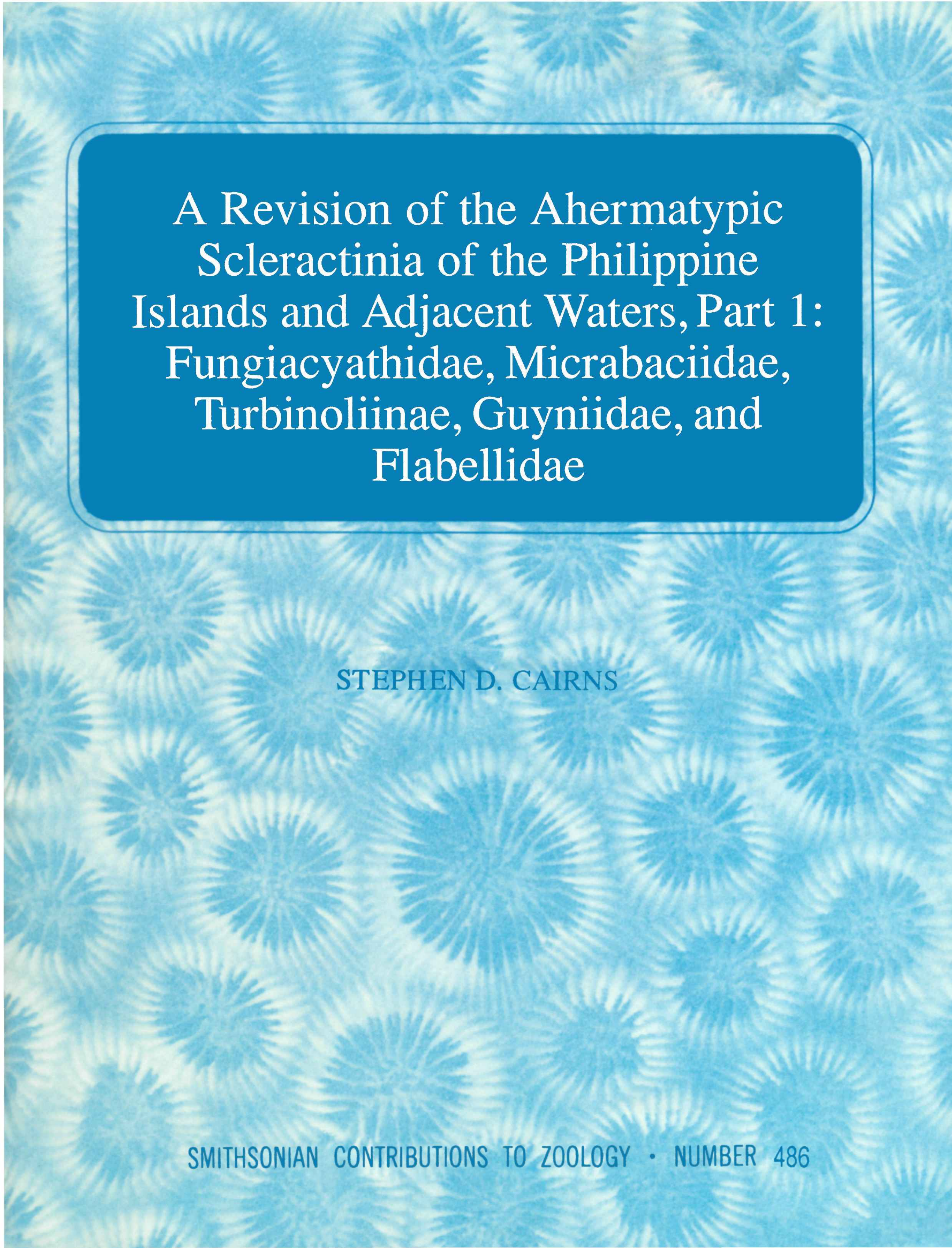

A Revision of the Ahermatypic Scleractinia of the Philippine Islands and Adjacent Waters, Part 1: Fungiacyathidae, Micrabaciidae, Turbinoliinae, Guyniidae, and Flabellidae

STEPHEN D. CAIRNS

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A Revision of the Ahermatypic Scleractinia of the Philippine Islands and Adjacent Waters, Part 1: Fungiacyathidae, Micrabaciidae, Turbinoliinae, Guyniidae, and Flabellidae

Stephen D. Cairns

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ABSTRACT

Cairns, Stephen D. A Revision of the Ahermatypic Scleractinia of the Philippine Islands and Adjacent Waters, Part 1: Fungiacyathidae, Micrabaciidae, Turbinoliinae, Guyniidae, and Flabellidae. *Smithsonian Contributions to Zoology*, number 486, 136 pages, 3 figures, 42 plates, 1989.—Fifty-three species of ahermatypic Scleractinia—about half of the Philippine ahermatypic fauna—belonging to four families and one subfamily are described and illustrated. Five additional species found in adjacent waters just north of the Philippines are also included in the faunistic revision. In order to better evaluate the genus *Leptopenus*, *L. antarcticus*, from Antarctica, is also included in this revision as a new species, making a total of 59 species revised. Concurrent with the species revision, higher-level taxa were reanalyzed and revised, resulting in the description of four new genera: *Endocyathopora*, *Thrypticotrochus*, *Truncatoguynia*, and *Truncatoflabellum* and 17 new species; the formation of 13 new species combinations; and the establishment of two new subgeneric ranks: *Fungiacyathus (Bathyactis)* and *Flabellum (Ulocyathus)*. To help stabilize the nomenclature of taxonomically confusing species, neotypes were designated for two species: *Flabellum (= Truncatoflabellum) cumingii* and *Flabellum (= Truncatoflabellum) candeanum;* and lectotypes were chosen for four other species: *Bathyactis (= Fungiacyathus) sibogae*, *Flabellum pavoninum*, *Flabellum distinctum*, and *Flabellum patens*. Approximately 4400 specimens were examined from 178 stations throughout the Philippines, as well as most of the previously reported specimens from this area. A historical resume is given of previous literature on ahermatypic Scleractinia in the Philippine Islands. Character tables or keys are provided for the genera of Micrabaciidae, Turbinoliinae, Guyniidae, and Flabellidae, and character tables are provided for the Philippine species of *Fungiacyathus*, *Stephanophyllia*, *Flabellum (Flabellum)*, and *Truncatoflabellum*.

