseris* is subdivided into three sister-groups, namely *Cycloseris* A, *Cycloseris* B and



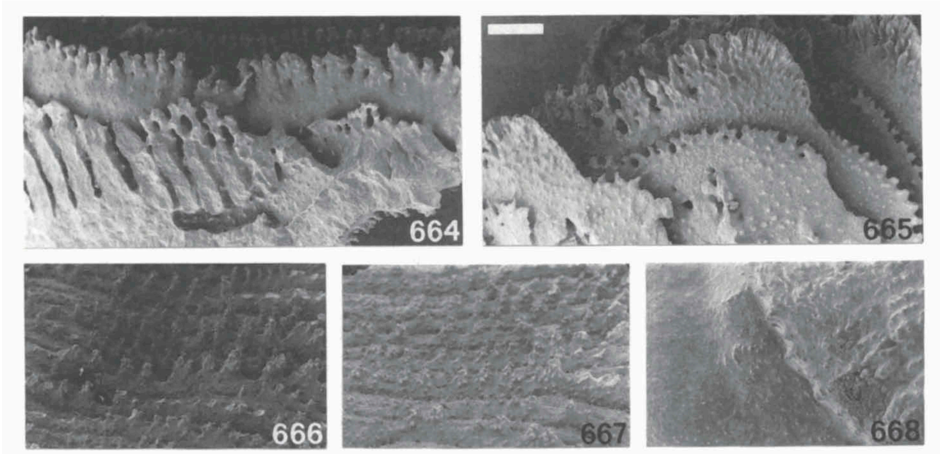
Figs. 656-659. SEM-photographs of septo-costal ornamentations in *Sandalolitha*. Scale bar: 1 mm. Figs. 656-657. Septa and costae *S. robusta* (RMNH 16207; SW Sulawesi, Indon.). Figs. 658-659. Septa and costae *S. dentata* (RMNH 22105; SW Sulawesi).



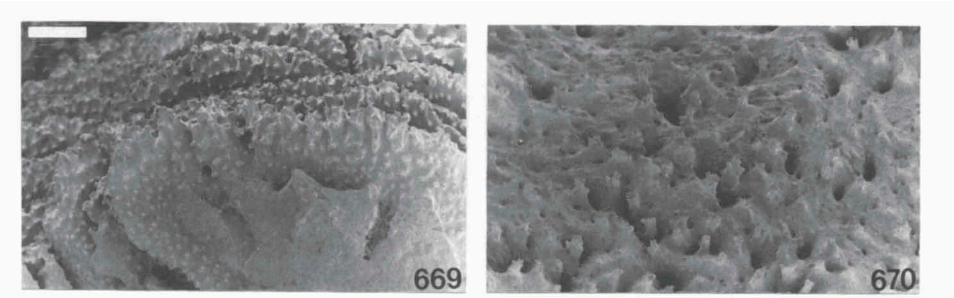
Figs. 660-661. SEM-photographs of septo-costal ornamentations in *Zoopilus*. Scale bar: 1 mm. Fig. 660. Septa *Z. echinatus* (RMNH 22116; SW Sulawesi, Indon.). Fig. 661. Costae of same specimen.



Figs. 662-663. SEM-photographs of septo-costal ornamentations in *Halomitra*. Scale bar: 1 mm. Fig. 662. Septa *H. pileus* (RMNH 8410; Banda, Indon.). Fig. 663. Costae of same specimen.



Figs. 664-668. SEM-photographs of septo-costal ornamentations in *Lithophyllon*. Scale bar: 1 mm. Fig. 664. Septa *L. undulatum* (RMNH 22133; SW Sulawesi, Indon.). Fig. 665. Septa *L. mokai* (RMNH 22150; SW Sulawesi). Figs. 666-667. Costae *L. undulatum* (RMNH 22133; SW Sulawesi). Fig. 668 Costae *L. mokai* (RMNH 22150; SW Sulawesi).



Figs. 669-670. SEM-photographs of septo-costal ornamentations in *Podabacia*. Scale bar: 1 mm. Fig. 669. Septa *P. crustacea* (RMNH 22120; SW Sulawesi, Indon.). Fig. 670. Costae of same specimen.

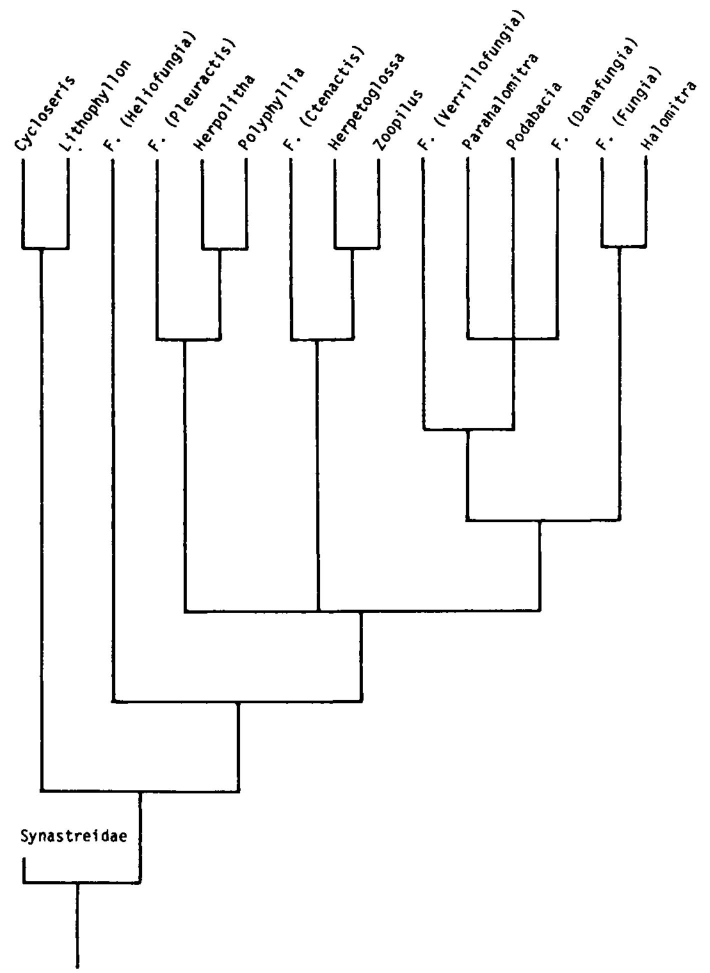


Fig. 671. Well's (1966: fig. 3) scheme of the evolutionary pattern of fungiid genera and subgenera transformed into a cladogram.

Diaseris. The division into *Cycloseris* A and *Cycloseris* B depends on whether the width of adjacent costae is equal or not. *Diaseris* is separated from its sister groups because its species show a capacity to fragment. *F. (Danafungia)* is the sister-group of *F. (Ctenactis)* with *Herpetoglossa*. *F. (Danafungia)* has been split into two sister-groups, A and B. Species of *F. (Danafungia)* A show a solid corallum wall and those of *F. (Danafungia)* B a perforated one. (Consequently this division should have been made for *F. (Verrillofungia)* as well, because in this subgenus species also display either a perforate or an imperforate corallum wall).

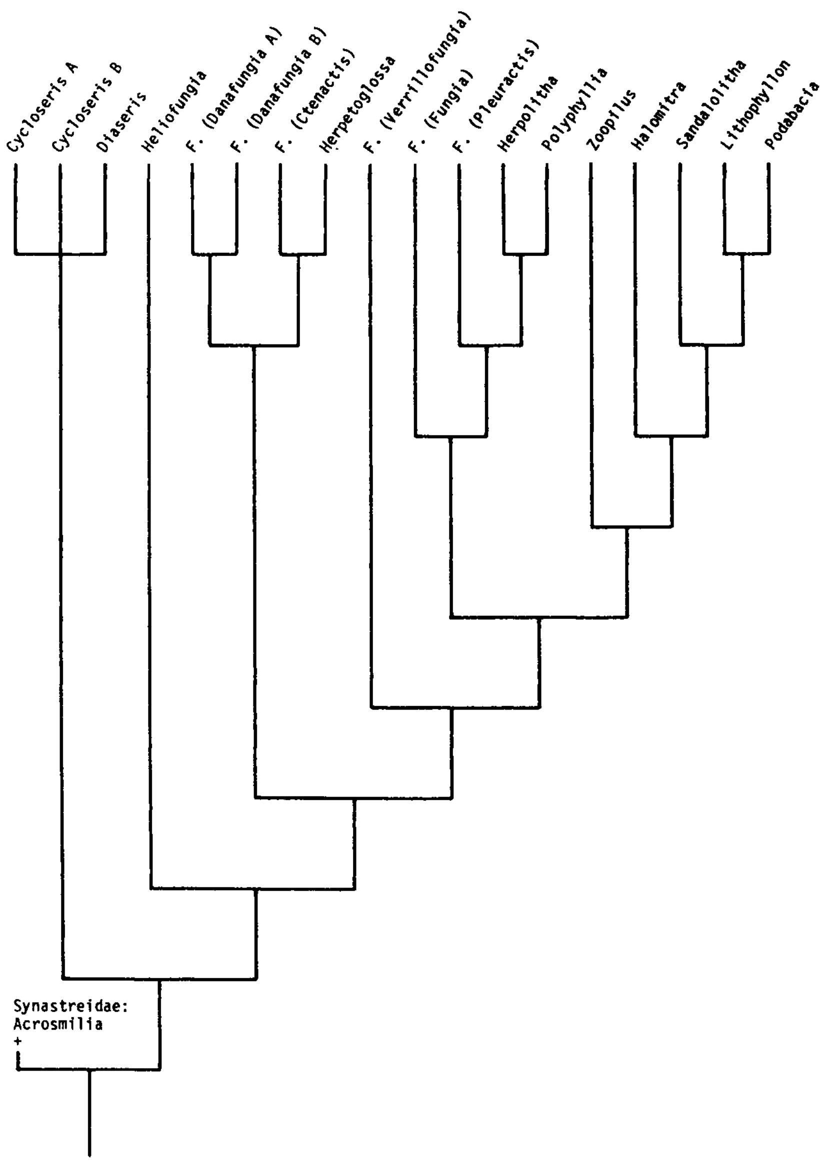


Fig. 672. A simplified version of Cairn's (1984: fig. 3) cladogram of fungiid (sub)genera to indicate hypothetical affinities within the Fungiidae.

In Cairns' (1984b) cladogram the generic name *Fungia* is maintained for a complicated paraphyletic group next to *Herpetoglossa* and also next to *Herpolitha* and *Polyphyllia*, i.e. *F. (Ctenactis)* is the sister-group of *Herpetoglossa*, and *F. (Pleuractis)* is the sister-group of *Herpolitha* with *Polyphyllia*. The major changes introduced in the taxonomic arrangement of the taxa in Cairns' (1984b) cladogram are due to its higher degree of parsimony. For instance, genera of corals showing circumoral budding are grouped together, with the sedentary genera *Lithophyllon* and *Podabacia* at the end of the transformation series. Nomenclatural modifications shown in Cairns' (1984b) cladogram comprise the upgrading of *Heliofungia* to genus level (after Veron & Pichon, 1979) and the change of *Parahalomitra* into its senior synonym *Sandalolitha* (after Pillai & Scheer, 1976).

Methods. — Döderlein (1901, 1902) and Wells (1966) considered differences in the shape of the septal dentations and the costal spines important for the taxonomy and the unravelling of the phylogeny of the Fungiidae. Döderlein (1901; 1902) did not give detailed illustrations of these differences. Drawings of generalized septo-costal structures were first presented by Vaughan & Wells (1947: figs. 30-31) and later by Wells (1966: fig. 4). In the present study SEM-photographs are given to show the differences between the septo-costal structures of the fungiid (sub)genera. When a subgenus or genus shows interspecific variation in these structures, extra illustrations are given to indicate its range (figs. 611-670).

The present analysis is the first in which the phylogeny of the Fungiidae is studied down to species level. The interspecific differences of the Fungiidae are critically examined in a phylogenetic perspective. With the help of outgroup comparison (the main criterion), geologic character precedence and the correlation of transformation series (De Jong, 1980; Wiley, 1980) is investigated which of the character states are plesiomorph (ancestral) and which are apomorph (derived). These techniques concern the morphology of the animals. Additional techniques, which mainly concern the ecology and biogeography of the groups (see De Jong, 1980) have not been used because the data necessary for these techniques have not been worked out yet. (The phylogenetic aspects of biogeography will be discussed in the section on historical and ecological biogeography).

Following Cairns (1984b), the genus *Acrosmilia* d'Orbigny, 1849, has been selected as out-group for the Fungiidae. *Acrosmilia* has the same septal structures as *F. (Cycloseris)* and it has a corallum shape which is very similar to that of the late anthocaulus-stage in the ontogeny of fungiids (Wells, 1966: 235). *Acrosmilia* (Synastreidae), which became extinct during the Cretaceous, is according to Wells (1956: fig. 259) more closely related to the Fungiidae than any other family (see also fig. 38). (The taxonomic position of the recently described Fungiacyathidae (see Chevalier & Beauvais, 1987) is not clear

Table 3. Character state transformations (#) on which the phylogenetic analysis of the Fungiidae is based.

Plesiomorph character states (0)	Apomorph character states (●)	#
Compound synapticulae absent	- Compound synapticulae present	01
Sedentary mode of life (turbinate)	- Free-living phase in life cycle	02
All septa with densely distributed perforations	Higher order septa densely perforated and those of lower orders usually	
	- thinly perforated or solid	03
03	- with irregularly distributed holes	04
Granulations at septal fringe arranged in crossing rows or predominantly in rows perpendicular to septal margin	- Granulations predominantly arranged in rows parallel to the septal margin	05
	- Granulations arranged in irregular patterns	06
	- Rows of granulations in a radiating pattern	07
Septal dentations simply trabeculate with granular appearance	Dentations compound and	
	- angular	08
"	- lacerate	09
"	- tapering towards their tip	10
"	- lobate	11
08	- club-shaped	12
10	- angular	13
10	- lobate	14
Number of septal dentations > 30 / cm	- Number of septal dentations < 30 / cm	15
Number of septal dentations > 15 / cm	- Number of septal dentations < 15 / cm	16
Full-grown costal spines simply trabeculate and acute	Costal spines compound trabeculate and	
	- short, spherical and granulated	17
"	- lacerate	18
"	- long, cylindrical-conical and granulated	19
19	- with coarse granulations (echinose)	20
19	- with granulations concentrated at their tip	21
Number of costal spines > 40 / cm	- Number of costal spines < 40 / cm	22
Number of costal spines > 20 / cm	- Number of costal spines < 20 / cm	23
Corallum wall not granulated	- Corallum wall granulated	24
Corallum wall solid	- Corallum wall perforated	25
Length of central fossa (axial furrow) < 1/8 length of corallum	- Length of central fossa (axial furrow) ≥1/8 length of corallum	26
Corallum outline circular or slightly oval	- Corallum outline hexagonal in juvenile stage	27
	- Corallum outline oval	28
28	- Corallum outline elongate	29
Animal monostomatous	Animal polystomatous by	
	- intrastomadaeal budding	30
"	- circumoral budding	31
"	- peripheral budding	32

Table 3 (continued).

Maximal corallum length ≤15 cm	- Maximal corallum length > 15 cm	33
Maximal corallum length ≤ 30 cm	- Maximal corallum length > 30 cm	34
Diameter detachment scar < 1 cm	- Diameter detachment scar > 1 cm	35
Detachment scar healing	- Detachment scar remaining	36
Free-living phase in life-cycle	- Coral remaining sedentary, turbinate	37
37	- Coral encrusting	38
37	- Coral foliacious	39
Auto-fragmentation ability absent	- Auto-fragmentation ability present	40
Corals in general not breaking easily	- Fragmentation due to thinness of corals	41
Corallum margin even	- Corallum margin undulating in adults	42
"	- Corallum margin folded in adults	43
Coral not humped at upper surface	- Upper surface humped around central fossa	44
Length of extended tentacle < 1 cm	- Maximal tentacle length > 1 cm	45
Tentacles not conspicuously pigmented	- Tentacles white	46
"	- Tips of tentacles violet	47
Tentacular lobes usually absent	- Tentacular lobes usually present	48
Septa densely packed	- Septa loosely arranged	49
Septa (almost) equally high	- Low order septa higher than adjacent septa	50
"	- First few cycles of septa distinctly protruding	51
Adjacent septa almost equally thick	- Low order septa thicker than adjacent ones	52
Adjacent costae (almost) equal in size	- Lower order costae relatively large	53
All costae with well-developed spines	- Higher order costae without developed spines	54
No distinct columella present	- Trabecular columella present in central stoma	55

enough to consider it useful as an out-group). The characters of *Acrosmilia* are briefly summarized by Wells (1956: 365).

The phylogenetic criterion of geologic character precedence is useful in the determination of the relative state of characters, in particular when these characters concern the stony coralla since these fossilize relatively easily. Use of this criterion implies that the apomorphic character states cannot be found in the oldest members of a monophyletic group, whereas any plesiomorphic character may still be present in the more recent members. In relation to the Fungiidae, the correlation of transformation series analysis is particularly useful for characters that are not preserved in the fossil record, such as those related to the soft body parts (for example tentacle size and colour).

An important problem for the reconstruction of the phylogeny of the Fungiidae, is their great intraspecific morphological variability. To overcome this problem character states may have to be generalized, thus neglecting anomalies. In the following paragraphs the character state transformations used in the cladistic analysis are discussed. In conclusion there is a discussion of the cladogram.

Table 4. Code numbers representing the Fungiidae as used in tables and diagrams

01.	Fungia (Cycloseris) sinensis	21.	Fungia (Pleuractis) moluccensis
02.	Fungia (Cycloseris) distorta	22.	Fungia (Pleuractis) gravis
03.	Fungia (Cycloseris) cyclolites	23.	Fungia (Pleuractis) paumotensis
04.	Fungia (Cycloseris) curvata	24.	Heliofungia actiniformis
05.	Fungia (Cycloseris) somervillei	25.	Ctenactis albitentaculata
06.	Fungia (Cycloseris) fragilis	26.	Ctenactis echinata
07.	Fungia (Cycloseris) hexagonalis	27.	Ctenactis crassa
08.	Fungia (Cycloseris) costulata	28.	Herpolitha limax
09.	Fungia (Cycloseris) tenuis	29.	Polyphyllia novaehiberniae
10.	Fungia (Cycloseris) vaughani	30.	Polyphyllia talpina
11.	Fungia (Verrillofungia) spinifer	31.	Sandalolitha dentata
12.	Fungia (Verrillofungia) scabra	32.	Sandalolitha robusta
13.	Fungia (Verrillofungia) concinna	33.	Zoopilus echinatus
14.	Fungia (Verrillofungia) repanda	34.	Halomitra pileus
15.	Fungia (Danafungia) fralinae	35.	Halomitra clavator
16.	Fungia (Danafungia) horrida	36.	Cantharellus doederleini
17.	Fungia (Danafungia) scruposa	37.	Cantharellus noumaea
18.	Fungia (Fungia) fungites	38.	Lithophyllon undulatum
19.	Fungia (Wellsofungia) granulosa	39.	Lithophyllon mokai
20.	Fungia (Lobactis) scutaria	40.	Podabacia crustacea

Character state transformations. — In total 55 character state transformations are used to analyze the phylogenetic relationships of the Fungiidae (table 3). Per species the character states are indicated in a matrix (table 5). In this matrix the species are represented by code numbers (see table 4) which are also used in the cladogram (fig. 673). In this cladogram each species is indicated by the first three letters of its specific name.

Transformation 1. The presence of compound synapticulae (01) is a synapomorph character of the Fungiidae, which distinguishes it from other scleractinian families.

Transformation 2. The presence of a free-living stage in the life cycle (02) is an apomorph character shared by most Fungiidae, but not by the species of *Cantharellus*, *Lithophyllon* and *Podabacia*, and also not by the out-group *Acrosmilia*. In these three fungiid genera the corals lack the free-living phase, which, following the criterion of the correlation of transformation series, is suggested to be an example of reversal (37) because in these monophyletic groups it co-occurs with several synapomorphies that do not occur in the out-group. Within the Scleractinia, the development of a free-living stage is not restricted to the Fungiidae. It may, for example, also be observed in the extinct Cyclolitidae and in the extant Fungiacyathidae (see Wells, 1956). The frequent evolution of free corallum shapes within the Scleractinia is considered an example of convergence.

Table 5. Plesiomorph (0) and apomorph (●) character states (table 3: #) per species (the out-group = 00; * = no character state is applicable).

	---------------------------- Fungiidae (see table 4) ----------------------------																				
#	00	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	#
01	0	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	01
02	0	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	02
03	0	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	03
04	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	04
05	0	0	0	0	0	0	0	0	0	0	0	●	●	●	●	0	0	0	0	0	05
06	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	●	●	0	0	06
07	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	07
08	0	0	0	0	0	0	0	0	0	0	0	●	●	●	●	●	●	●	●	●	08
09	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	09
10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10
11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11
12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12
13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13
14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14
15	0	0	0	0	0	0	0	0	0	0	0	0	0	●	●	●	●	●	●	0	15
16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	●	●	0	0	16
17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	●	17
18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	18
19	0	0	0	0	0	0	0	0	0	0	0	●	●	●	●	●	●	●	●	0	19
20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20
21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	●	0	21
22	0	0	0	0	0	0	0	0	0	0	0	●	●	●	●	●	●	●	●	0	22
23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	●	0	●	●	●	0	23
24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	●	●	●	●	0	24
25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	●	0	0	●	●	●	25
26	0	0	●	●	●	●	0	0	●	●	●	●	●	●	●	●	●	●	●	●	26
27	0	0	0	0	0	0	0	●	0	0	●	0	0	0	0	0	0	0	0	0	27
28	0	0	0	●	0	●	0	0	0	●	0	0	0	0	0	0	0	0	0	0	28
29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	29
30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	30
31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	31
32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	32
33	0	0	0	0	0	0	0	0	0	0	0	0	0	●	●	●	●	●	●	●	33
34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	●	●	0	34
35	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	35
36	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	●	0	0	0	0	36
37	*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	37
38	0	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	38
39	0	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	39
40	0	●	●	●	●	●	●	●	0	0	●	0	0	0	0	0	0	0	0	0	40
41	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	41
42	0	0	0	0	0	0	0	●	0	0	0	0	0	0	0	0	0	0	0	0	42
43	0	0	0	0	●	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	43
44	0	0	0	0	0	●	0	0	0	0	0	0	0	0	0	0	0	0	0	0	44
45	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	●	0	0	0	0	45
46	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	46
47	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	●	0	0	0	0	47
48	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	48
49	0	0	0	0	0	0	●	0	0	0	0	0	0	●	●	●	●	●	●	0	49
50	0	0	0	●	●	●	●	●	0	0	●	●	●	●	●	●	●	●	●	0	50
51	0	0	0	0	0	0	●	0	0	0	0	0	0	0	0	0	0	0	0	0	51
52	0	0	0	●	●	0	0	0	●	●	0	0	0	0	0	0	0	0	0	0	52
53	0	0	0	0	0	●	0	0	0	●	●	●	0	●	●	●	●	●	0	0	53
54	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	●	●	●	0	0	54
55	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	55

Table 5 (continued).

	------------------------------ Fungiidae (see table 4) ------------------------------																					
#	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	#
01	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	01
02	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	0	0	0	0	0	02
03	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	03
04	0	0	0	0	0	0	0	0	0	0	0	●	●	●	0	0	0	0	●	●	●	04
05	0	0	●	●	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	05
06	0	0	0	0	0	●	●	●	0	0	0	●	●	●	●	●	0	0	●	●	●	06
07	0	0	0	0	●	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	07
08	●	●	●	●	0	0	0	0	●	●	●	0	0	0	●	●	0	0	0	0	0	08
09	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	●	●	0	09
10	0	0	0	0	0	●	●	●	0	0	0	●	●	●	0	0	0	0	0	0	●	10
11	0	0	0	0	●	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11
12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	●	0	0	0	0	0	12
13	0	0	0	0	0	0	0	●	0	0	0	0	0	0	0	0	0	0	0	0	0	13
14	0	0	0	0	0	0	0	0	0	0	0	0	●	0	0	0	0	0	0	0	●	14
15	0	0	0	●	●	●	●	●	0	●	●	●	●	●	●	●	0	0	0	0	●	15
16	0	0	0	0	●	●	●	●	0	0	0	0	0	●	●	●	0	0	0	0	0	16
17	0	●	●	●	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17
18	0	0	0	0	●	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	18
19	●	0	0	0	0	●	●	●	●	●	●	●	●	●	●	●	0	0	●	●	●	19
20	0	0	0	0	0	●	●	●	0	0	0	0	0	●	0	0	0	0	0	0	0	20
21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	●	●	0	0	0	0	0	21
22	●	0	●	●	●	●	●	●	●	●	●	●	●	●	●	●	0	0	0	0	●	22
23	0	0	0	0	0	0	●	●	0	0	0	0	0	●	●	●	0	0	0	0	0	23
24	0	0	0	0	0	0	●	●	0	0	0	●	●	●	●	●	0	0	●	●	●	24
25	●	●	●	●	0	●	●	●	●	●	●	●	●	●	●	●	0	0	0	0	●	25
26	●	●	●	●	●	●	●	●	●	●	●	0	0	0	0	0	0	0	0	0	0	26
27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	27
28	●	●	●	●	0	●	●	●	●	●	●	●	●	●	0	0	0	0	0	0	0	28
29	0	0	0	0	0	●	●	●	●	●	●	0	0	0	0	0	0	0	0	0	0	29
30	0	0	0	0	0	0	●	●	●	●	●	0	0	0	0	0	0	0	0	0	0	30
31	0	0	0	0	0	0	0	0	0	●	●	●	●	●	●	●	0	0	●	●	●	31
32	0	0	0	0	0	0	0	0	●	●	●	0	●	●	●	●	0	0	●	●	●	32
33	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	0	0	●	0	●	33
34	0	0	0	0	0	●	●	●	●	●	●	●	●	●	●	●	0	0	●	0	●	34
35	0	●	0	0	0	0	0	0	0	0	0	●	●	0	0	0	*	*	*	*	*	35
36	0	●	0	0	●	0	0	0	0	0	0	0	0	0	●	0	*	*	*	*	*	36
37	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	●	●	●	●	●	37
38	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	0	0	0	●	0	38
39	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	0	0	●	0	●	39
40	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	40
41	0	0	0	0	0	0	0	0	0	●	0	0	0	●	0	●	0	0	0	0	0	41
42	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	●	0	●	42
43	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	●	●	0	●	43
44	0	●	●	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	44
45	0	0	0	0	●	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	45
46	0	0	0	0	0	●	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	46
47	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	47
48	●	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	48
49	0	0	0	●	0	●	●	0	0	0	0	0	0	●	●	●	0	0	0	0	0	49
50	0	0	0	●	●	●	●	0	●	0	0	0	0	0	●	●	0	●	0	0	0	50
51	0	0	0	0	0	0	0	0	0	0	0	●	0	0	0	0	0	0	0	0	0	51
52	●	●	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	52
53	0	●	0	0	0	0	0	0	0	0	0	0	0	0	0	●	0	0	0	0	0	53
54	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	●	0	0	0	0	0	54
55	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	55

Transformations 3-4. In adult specimens of most Fungiidae, the lower order septa are either solid or thinly perforated only (03; see figs. 638, 640), whereas their higher order septa are more densely perforated. In juveniles these septa may still be completely perforated. In both the out-group and the extinct genus *Cyclolites* Lamarck, 1801 (Cyclolitidae), in all specimens, all septa are densely perforated in an almost regular pattern (see Wells, 1956: figs. 233, 277), which is considered the plesiomorph character state. Hence, solid or thinly perforated lower order septa of adult corals is the apomorph character state. Most adults of *Fungia (Cycloseris) sinensis* show this apomorph character state (fig. 611), whereas a minority of the adult specimens still has completely perforated lower order septa. In the latter group of adult specimens the character septal perforation is expressed as if these corals were still juveniles (neoteny). In the analysis, the occasional occurence of fully perforated lower order septa in full-grown specimens is neglected. The presence of few small perforations in the lower order septa (03) is considered a plesiomorph character state as compared to the presence of relatively large perforations, which give these septa a fenestrate appearance (04). Only a few fungiid species show this character state (see fig. 650).

Transformations 5-7. Within the Fungiidae four distinct patterns of septal granulations can be observed. In the out-group these granulations are distributed in crossing rows, parallel and (predominantly) perpendicular to the septal margins. This may also be observed in some of the fungiids (figs. 611-615), but in most species the septal granulations are either arranged in rows parallel to the septal margin (05; see fig. 621), in an irregular pattern (06; see fig. 650), or in a radiating pattern (07; see fig. 648). As an exception, the granulation pattern is hardly visible; this is displayed by specimens that have grown anomalously large and sometimes by corals that have lived in an environment much exposed to wave action.

Transformations 8-14. With the help of out-group comparison it can be assumed that within the Fungiidae the septal dentations have evolved from structures consisting of simple, granular trabeculae towards compositions of compound trabeculae (compare Wells, 1956: fig. 236). The plesiomorph character state of simply trabeculate dentations is common in juvenile specimens of most species and also in some adults, such as those of *F. (Cycloseris)* (figs. 611-615). Rarely adults of the latter species form dentations that are compound lacerate (figs. 153-156). This effect of the septal fringe being frayed (09) is common in species of *Lithophyllon* (figs. 664-665). In many fungiids the septal margin is ornamented with compound angular dentations (08), which are either regular or irregular in shape (figs. 625-628). In a single species these angular dentations have developed into club-shaped ornamentations (12; see figs. 544-545, 549-550). In some species the dentations are compound and tapering towards their tip (10; see figs. 650, 658), whereas in others they may have developed into septal teeth which are compound and angular (13; see figs. 435-437) or compound and lobate (14; see fig. 656). Because angular and lobate septal dentations occur in different monophyletic groups, they are supposed to have evolved in two ways, i.e. directly from simple septal teeth (08 and 11) and indirectly, through transformation 10, in which the compound tapering dentations become angular by developing a wider base (13) or lobate by getting a wider tip (14).

Transformations 15-16. While becoming more compound, the septal dentations also become larger, which results in smaller densities of septal dentations. Cairns (1984b) considered this density a multistate character: small dentations (30-60 teeth per cm), large ones (10-20 teeth per cm) and very large ones (less than 10 teeth per cm). When defined as such, it appears that in the present study two character states may be observed within a single species. Therefore they are now redefined as: fine (more than 30 teeth per cm; the plesiomorph character state); small (15-30 teeth per cm; apomorph character state 15) and large (less than 15 teeth per cm; apomorph character state 16).

Transformations 17-21. Like the septa, the costae show differentiation in their ornamentation. Simply trabeculate spines are considered plesiomorph (figs. 616-618). The granulated compound trabeculate spines derived from this form are either relatively short and spherical (17; see figs. 639, 643, 645, 647), lacerate (18; see fig. 649) or relatively long and cylindrical (19; see figs. 622-624, 629-632). When the criterion of the correlation of transformation series is applied, it can be assumed that character state 19 is the plesiomorph state related to spines covered by very coarse granulations (20; see fig. 651), and to spines with granulations concentrated at the tip (21; see figs. 636-637).

Transformations 22-23. The density of the costal spines is defined as a multistate character: fine (more than 40 spines per cm) is the plesiomorph character state; large (less than 40 spines per cm) is an apomorph character state (22); very large (less than 20 spines per cm) is considered apomorph (23) related to character state 22. Cairns (1984b) made a subdivision between fine costal spines (30-70 per cm) as plesiomorph and coarse ones (5-20 per cm) as apomorph. With these limits maintained, two character states might be observed within one species. The limits of the newly defined character states occur not within the density ranges of the individual species.

Transformation 24. Up to the present, very little attention has been paid to the presence of granulations on the aboral side of the corallum wall, with the exception of those on the spines. In the present study the absence of these granulations is regarded as a plesiomorph character state (fig. 616) and their presence as the apomorph one (24; see figs. 629-632).

Transformation 25. Cairns (1984b) considered a solid corallum wall the plesiomorph character state (figs. 666-668) and a perforated one apomorph (25; see fig. 670). This view is followed in the present study.

Transformation 26. A central fossa distinctly shorter than 1/8 of the corallum length is considered a plesiomorph character state. It occurs in the outgroup *Acrosmilia* and in some fungiid species. A fossa which measures at least 1/8 of the corallum length is considered apomorph (26).

Transformations 27-29. In the out-group the corallum outline is circular to slightly oval (Vaughan & Wells, 1943: pl. 16 figs. 1-2), which is therefore considered a plesiomorph character state. Most fungiids show a similar outline (fig. 41a) whereas some species of *Fungia* show a hexagonal outline in juvenile stage (27; see fig. 40b) which in the course of the anthocyathus-phase may become more circular. In other species the corallum outline is distinctly oval (28; figs. 41d-f) or even elongate (29; see figs. 41g-h).

Transformations 30-32. The more elongate the corallum outline of a fungiid coral, the longer the length of its axial furrow (fig. 41b), and when such an oblong coral shows intrastomadaeal budding (figs. 41c, g-h) the more stomata it develops inside the axial furrow. The monostomatous coral shape (figs. 41a-b) is considered the plesiomorph character state, whereas corals showing intrastomadaeal budding represent an apomorph character state (30). Circular and oval corals may become polystomatous by circumoral budding (31; see fig. 41d), peripheral budding (32; see fig. 41j) or by a combination of these (fig. 41). In some species apomorphy 30 may be observed in combination with either apomorph character state 32 (figs. 40f, 41h) or with both apomorphies 31 and 32 together (fig. 41g). It is possible that specimens of species which usually show a single mouth (the plesiomorph character state) produce supernumerary mouths in the form of either one of the three apomorph character states. In the analysis these anomalies have not been taken into account.

Transformations 33-34. The maximum corallum diameter of fungiid corals is defined as a multistate character. A maximum coral length of 15 cm or less is considered plesiomorph. Lengths of more than 15 cm, and more than 30 cm are apomorph character states 33 and 34, respectively. Cairns (1984b), following Wells (1966), defined a corallum diameter of less than 5 cm as the plesiomorph character state and all larger sizes as the apomorph character state. During the present study it appeared that the maximum diameter of 5 cm which was supposed to be observed in *F. (Cycloseris)* (see Wells, 1966), actually should be 15 cm.

Transformations 35-36. Specimens of most species reaching the anthocyathus phase have a quickly healing small detachment scar. Within the

Fungiidae this is considered a plesiomorph character state. In a few species the corallum shows a relatively large detachment scar, with a diameter of more than 1 cm, which is considered an apomorph character state (35; see fig. 350). A failure to perform the healing process, which is seen in two species, is also regarded as an apomorphy (36; see figs. 390-391).

Transformations 37-39. A few species have lost the ability to detach and remain in the anthocaulus phase with a turbinate corallum shape (37; figs. 558-561). In relation to transformation 2 this is an example of reversal. In Cairns' (1984b) analysis a fixed adult corallum is considered a plesiomorph state within the Fungiidae, whereas in the present study Wells' (1966) view is followed in which it is regarded as a loss of the free-living stage. Within the Fungiidae a loss of the free-living phase (37) has apparently occurred three times, independantly, and therefore this may be considered an example of homoplastic reversal. The reversal towards a turbinate corallum shape in its turn is plesiomorph related to an encrusting shape (apomorph character state 38; see figs. 583-589) and a foliacious corallum (apomorph character state 39; see figs. 567, 596).

Transformations 40-41. Corals of most Fungiidae do not break easily, which is considered the plesiomorph character state. Corals (in the anthocyathus phase) of some species are able to break into fragments, after fissures in the corallum wall have been developed, to facilitate fragmentation (40; see figs. 100, 120). Within the Scleractinia this process is best known to occur in some fungiid species, although it may also be observed in some of the Fungiacyathidae (see Cairns, 1984a: pl. 1 fig. A). Most fungiids not producing these fissures usually do not break because their corallum is too thick for easy fragmentation. A few species have coralla which have evolved into such a thin and fragile shape, that their fragmentation is almost inevitable (apomorph character state 41; figs. 461-462). Both character state transformations, 40 and 41, increase the chance for asexual reproduction, since the loose fragments usually regenerate very easily.

Transformations 42-44. In most Fungiidae the corallum margin is even and relatively smooth, which is considered a plesiomorphy. There are also species in which the corallum margin becomes undulating (apomorph character state 42; see figs. 123-126) or folded (apomorph character state 43; see fig. 88) in adult specimens. The oral surface of the animals is usually also even (plesiomorphy), although in some species the central part of the upper surface has evolved into a hump (apomorph character state 44; see figs. 349, 351).

Transformations 45-48. Short tentacles and colourless translucent tentacles are considered plesiomorph character states. Examples of apomorph character states are relatively long tentacles with acrospheres (45; see fig. 24), white tentacles (46; see fig. 25) and violet tentacle tips (47; see fig. 12). Most Fungiidae usually show no septal structures supporting the tentacles (tentacular lobes), which is the plesiomorph character state; a single species, *Fungia (Lobactis) scutaria*, does almost consistently show such structures, on each septum one, which is the apomorph character state (48; see fig. 20). Apomorphies related to polyp coloration (excluding the tentacles) are not used in the analysis; within the Fungiidae they are apomorphies such as particularly coloured mouth areas and peripheral zones. None of the observed soft body parts related character state transfomations helped to find phylogenetic affinities because each of them occurs in only one species.

Transformations 49-51. In comparing the septal arrangement of *Acrosmilia* with that of the Fungiidae several apomorph character states in the latter group can be distinguished. In *Acrosmilia* the septa are densely packed and almost equally exsert and thick (Vaughan & Wells, 1943: pl. 1 figs. 1-2), whereas some of the fungiids have the septa loosely arranged, i.e. with relatively much space between them (character state 49; see fig. 248). Several fungiids have the low order septa distinctly more exsert than the adjacent septa (character state 50; see fig. 248). Some species have only the first few cycles of septa distinctly protruding related to the other septa (character state 51; see fig. 123). Others show low order septa which are much thicker than the adjacent ones (apomorph character state 52; see fig. 94).

Transformations 53-54. Some character state transformations can be observed in the costal arrangement of the Fungiidae. Adjacent costae (almost) equal in size and costae with well-developed spines are regarded as plesiomorphies. The presence of relatively large lower order costae in adult specimens is an apomorph character state (53; see fig. 178) and the relative small size of higher order costae and the loss of their spines is another one (54; see figs. 275-280, 551-552).

Transformation 55. The presence of a trabecular columella in the central stoma, which the out-group and the Fungiidae have in common, may be a synapomorphy (55) for these sister-groups related to its absence in *Cyclolites* (Cyclolitidae; see Wells, 1956: 386), which may act as an out-group for both *Acrosmilia* and the Fungiidae together. The significance of the development of a columella in the phylogeny of the Scleractinia is not clear yet. The presence of a columella as such is not rare within the Scleractinia, although its structure may vary a lot and contain characters which may be useful for a cladistic analysis of the scleractinian families.

Cladograms, relations and classifications. — In the resulting cladogram concerning the Fungiidae (fig. 673) an apomorph character state is indicated by the number of its character state transformation and monophyly is symbolized by a solid clade line. When only a symplesiomorph character state is the most distinctive character for a species-group, this is symbolized by a broken clade line and by indicating the distinguishing character state transformation of the sister-group between brackets.

In the cladogram, the superspecific taxa as used in the systematic account are presented without a distinction between genera and subgenera. In a classification based on character weighting (such as in the systematic account) the tree could only be regarded as a cladogram (according to the terminology of Wiley, 1981) in which the genus *Fungia* is paraphyletic. *Fungia* can be distinguished by a combination of characters which in the cladistic analysis are considered plesiomorphies: a single mouth, no loss of the free-living phase, relatively small tentacles and relatively small coralla, which are either circular or oval.

In the present classification of the Fungiidae, genera are distinguished by easily recognized (diagnostic) characters such as the presence of a free-living phase versus its absence, a circular corallum outline versus an oval one, and monostomatous corals versus polystomatous ones. Such a classification based on character weighting, fundamental to evolutionary taxonomy, is theoretically difficult to support (Eldredge & Cracraft, 1980; Ridley, 1986). Some of these diagnostic "characters" are considered plesiomorph character states and, therefore, cannot be used in a phylogenetic classification. For example, *Cycloseris* is distinguished from its sister-group *Cantharellus* because its species have not lost the anthocyathus phase (apomorph character state 37). *Wellsofungia* is separated from *Pleuractis* because it does not contain species that show an oval corallum outline (apomorph character state 28). Phylogenetically such groups of which the monophyly cannot be demonstrated by the presence of synapomorphies are of a reduced interest, whereas symplesiomorph character states can be used in character weighting to define them for practical use.

An important problem met with in the study of fungiid phylogeny is the abundance of convergence. In a cladistic analysis it may be difficult to see whether an apomorph character state that two or more species have in common is an autapomorphy or a synapomorphy (terminology after De Jong, 1980). If one comes to the conclusion that such a character state that two taxa have in common is an autapomorphy, another one may appear to be a homoplasy and vice versa. Several combinations of branches resulting in many different cladograms are possible, which implies that each cladogram is very hypothetical. In such a case it is not advisable to base the nomenclature on a cladogram. In the present analysis, the number of autapomorphies found (in

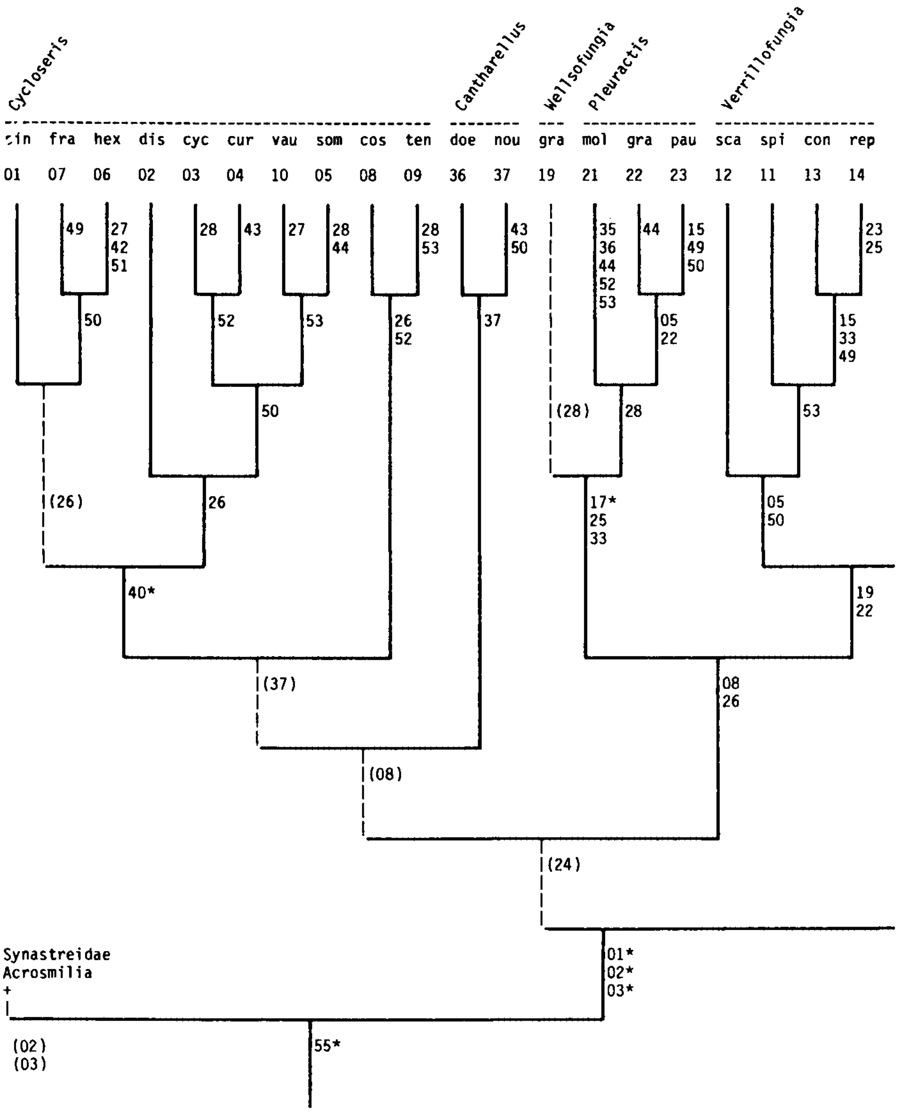
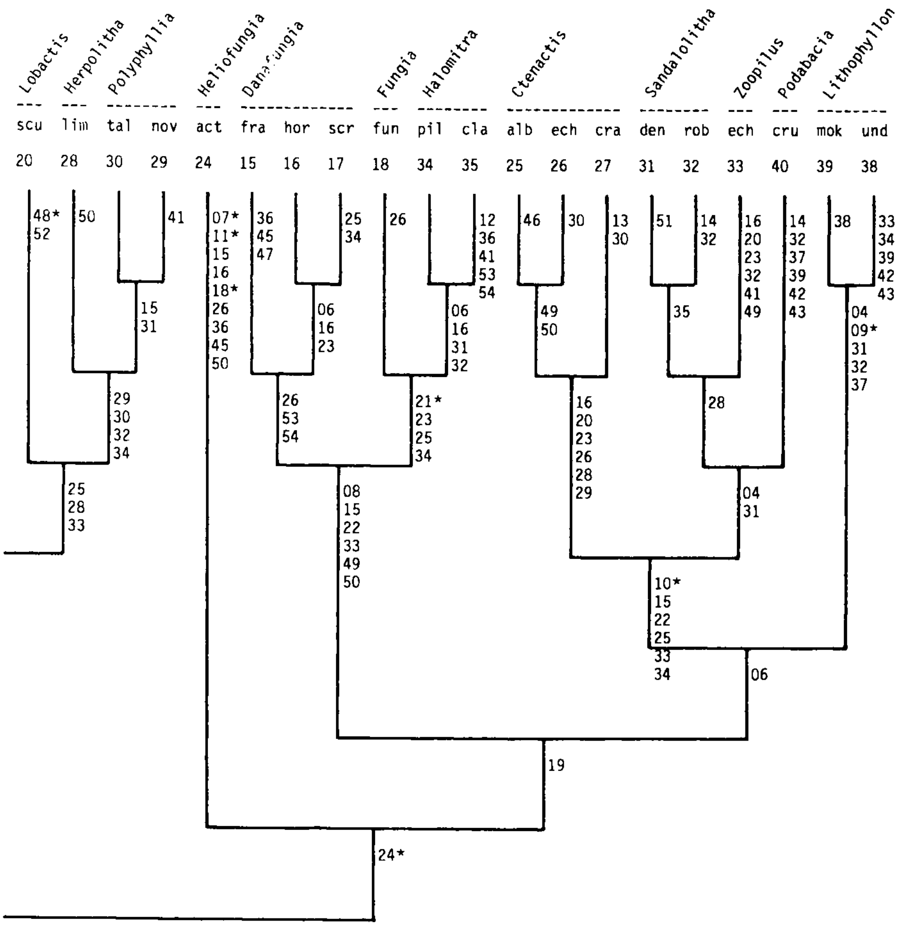


Fig. 673. A cladogram of the Fungiidae based on the character state transformations listed in table 3. The species are indicated with a code number (see table 4) and with the first three letters of the specific name. On top of the cladogram the superspecific taxa as used in the systematic account are displayed, genera and subgenera likewise. Autapomorphies are marked with an ★ to distinguish them from the synapomorphies that occur as homoplastic similarities. When of two sister-groups



only one results from a character state transformation, this one is symbolized by a solid line with the number(s) of the character state transformation(s) alongside. The sister-group that shows no synapomorphy is represented by a broken line with the concerning character state transformation displayed between brackets to indicate by which symplesiomorph character state this sister-group is recognized.

fig. 673 marked with an asterisk) is 14 among a total of 55 apomorph character states, in spite of the maximum of parsimony that has been sought.

Another problem in cladistic analyses is the occurence of reversal. Within the Fungiidae, some species have lost the free-living, anthocyathus-stage. An evolutionary tendency in which corals loose the ability to detach themselves from the substratum is not unlikely to occur. Such reversals may be difficult to recognize because they represent a multistate character (i.e. a series of successive character states) in which the final state resembles the initial one. The way in which reversals and homoplasy are interpreted influences the degree to which the taxa are considered to be related to each other.

The relations between the taxa as indicated in the present cladogram differ in several aspects from those indicated in Cairns' (1984b) cladogram and in Wells' (1966) diagram (compare fig. 673 with figs. 672 and 671, respectively). Some of the differences result from the taxonomic revision treated in the preceding systematic account, without any use of cladisistic principles: the fusion of *Cycloseris* with *Diaseris*, that of *Ctenactis* with *Herpetoglossa* and the addition of *Cantharellus*, *Wellsofungia* and *Lobactis*. The other differences are due to the use of more characters, to different observations and to a different interpretation of similarities due to either synapomorphy or homoplasy and to either symplesiomorphy or reversal.

For example, Wells (1966: 236) considered *Cycloseris* and *Lithophyllon* most closely related (fig. 671) because both should have simple and acute costal spines, which is however a symplesiomorphy (character state transformation 19). According to Cairns' cladogram (1984b: fig. 3), *Cycloseris* and *Lithophyllon* are not closely related (fig. 672) and the presence of simple costal spines in *Lithophyllon* is to be considered a reversal from arborescent to simple. Cairns (1984b) used data from Wells (1966), whereas during the present study it was observed that the costal spines of *Lithophyllon* are not necessarily simple. Adult corals of *Lithophyllon* may show spines which are arborescent (figs. 666-667), whereas in specimens which are still juvenile this character may be less clearly developed (fig. 668). Cairns (1984b) is probably right in considering *Cycloseris* and *Lithophyllon* remotely related, although according to the present study, this view cannot be based on a character state reversal.

Another example of distinct differences between the various cladograms (figs. 671-673) concerns the mutual relationships of three genera of polystomatous corals which resemble each other considerably in general shape and, therefore, are often confused in identifications: *Zoopilus*, *Halomitra* and *Sandalolitha*. In Wells' (1966) diagram (see fig. 671; *Parahalomitra* = *Sandalolitha*), the three genera are not indicated as closely related to each other, whereas they are apparently more akin to either one of the subgenera of *Fungia*. In Cairns' (1984b) cladogram the three genera are situated rather close to each other (fig. 672). According to the present phylogenetic study (fig. 673), *Halomitra* is the sister-group of *Fungia*, and *Zoopilus* and *Sandalolitha* are sister-groups of each other. For *Fungia* and *Halomitra* the opinion concerning the sister-group relationship is mainly based on the shape of the costal spines (character state transformation 21), whereas the interpretation of the relation between *Zoopilus* and *Sandalolitha* is based on the corallum outline (character state transformation 28). In earlier studies, it was not recognized that *Zoopilus* should be considered to have an oval corallum shape, like *Sandalolitha*. Usually this is difficult to see because the corals of *Zoopilus* break easily, involving the loss of the oval shape. Only an examination of the relatively rare unfragmented specimens, most likely to be juveniles, reveals the originally oval shape. At first sight, the broken specimens resemble fragments of *Halomitra*, but the two genera differ distinctly in the shape of the costal spines.

Cycloseris could not be defined by a synapomorph character state, which implies that it may be a para- or a polyphyletic group (fig. 673). The suggested sister-group relationship between *Cycloseris* and *Cantharellus* is uncertain because it has not been demonstrated that these taxa share a synapomorphy (but only symplesiomorphies; see character state transformations 08, 17 and 19).

For a large part the taxonomy as presented in the systematic account can be defended with cladistic arguments. For example, in the cladogram *Wellsofungia* does not share a synapomorph character state with *Verrillofungia*, from which it was separated in the systematic account. Instead, it has three synapomorphies in common with *Pleuractis*, one of which is an autapomorphy (through character state transformation 17). *Lobactis* is not the sister-group of *Pleuractis*, which supports their separation. The oval corallum shape, which the two taxa have in common (character state transformation 28), appears to be a homoplastic similarity.

Several taxonomic changes introduced in the present revision are supported by parts of the largely still hypothetical cladogram that resulted from the phylogenetic studies. A nomenclature strictly based on the present cladistic analysis would be premature because many phylogenetic affinities are not clear yet. When additional data become available an amended cladogram may be preferred.

BIOGEOGRAPHY

Descriptive and phenetic biogeography. — In this section the various ranges of the Fungiidae are compared. To investigate the pattern of regional species richness, the species numbers of 29 areas are counted; in addition the similarity in fungiid faunal composition of these areas is studied.

The geographic distribution ranges of various taxa within the Fungiidae published to date, include a selection of species (Ekman, 1953; Wells, 1966; Gill & Coates, 1977; Wood, 1983; Lamberts, 1984; Veron, 1986b). Some authors have subdivided species into geographic races or subspecies (see the synonymies of *Fungia (Fungia) fungites* and *Heliofungia actiniformis*). Several of these so-called "geographical varieties" proved to be sympatric (Gardiner, 1905; 1909; Boschma, 1925; Wells, 1966), which implies that they cannot be considered subspecies. The ecophenotypical variation of mushroom corals is thus great (Rossi, 1956; Hoeksema & Moka, 1989), that geographic races, should they exist, cannot easily be detected on classical morphological grounds (Rensch, 1929; Wells, 1966; this study). Any attempt to discern their presence and their ranges without using additional methods, such as for example genetical or biochemical ones, would be highly speculative.

For plotting the pattern of regional species richness on a map, distinct geographical areas are selected, which consist mainly of continental coasts bordered by major river outlets and groups of islands situated on shallow oceanic platforms (fig. 674). Despite the fact that these areas are large enough

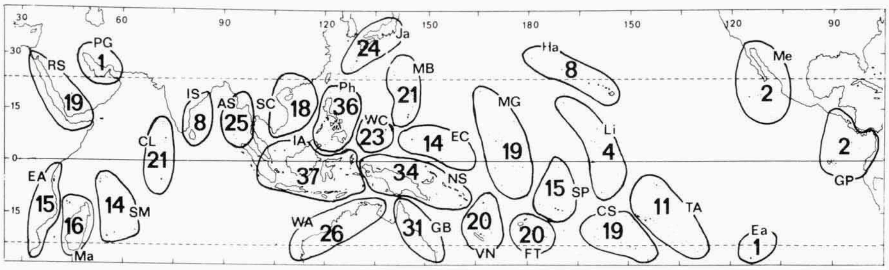


Fig. 674. Areas in the Indo-Pacific and their number of recorded Fungiidae: AS = Andaman Sea; CL = Chagos-Laccadive Plateau; CS = Cook Is. + Society Is.; EA = Eastern Africa; Ea = Easter I.; EC = East Carolines; FT = Fiji + Tonga Is.; GB = Great Barrier Reef; GP = Galapagos + Cocos Is. + Gulf of Panama; Ha = Hawaii Is.; IA = Indonesian Arch.; IS = SE India + Sri Lanka; Ja = Japan; Li = Line Is.; Ma = Madagascar; MB = Marianas + Bonin Is.; Me = Mexico; MG = Marshall + Gilbert Is.; NS = New Guinea + Solomon Is.; PG = Persian Gulf; Ph = Philippines; RS = Red Sea; SC = South China Sea; SM = Seychelles-Mauritius Plateau; SP = Samoa + Phoenix Is.; TA = Tuamoto Arch. + Marquesas; VN = Vanuatu + New Caledonia; WA = Western Australia; WC = West Carolines.

for adequate collection of Fungiidae, the problem remains that poorly known species, in particular those usually occurring deeper than 20 m, are not recorded as frequently as species that are easier to find.

Within the selected areas (fig. 674) differences in species richness may exist, especially at the periphery of the tropical Indo-Pacific. Some of these differences merely reflect the decreasing diversity gradients from lower to higher latitudes which are commonly recognized in biogeography (Briggs, 1974; Pielou, 1979; Stevens, 1989). For example, the Ryukyu Islands are richer in species of Fungiidae than the more northern main island of Japan (Honshu), and along the coastlines of Mozambique (EA) and Western Australia (WA) the species number decreases towards the south. These differences within the selected areas are not considered further.

Of the 40 species dealt with in this paper, 37 (93 %) are known to occur in the Indonesian Archipelago (IA) and 36 (90 %) in the Philippine Islands plus northern Borneo (Ph) (fig. 674). *Ctenactis albitentaculata* has not been recorded for the Philippines, where it is expected to occur because it has been collected from the Talaud Islands (Indonesia) near Mindanao. The area of New Guinea and the Solomons (NS) approaches the maximal species richness with a total number of 34 (85 %). Around the distinct concentration of Fungiidae in the central Indo-Pacific (IA, Ph and NS) the species richness decreases gradually in both longitudinal and latitudinal directions. Southward, Western Australia (WA) and the Great Barrier Reef (GB) have lower species numbers, 26 (65 %) and 31 (78 %), respectively. North of the Philippines, Japan (Ja) with 24 (60 %) has a distinctly lower species diversity and from the West Carolines (WC), including the Palau Islands, only 23 species (58 %) are known. The lowest species richness is observed in peripheral areas like the Persian Gulf (PG) and Easter Island (Ea), each with a single species (3 %). Only two species (5 %) have been recorded for the East Pacific (Galapagos, Mexico and Panama).

A concentration of species in the area formed by the Philippines, the Malay Archipelago and New Guinea is common among groups of tropical shallow-water animals (Ekman, 1953; Briggs, 1974; 1987). Ekman (1953: 16) called this center of high diversity the "Indo-Malayan region", whereas Briggs (1987: fig. 17) distinguished it as a "central triangle" within an "Indo-Polynesian province". This Indo-Polynesian biogeographic province cannot be easily distinguished for the Fungiidae. The adjoining western Indian Ocean, i.e. the Red Sea (RS) and eastern Africa (EA) with Madagascar (Ma), also shows a rather high species diversity of mushroom corals. Towards the eastern Pacific, at for instance the Tuamotu Archipelago (TA), the Line Islands (Li) and the Hawaiian Islands (Ha), the species diversity decreases more abruptly, which accords approximately with the eastern boundary of the Indo-Polynesian province sensu Briggs (1987).

Very few geographic diversity patterns have been published for species of tropical Indo-Pacific shallow water organisms that can be compared with the data on the Fungiidae. However, patterns for the gastropod genus *Strombus* (Mollusca, Strombidae) and the fish family Siganidae enable a comparison and show striking similarities.

Strombus is a well-known gastropod genus with 38 species and subspecies in the tropical Indo-Pacific (Abbott, 1960). Its distribution is less pan-tropical (East Africa — Easter Island) than that of the Fungiidae (East Africa — Panama). The geographic diversity patterns of these taxa can easily be compared because the areas selected in the present study (fig. 674) are almost the same as those used by Abbott (1960: pl. 19). The diversity of *Strombus* is, like that of the Fungiidae, highest in the Indo-Malayan region (68 %) decreasing east- and westward. As in the Fungiidae, the decline of species richness is greatest towards the east. Some (sub)species of *Strombus* have restricted distributions, either continental or oceanic, and several do not include the centre of diversity (Abbott, 1960). Such a distinction in restricted continental and oceanic ranges is not applicable to the Fungiidae, which explains why the Fungiidae with their wide distributions show a higher species diversity in the Indo-Malayan region.

The distribution of the Siganidae (26 species) ranges from East Africa towards French Polynesia (Woodland, 1983: fig. 1). Its diversity pattern is similar to those of *Strombus* and the Fungiidae. Again there is a distinct diversity centre in the Indo-Malayan region where 50 % of the Indo-Pacific Siganidae have been recorded. The declines of species richness in the Siganidae, Fungiidae and *Strombus* from the central Indo-Pacific towards eastern Africa and Polynesia are very similar. Woodland (1983) distinguished two faunas with an overlap in Indonesia, i.e. one in the Indian Ocean from Indonesia to the Gulf of Oman and a second in the Pacific Ocean from Indonesia to French Polynesia. Such a distinction cannot be made for the Fungiidae. There are only a few Fungiidae with a predominantly Pacific distribution (e.g. *Zoopilus echinatus* [fig. 524], and *Polyphyllia novaehiberniae* [fig. 472]) and none occurs exclusively in the Indian Ocean.

The generic diversity contours ("isopleths") of zooxanthellate Scleractinia given by Rosen (1971b) and by Stehli & Wells (1971) for the Indo-Pacific were updated by Rosen (1984), Veron (1985; 1986b), and more specifically for the Indo-Malayan region by Best et al. (1989). As far as known, the area of the highest generic diversity (70-75 genera) is located at the Philippines and eastern Indonesia and might even reach as far as northern New Guinea (Best et al., 1989: fig. 2). The existence of a second generic centre of high diversity in the western Indian Ocean, as indicated by Rosen (1971b: fig. 3), Stehli &

Wells (1971: fig. 2) and Coudray & Montaggioni (1982), was not confirmed by Rosen (1984: fig. 11.1) and Veron (1985: fig. 1; 1986b: 630). Most of the genera originally supposed to be restricted to the western Indian Ocean have subsequently been discovered to be more widespread (Sheppard, 1987). The diversity patterns of the scleractinian genera and that of the fungiid species (fig. 674) are much alike. Approximately 90 % of the Indo-Pacific zooxanthellate scleractinian genera (see Best et al., 1989) and 93 % of the fungiid species occur in Indonesia and the Philippines. For eastern Africa and the Red Sea up to 65 % of the scleractinian genera have been recorded, and for western central America about 5 % (see Veron, 1986b). The values for the Fungiidae in these areas are 48 % and 5 %, respectively.

In addition to the comparison of species richness of areas (a quantitative approach), their similarities in fungiid species composition were investigated (a qualitative approach). This has rarely been done for any group of shallow-water organisms in the tropical Indo-Pacific. (For examples of analyses on scleractinian species compositions on a more regional scale, see Veron, 1986b; Sheppard, 1987; Veron & Marsh, 1988; Hoeksema & Moka, 1989). In the present analysis the areas (outlined in fig. 674) are the entities and the species their attributes. The data are binary since each species has been recorded either present or absent for an area. The species compositions of the areas are therefore compared with a UPGMA-cluster analysis of the mean differences in Q-mode group averaging (see Sneath & Sokal, 1973) with the help of BIOPAT (Hogeweg & Hesper, 1972). Within each cluster further subdivisions were performed as far as they are of biogeographic relevance and not, for the sake of consistency, according to the same dissimilarity limits used in neighbouring clusters. If, for example, a dissimilarity limit of 0.25 could be applied everywhere in the analysis, this would result in a few large clusters next to many small ones.

In the resulting cluster diagram (fig. 675) a first separation (at dissimilarity limit 0.50) is made between areas in the Central Indo-Pacific (A) and those either east or west of it (B).

Within the principal cluster A, a distinction is made between the Indo-Malayan region (cluster 1: Ph, IA and NS) and the adjoining areas (cluster 2: AS, GB, WA, WC and Ja; see fig. 676). Possibly a distinction has to be made between western and eastern Indonesia because west of the Makassar Strait (apart from N Borneo), i.e. on the Sunda shelf, fewer species have been recorded (e.g. *Zoopilus echinatus* is absent there). West of New Guinea there is no record of *Polyphyllia novaehiberniae*, which distinguishes this area from Indonesia and the Philippines. The Philippines, in contrast with the two other areas, has no record yet of *Ctenactis albitentaculata* spec. nov. Indonesia and

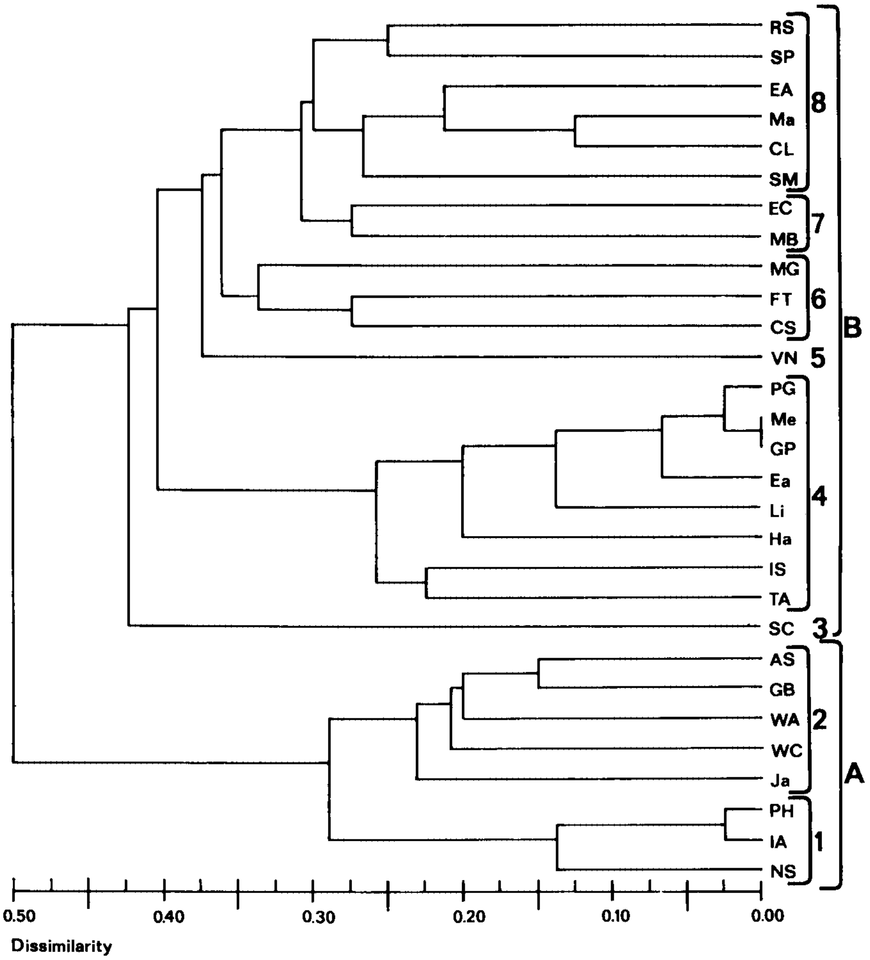


Fig. 675. Unweighted Pair-Group arithmetic Mean Average (UPGMA) dendrogram showing correlations between areas (fig. 674) in fungiid species composition.

the Philippines are the only two areas where *Halomitra clavator* spec. nov. has been found.

In cluster 2 the highest similarity is found between the Andaman Sea (AS) and the Great Barrier Reef (GB), whereas Western Australia (WA), the West Carolines (WC) and Japan (Ja) are slightly more dissimilar in species composition.

The separate position in the diagram of the South China Sea (SC), as cluster 3, is conspicuous. In cluster 4 eastern India with Sri Lanka (IS) and the Persian Gulf (PG) are grouped together with areas representing the eastern Pacific, namely Mexico (Me), Galapagos to the Gulf of Panama (GP), Easter Island (Ea), the Line Islands (Li), Hawaii (Ha) and the Tuamotu Archipelago (TA). In marine zoogeographical literature, the eastern Pacific is generally known as depauperate compared to the Indo-West Pacific (Briggs, 1987). The incorporation of the Persian Gulf in cluster 3 is mainly due to the record of *Fungia (Cycloseris) curvata* in this area. This species is one of the two species ocurring at western central America. The eastern coast of India (IS) probably has a poor species record caused by the fluvial discharge in the Gulf of Bengal and therefore shows a fungiid fauna which is relatively similar to that of the eastern Pacific.

New Caledonia and Vanuatu (VN), cluster 5 in the diagram, have a mushroom coral fauna which is dissimilar to those of the areas in clusters 6, 7 and 8. This is partly due to the endemic species *Cantharellus noumeae* at New Caledonia and to some species which have New Caledonia and Vanuatu as their (south)easternmost distribution boundary: *Heliofungia actiniformis*, *Ctenactis albitentaculata* and *Polyphyllia talpina*. Some areas more eastward (see fig. 676) form cluster 6 (MG, FT and CS), while further north an area forming cluster 7 (MB and EC) is located. Cluster 8 contains the areas of the eastern Indian Ocean (apart from the Persian Gulf) with the Samoan and Phoenix Islands (SP). The fungiid species compositions of these areas are all poor in relation to the central Indo-Pacific.

Future research should concentrate on areas where disjunctions in the recorded ranges of several Fungiidae have appeared. Such areas are located in the central Indian Ocean (SM, CL and IS) and the central Pacific (EC and SP). Special attention should be given to the species that usually live relatively deep, on the sandy bottoms below the reef slopes.

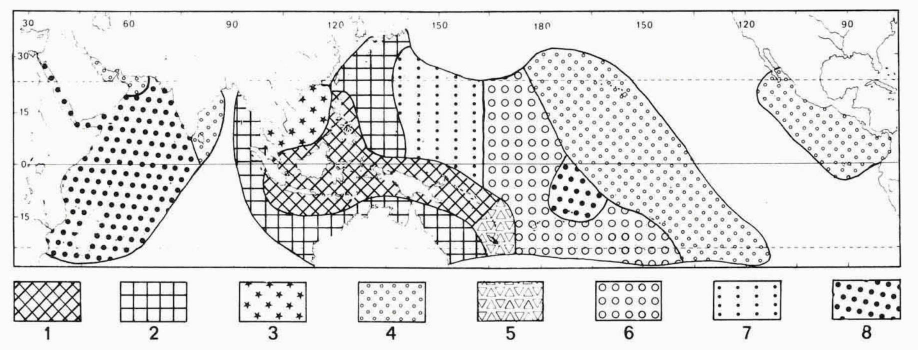


Fig. 676. The area clusters 1-8 distinguished in the cluster analysis (fig.675) plotted on a map. Cluster 1 comprises the centre of highest fungiid species diversity; the areas around it represent dissimilar species compositions in which a depauperation towards the periphery is recognized.

In conclusion, the change in fungiid species composition from the central Indo-Pacific towards the periphery of the tropical Indo-Pacific (fig. 676) is mainly a decrease in species richness (figs. 674). The endemism observed at the northern Red Sea, New Caledonia and the Indonesian-Philippine Islands plays a minor part in the dissimilarities observed. Because the fungiid fauna is concentrated in the central Indo-Pacific and becomes depauperate towards the eastern Pacific, as well as towards the western Indian Ocean, the tropical Indo-Pacific can be considered one large faunal province for these corals. An Indo-West Pacific "sub-province", as originally defined by Ekman (1953), cannot be distinguished with respect to the Fungiidae.

Stehli & Wells (1971) used a cluster analysis to look at similarities in generic assemblages of Scleractinia. The data they used were mainly obtained from records of restricted locations ("stations") reported in the literature, part of which was not up to date. Therefore their area cluster diagram cannot be interpreted very precisely (Stehli & Wells, 1971: fig. 7). Three main area clusters were distinguished in the Indo-Pacific, namely (1) a cluster representing the eastern Pacific, (2) a cluster comprising the south-west Pacific, the southern Indian Ocean and the Persian Gulf, and (3) another one containing the remainder of the Indo-Pacific. For the eastern Pacific the area analysis of the generic assemblages agrees particularly well with that of the Fungiidae. In contrast, a cluster formed by the Persian Gulf and the southern Indo-West Pacific cannot be distinguished for the Fungiidae.

Because zooxanthellate corals can be regarded as "photosynthetic animals" or "living greenhouses" (Rosen, 1988b), a comparison between fungiid distributions with that of marine algal floras can be made. In a world-wide phytogeographical study, the distributions of rhodophytan genera along the continents of the Indo-Pacific have been noted, with exception of western Australia (Van den Hoek, 1984; Joosten & Van den Hoek, 1986). Within the Indo-Pacific the rhodophytan flora of the Indo-West Pacific is most similar to that of Japan and the red algal flora of the tropical East Pacific mostly resembles that of the temperate warm SE Pacific. These patterns are also shown by the Fungiidae: the mushroom coral fauna of southern Japan has many elements in common with that of the Indo-West Pacific and the fungiid fauna of the tropical east Pacific is identical to that of the Galapagos islands.

Following a paper by Valentine (1971) the relation between allopatric speciation of shallow-water organisms and lithospheric plate tectonics has received attention with regard to groups of gastropods (Foin, 1976; Kay, 1980), fishes (Springer, 1982) and corals (Coudray & Montaggioni, 1982). In biogeography plate tectonics is considered particularly relevant in relation to the forming of dispersal bridges (island arcs associated with subduction zones

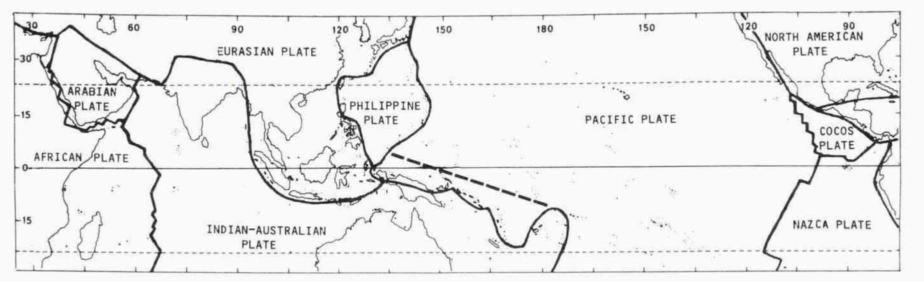


Fig. 677. The lithospheric plates on which Fungiidae occur. On the Pacific Plate the Andesite Line is indicated as a broken line (see Springer, 1982). The fungiid species compositions of the plates are given in table 6.

and volcanic islands chains) and dispersal barriers (increasing distance by sea floor spreading from oceanic ridges). With reference to the present study, major zones of sea floor spreading are located in the central Indian Ocean and in the eastern Pacific (East Pacific Barrier). The Sunda Islands of Indonesia and the Solomons exemplify island arcs, whereas the Hawaiian Islands and the Line Islands are midplate volcanic chains (see Valentine, 1971: fig. 1). Emphasis in relation to plate tectonics is generally put on Pacific Plate endemism, with the distinction of the Pacific Basin as a major biogeographic region (Springer, 1982).

When the ranges of the fungiid species are superimposed on the major lithosperic plates (fig. 677), it becomes obvious that none of the species is distributed solely on the Pacific Plate (table 6). The Andesite Line (fig. 677), actually demarcating a difference in petrologic composition, is suggested to be of biogeographic importance by running parallel with the easternmost limits of several Indo-Pacific species (Springer, 1982). On the Pacific Plate, slightly more fungiids (34 species) have been recorded at the continental side of this line (see table 6) than at the oceanic side (31 species), which suggests that the occurrence of some species in the Pacific Basin is related to the proximity of land masses and not to the presence of isolated groups of islands.

Historical and ecological biogeography. — The main biogeographic problems with respect to the Fungiidae are: (1) how can the Indo-Malayan centre of diversity be explained and (2) why are the ranges of most species large. These questions are relevant for the biogeography of several other taxa of marine shallow-water organisms as well (Kohn, 1983). For the Fungiidae in particular the question arises (3) why are there relatively few endemic species in relation to many other taxa (Briggs, 1974). Because too little is known about which speciation process occurred within the Fungiidae, the cluster analysis used to

Table 6. Fungiidae (sp. in table 4) recorded on the lithospheric plates of the Indo Pacific (see fig. 677). The Pacific Plate is subdivided into two areas, one at the continental side (C) of the Andesite Line and one at the oceanic side (O).

Sp.	Afric. Plate	Arab. Plate	Ind. Austr. Plate	Euras. Plate	Philipp. Plate	Pacific Plate		N.Am. Plate	Cocos Plate	Nazca Plate
						C	O			
01	+		+	+	+	+	+			
02	+		+	+	+	+	+	+	+	+
03	+	+	+	+	+	+	+			
04	+	+		+		+		+	+	+
05	+		+	+	+	+				
06	+	+	+	+	+	+	+			
07			+	+		+				
08	+	+	+	+	+	+	+			
09	+	+	+	+	+	+	+			
10	+		+	+	+	+	+			
11				+	+	+				
12	+		+	+			+			
13	+	+	+	+	+	+	+			
14	+	+	+	+	+	+	+			
15			+	+		+	+			
16	+	+	+	+	+	+	+			
17	+	+	+	+	+	+	+			
18	+	+	+	+	+	+	+			
19	+	+	+	+	+	+	+			
20	+	+	+	+	+	+	+			
21	+	+	+	+	+	+	+			
22	+		+	+	+	+	+			
23	+	+	+	+	+	+	+			
24			+	+	+	+				
25			+	+	+	+	+			
26	+	+	+	+	+	+	+			
27	+	+	+	+	+	+	+			
28	+	+	+	+	+	+	+			
29			+			+				
30	+		+	+	+	+	+			
31			+	+	+	+	+			
32			+	+	+	+	+			
33			+	+		+	+			
34	+		+	+	+	+	+			
35				+						
36	+									
37			+							
38			+	+			+			
39			+	+		+	+			
40	+		+	+	+		+			
Total	27	17	36	37	29	34	31	2	2	3

compare the species compositions of areas cannot be used to solve the three main biogeographic problems (see McCoy & Heck, 1987).

Sympatric speciation (see e.g. Pielou, 1979; Myers & Giller, 1988) might have occurred within the Fungiidae, but it is hard to relate this to a particular model, since these animals may simply release their sperm into the water. Nevertheless, there may exist some differentiation amongst the fungiids regarding the timing of sperm release and ovogenesis, but virtually nothing has been published about this (review by Fadlallah, 1983).

According to the principles of evolutionary biogeography (sensu Darlington, 1957; 1959; Briggs, 1973) a centre of diversity is an area with much ecosystem stability, where the newly derived, most competitive species or higher taxa are expected to occur by having displaced the older ones towards peripheral areas. With respect to the Fungiidae, there is no evidence supporting the theory (Briggs, 1966; 1974; 1981; 1987) that the Indo-Malayan area is such a centre of origin. The assumption that the oldest fossils are expected to be located close to the centre of origin of the family (Darlington, 1957) is also not applicable to the Fungiidae, of which the oldest fossil record comes from India (table 2). However, it is unknown to what extent the known stratigraphic and paleogeographic distribution of each species represents its real occurrence in time. Rosen (1981) argued that coral taxa could have originated in other areas than the centre of diversity, and that such areas could have subsequently been destroyed or transformed by tectonic events.

The isolation of oceanic islands may have caused allopatric speciation among the Fungiidae, whereas the presence of long coastlines may have resulted in parapatric speciation. Evidence for speciation areas can hardly be deducted from the present-day wide distributions (fig. 678). The ranges of most species show much mutual overlap and are therefore irrelevant to elucidate interrelationships of areas of endemism (Nelson & Platnick, 1978). Some endemism is shown by *Cantharellus* with *C. doederleini* as an endemic for the northern Red Sea and *C. noumeae* for New Caledonia (also recorded from the Miocene of Indonesia). However, the ranges of these sister-species are too far apart to trace where their evolution has taken place. In contrast, sister-species showing much range overlap are e.g. *F. (Cycloseris) costulata* with *F. (C.) tenuis*, *F. (Verrillofungia) concinna* with *F. (V.) repanda*, *Ctenactis echinata* with *C. crassa* and *Polyphyllia novaehiberniae* with *P. talpina* (fig. 678). Because of these large overlaps allopatric patterns cannot be recognized. If allopatric speciation has occurred, subsequent dispersal must have wiped out the traces of where this took place. Hence, it is difficult to explain the present-day distributional patterns of the Fungiidae with the help of methods used in cladistic biogeography (see Nelson & Platnick, 1981; Humphries & Parenti, 1986; Humphries et al., 1988).

Among the Fungiidae occurring in the centre of diversity some species with many apomorph character states (fig. 673) have a restricted range. For example, *Heliofungia actiniformis* (14 apomorphies) and *Lithophyllon undulatum* (17 apomorphies) are rather stenotopic and the species showing most apomorphies (25), *Halomitra clavator*, is endemic for Indonesia and the Philippines.

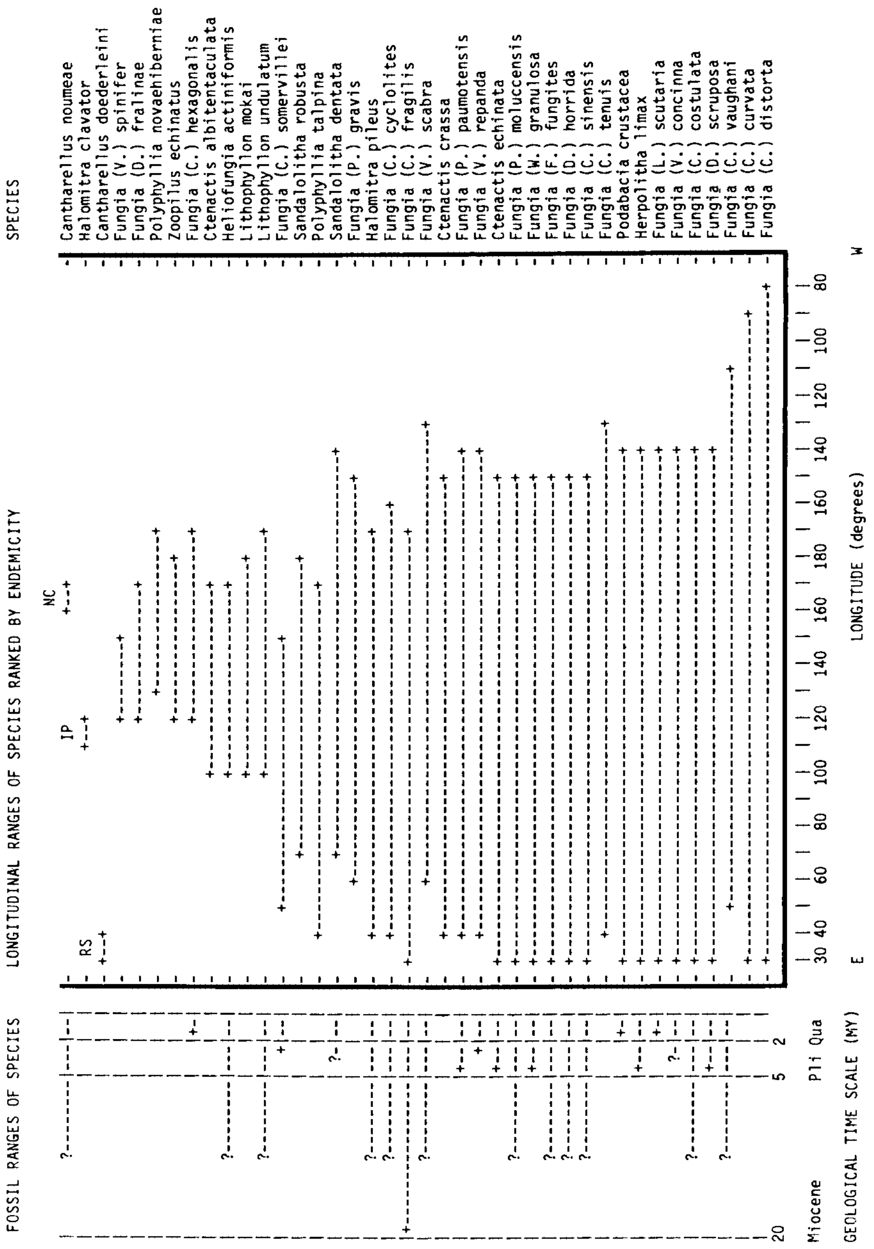


Fig. 678. The stratigraphic and longitudinal ranges of Fungiidae as recorded during the present study. The species are ranked according to endemicity, i.e. the stenotopic species above and the eurytopic ones below (RS = Red Sea; IP = Indonesia + Philippines; NC = New Caledonia). In case it is unknown whether the fossil record of a species can be traced to the "early", "middle" or "late" part of an epoch, this is indicated with a "?" in the middle of the earliest epoch concerned.

This implies that phylogenetically derived fungiids do not necessarily occur at the periphery of the family's range as predicted in phylogenetic biogeography (sensu Brundin, 1972; 1988). On the other hand, there are several stenotopic species at the centre of the family's range with relatively few apomorph character states, such as *F. (C.) hexagonalis* (9 apomorphies). *Fungia (C.) distorta* (6 apomorphies) and *F. (C.) curvata* (9 apomorphies) with many symplesiomorph character states are the only two fungiids showing a pantropical distribution. In other words, within the Fungiidae there is no distinct relation between phylogeny and biogeographic range at the species level.

At superspecific levels, it appears that symplesiomorphies may be more widespread than synapomorphies. For example species-groups showing a single mouth have a larger range than species-groups with more mouths (character state transformations 30-32). Likewise, species with small tentacles have a wider distribution than those with long tentacles (character state transformation 45). This suggests that synapomorphies are evolutionary novelties that have got less time to disperse than the symplesiomorphies.

Among the Fungiidae, *Fungia* shows more plesiomorph character states than does any other genus (fig. 673), while it has the oldest traceable record (table 2) and the largest recent range (fig. 678). This agrees with the observations of Wells (1969) and Stehli & Wells (1971) that the most widely distributed reef coral genera of the Indo-Pacific have the longest paleontological record. The long fossil record known for several Fungiidae, the large ranges of many species, the distributional overlap shown by sister-species, and the small number of endemic species imply that it may be too difficult to interpret past biogeographic processes with present-day distributions. The present-day distributional patterns of the Scleractinia and some other taxa may be considered as the modification of a previously widespread, pan-Tethyan biota by tectonic events, speciation and extinction (cf. McCoy & Heck, 1976; 1983; Heck & McCoy, 1978).

The large ranges shown by most Fungiidae are most probably the result of long-distance dispersal over a long time. The long-distance dispersal of sedentary animals such as corals is expected to occur mainly during the planktonic larval phase (Dana, 1975; Richmond, 1987). Although rafting by adult coral colonies may occur (Jokiel, 1984; 1989; Newman, 1986), this kind of dispersion is not considered relevant for free-living mushroom corals after they have reached the anthocyathus-stage (fig. 42). Some species of corals are capable of floating by the intake of air during temporary drought (Kornicker & Squires, 1962), which is theoretically likely to occur among free-living corals, but there are no actual records.

The maximal potential distance that larvae can bridge is affected by the length of the planktonic larval phase and by the rate and the direction of the currents that transport them (Scheltema, 1986b). In the tropical belt of the Indo-Pacific, the transoceanic warm surface currents run mainly eastward or westward, whereas along the coast of the continents smaller currents run either northward or southward (Dietrich & Ulrich, 1968; Garrett, 1981; 1983). The oceanic circulation system is more variable than this, due to the reversing monsoon winds (Wyrtki, 1961) and mesoscale counter currents or eddies (Owen, 1981; Dickson, 1983).

Although there is as yet no direct evidence, transportation of larvae by currents may still be responsible for maintaining the wide ranges of many Fungiidae. Species that occur in isolated areas, such as *Fungia (Cycloseris) distorta* and *F. (C.) curvata*, would otherwise have undergone diversification, like other near-shore animals with a low dispersability (Vermeij, 1978). The distances over which larvae of many marine benthic invertebrates are transported (Scheltema, 1986a; 1986b; 1988) strongly suggest that there is a gene flow between the islands of the Indo-Pacific which is frequent enough to account for the persistence of the widespread species and the absence of local endemism. The predominant occurrence of reef-dwelling invertebrates with planktonic larvae at midoceanic volcanic islands that have never been connected with major land masses, is consistent with the interpretation that these islands were colonized by dispersing propagules (Scheltema & Williams, 1983; Perron & Kohn, 1985).

There is a decrease in fungiid species richness (figs. 674, 678) from the centre of diversity in both longitudinal directions. For the widespread Fungiidae that are not pantropical, stretches of deep ocean may constitute barriers to transoceanic dispersal. Such barriers act as a filter by allowing only species with great larval longevity to pass (Scheltema, 1988). Eleven species have their eastern distribution limit at the Tuamotu Archipelago, while a single one, *Fungia (Cycloseris) vaughani*, does not occur east of Easter Island. These species might have been unable to cross the East Pacific Barrier (the East Pacific Filter, see Newell, 1971: fig. 11), which is slowly increasing in width as the sea floor spreads from the East Pacific Rise (Springer, 1982: fig. 4; Garrett, 1983). In the Indian Ocean and between many island groups in the west Pacific there is usually a less distinct decrease in fungiid species richness (fig. 674). Here islands may facilitate long-distance dispersal by functioning as "stepping stones", or "staging posts" (Rosen, 1984), which, in the form of island arcs and volcanic island chains, may constitute "corridors" (Valentine, 1973).

According to the paleontologic record (tables 1-2) most fungiid taxa may have developed after the separation of the Indo-Pacific from the previously continuous Tethyan-Indopacific realm in the Early Miocene. During the Early

Miocene there was a temporal closure of the Indonesian seaway after which the sea level started to rise (Grigg, 1988: fig. 2). In the Mid Miocene some sea level fluctuations occurred with a subsequent drop in sea level that continued until a new series of sea level fluctuations started at the end of the Pliocene. Since the Miocene there has been much tectonic and climatic instability, which must have altered the position of dispersal barriers (Rosen, 1981). The currents transporting planktonic larvae must have been influenced by the various changes in sea level (Grigg, 1988: fig. 5), which makes it very difficult to deduce past dispersal routes.

There are no published examples of biotic factors limiting the ranges of fungiid species. With respect to predation affecting species ranges, some corallivorous sea stars seem to reject mushroom corals (Ormond et al, 1976; Glynn & Krupp, 1986), which favours the competitive capacity of Fungiidae. In competition for space among other coral species, free-living mushroom corals are known to rank high in the aggression hierarchy, while they do not seem to be disturbed by close proximity to each other (Sheppard, 1979).

The present-day distributions of the Fungiidae seem to be limited mainly by abiotic factors, such as temperature, salinity and sediment load of the sea water. There is a clear latitudinal diversity-temperature gradient (fig. 674) indicating that low temperatures limit the distribution ranges, as for all zooxanthellate Scleractinia (Rosen, 1981; 1984; 1988b). Many tropical marine species are unable to live in waters where the average temperature for the coldest month drops below 20 °C (Briggs, 1974). In areas outside the circumtropical reef coral belt the winter temperature of the surface water may drop too far below the minimum tolerance limit for most corals to survive. Some areas in relatively high latitudes may be rich in Fungiidae in relation to other areas of the same latitude (fig. 674) because of the occurrence of either warm surface currents, as in southern Japan (Garrett, 1983), or a combination of e.g. climate, high evaporation rate and restricted circulation, like in the Red Sea (Ross, 1983). In the Persian Gulf, where only one species is recorded, the minimum winter temperature is probably too low for additional species to occur (Basson et al., 1977). At Easter Island, with a single species (fig. 674), the number of species might have been higher but for the cooling effect on the surface water of the upwelling along the west coast of South America (Dietrich & Ulrich, 1968).

Some areas with dissimilar (poorer) species compositions relative to the adjacent areas (such as eastern India with Sri Lanka and the South China Sea; figs. 676, 674: IS, SC), are considerably influenced by river outflow. Anomalously low salinities (Dietrich & Ulrich, 1968: 32) and high sediment loads (Milliman & Meade, 1983) may be too extreme here for most species of zooxanthellate corals to survive (Schuhmacher, 1976; Longhurst & Pauly, 1987). For Fungiidae showing a mainly Pacific range the large river outflow in SE Asia may determine the easternmost distribution boundary.

To explain the Indo-Malayan centre of diversity several general models have been developed (reviews by Rosen, 1988a; 1988b) that are applicable to the Fungiidae. In these models much attention is given to sea level fluctuations (an important element in historical biogeography) and the the quantitative area-species relationship (an aspect relevant to ecological biogeography; see e.g. Connor & McCoy, 1979; Williamson, 1988). According to some models new species develop during regressions in a restricted number of suitable habitats along the Australasian continental shelves (Potts, 1983; 1984; 1985) or by the limitation of species ranges after the appearance of new barriers (Wise & Schopf, 1981; McManus, 1985). In another model species evolve during transgressions at isolated oceanic islands (Rosen, 1984). In Potts' model the Plio-Pleistocene regressions occurred too frequently and lasted too shortly for speciation, in contrast to the longer lasting Miocene sea level fluctuations. In Rosen's (1984) "vicariance and refuge" model a repetitive addition of oceanically evolved species would have caused an accumulation of species and faunal intermixing in the heterogeneous shelf environments during periods of low sea level. In the less heterogeneous habitats of the oceanic islands subsequent sea level fluctuations might cause the extinction of the more vulnerable newly evolved forms.

A species-area effect may be observed on the Australasian continental shelves, which serve as a refuge by including 53 % of the total area of Indo-Pacific reefs with the highest environmental heterogeneity (Potts, 1984). The occurrence of large continental islands give it a two-dimensional appearance instead of a linear one, which is expected to give planktonic larvae a much higher chance of reaching a suitable habitat than in oceanic areas (Valentine, 1973; Valentine & Jablonski, 1983).

In the literature dealing with the biogeography of zooxanthellate corals in the Indo-Malayan region, habitats not occurring on continental shelves received little attention. During a two-year research programme up to 35 (88 %) species of mushroom corals were found co-occuring on small reefs in the shelf area of SW Sulawesi (Hoeksema, unpubl.). In addition to shelf areas the Indonesian seas contain other kinds of areas rich in Fungiidae and thus show more habitat heterogeneity than expected only on the criterion of available shelf area. Many species were encountered during short surveys in areas that are not shelf-based, such as Sumbawa with 32 (80 %) fungiid species and Komodo with 33 (83 %). Habitats occurring on volcanic slopes and in silty bays, either with or without terrigenous run-off and river outflow, may add to the habitat heterogeneity, which is greater than that of the more oceanic areas, such as Taka Bone Rate with only 25 (63 %) fungiid species (Hoeksema & Moka, 1989). Free-living Fungiidae are very well able to survive in non-reefal oceanic habitats, such as unconsolidated rubble slopes (Potts, 1985), because the mobility of these species may promote a survival mechanism (Hoeksema, 1989). The phenotypic plasticity shown by many species also suggests that most Fungiidae are very well able to live in oceanic as well as in continental habitats (Hoeksema & Moka, 1989).

There is no indication that differentiation of species occurred because of past Indonesian interoceanic dispersal barriers. Separate populations in both the Indian and the Pacific ocean may have remained too large to cause a clear differentiation. Furthermore, corals have a great longevity with much generation overlap which may inhibit speciation (Potts, 1984). Mushroom corals showing asexual reproduction by fragmentation (character state transformation 40) in fact may live for a long time (Hoeksema, 1989). It is interesting to note that in addition to this autapomorphy, these species show remarkably few other apomorph character states (fig. 673). Therefore a short separation of the oceans may only have caused speciation in species with shorter generation overlaps, such as some fishes (Allen, 1975; Woodland, 1983) and crabs (Crane, 1975).

McManus' (1985) model of isolated sea basins at the periphery of the oceans during regressions is plausible for the species which are supposed to have evolved since the Late Pliocene, despite the fact that there are no extant mushroom coral species known to be endemic for such areas. Newly evolved species must have had enough time to expand their range during subsequent transgressions. The isolated basins resulting from Plio-Pleistocene regressions may be compared with the recent Red Sea, where *Cantharellus doederleini* is endemic for the Gulf of Aqaba. Potts' (1985) drew attention to the scarcity of Pacific endemism among corals compared to some groups of gastropods (e.g. *Conus*) and fishes, some of which are specialized predators (Kohn, 1971). Possibly the carnivorous fungiids, because they have a less specialized diet (Yonge, 1930; Abe, 1938), with perhaps *Heliofungia actiniformis* as an exception (Sisson, 1973), did not diversify during isolation as quickly as the other groups.

Isolated environments in which gene pools are most likely to change are those where terrigenous influences increase the heterogeneity of habitats by causing extreme local conditions (e.g. anomalous salinities and temperatures, eutrophication and siltation). The temporarily isolated sea basins in McManus' (1985) model, situated near the Australasian continents, were deep and large but nevertheless became more deprived of oceanic influences, which might have accelerated speciation according to the "punctuated equilibria model" (Eldredge & Gould, 1972; Gould & Eldredge, 1977; Cracraft & Eldredge, 1979; Stanley, 1979; Schopf, 1981) and increased the number of species in the Indo-Malayan area.

In Rosen's (1984) model speciation depends upon the vagility of the oceanically evolved species. During sea level transgressions or as a result of tectonic events (Grigg, 1982), shallow oceanic islands would submerge, thus causing extinction of the coral species. Rosen's (1984) model requires the assumption that the wide present-day ranges of Fungiidae cannot be explained without recolonization of the oceanic islands from continental refugia. An extreme specialization towards oceanic conditions would have been a disadvantage, and perhaps therefore there are no extant fungiid species endemic to oceanic islands. An interrupted occurrence of species at oceanic islands by extinction and recolonization is not unlikely, because there are indications from the scleractinian fossil record that this may have happened at the Hawaiian and Line Islands (Grigg, 1981; 1988; Wells, 1982; Maragos & Jokiel, 1986).

In conclusion, allopatric speciation of the Fungiidae may have occurred along the continents during regressions (Potts, 1983; 1984; 1985; McManus, 1985) and around oceanic islands during transgressions (Rosen, 1984). Refugia have probably been important to maintain a high species richness in the Indo-Pacific convergence, whereas dispersal must be accepted to explain the actual wide ranges. In general the present-day biogeographical patterns of the Fungiidae with many wide ranges can be explained better by an addition of disperal to vicariance and refugiality, than by Rosen's (1984) "vicariance and refuge" model alone.

Potts (1983) and Rosen (1984) expressed the need for research on species level distributions of Scleractinia to obtain more insight in the biogeographic history of shallow-water corals. During the present study the past biogeographic processes that have lead to the actual distributions of the Fungiidae could not be satisfactorily explained because most crucial events occurred too long ago. Moreover, the Pleistocene sea level fluctuations may have wiped out much of the original biogeographic pattern in this group which partly originated millions of years earlier. Additional data on a much more local scale may lead to a better insight in the ecological aspects of the distributional patterns (Best et al., 1989: fig. 1).

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TAXONOMIC INDEX

Names in *italic* letters are junior synonyms, junior homonyms, nomina nudae, misidentifications, names proposed for suppression, and those with an incorrect or invalid spelling.

Page numbers refer to taxa mentioned in the systemic account; those in *italics* refer to nomina nudae and to citations in the synonymy.