The Philippine Islands and Indonesia, especially the Sulu Sea, are considered to be at or near the center of ahermatypic species diversity and thus represent the most diverse ahermatypic fauna in the world. East and west of the Philippines the number of species held in common falls rapidly, but relatively high percentages of shared species are found to the north: 30%–32% for the South China Sea off Hong Kong, and 36%–38% for off Japan. The highest number of shared species, however, is with Indonesia (25–27 species, 47%–51%), with which the Philippines probably forms a zoogeographic unit. Of the 53 species reported from the Philippines, 27 are new records for this island group.

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Epigraph

The southern end of the Sulu Sea seems to be one of the richest places in the world for deep-sea corals.—Alcock (1902a:3)

The deep-water coral fauna of the East Indies, like that of the reef corals, is the richest in the world in numbers and species . . . .—Vaughan and Wells (1943:88)

A Revision of the Ahermatypic Scleractinia of the Philippine Islands and Adjacent Waters, Part 1: Fungiacyathidae, Micrabaciidae, Turbinoliinae, Guyniidae, and Flabellidae

Stephen D. Cairns

Introduction

As the quotations in the Epigraph imply, the Philippines and adjacent waters lie at the center of scleractinian species diversity for both hermatypic (zooxanthellate) and ahermatypic (azooxanthellate) species. Although the ratio of ahermatypic to hermatypic species is not as high as 2:1, as in the western Atlantic (Cairns, 1979), it is as high as 1:2, i.e., about 110 ahermatypic species to about 220 hermatypic species (Vaughan and Wells, 1943) for the Philippine Islands.

Approximately 150 papers have been written on the systematics of fossil and Recent Indo-West Pacific ahermatypes (see Literature Cited). Most of these papers are short descriptive accounts of species, but several are longer expedition reports or reviews of particular taxa. Notwithstanding the review by Faustino (1927), no author has attempted to synthesize this diverse literature and examine the specimens on which it is based in the context of a faunistic or taxonomic revision. It is the purpose of this paper to revise the ahermatypic species of the families Fungiacyathidae, Micrabaciidae, Guyniidae, and Flabellidae, and the subfamily Turbinoliinae known from the Philippine Islands and adjacent waters, including a comparison to previously described species and specimens from the Indo-West Pacific region. In so doing, the higher taxa containing these species (i.e., genera, subfamilies, families) have also been revised. It is hoped that the species-level revision will serve as a foundation for further revisionary studies on Indo-West Pacific deep-water coral species, particularly the Indonesian fauna.

The four families and one subfamily that constitute part 1 of this revision were chosen arbitrarily and therefore do not form a monophyletic unit but do represent about half of the ahermatypic species known from the Philippine Islands. The remaining families containing ahermatypic species represented in the Philippines are Pocilloporidae (*Madracis*), Rhizangiidae (*Culicia*), Oculinidae (*Cyathelia, Madrepora*), Anthemiphylliidae (*Anthemiphyllia*), Caryophylliidae (*Aulocycthus, Caryophyllia, Conotrochus, Cyathoceras, Deltocyathus, Lochmaeotrochus, Heterocyathus, Paracyathus, Stephanocyathus, Trochocyathus, Asterosmilia, Goniocorella, Desmophyllum*), and Dendrophylliidae (*Balanophyllia, Dendrophyllia, Enallopsammia, Leptopsammia, Heteropsammia, Endopachys*), which will form the basis for part 2.

ABBREVIATIONS.—The following abbreviations are used in the text.

Museums and Collections

AHF	Allan Hancock Foundation, University of Southern California, Los Angeles
AM	Australian Museum, Sydney
BM	British Museum (Natural History), London
MNHNP	Muséum National d'Histoire Naturelle, Paris
NMW	Naturhistorisches Museum Wien, Vienna
RGM	National Museum of Geology and Mineralogy, Leiden
TIUS	Institute of Geology and Paleontology, Tôhoku Imperial University, Sendai, Japan
USNM	collections of the former United States National Museum, now in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.
ZMA	Zöologisch Museum, Amsterdam
ZMB	Zoologisches Museum, Berlin
ZMC	Zoologisk Museum, Copenhagen

Vessels, Expeditions, and Collecting Institutions

ALB	U.S. Fish Commission Steamer *Albatross*

Stephen D. Cairns, Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

JM	John Murray Expedition (1933-1934), H.E.M.S. *Mabahiss*
MUSORSTOM	Muséum National d'Histoire Naturelle Office de la Recherche Scientifique et Technique d'Outre-Mer
NMNH	National Museum of Natural History, Smithsonian Institution, Washington, D.C.
NZGS	New Zealand Geological Survey
NZOI	New Zealand Oceanographic Institute
SME	Station Marine d'Endoume, Marseille
USGS	United States Geological Survey

Other Terms

CRE	Crest Height: linear measure of maximum height attained by crest on lateral edges.
EAN	Edge Angle: angle formed by intersection of two lateral corallum edges (exclusive of pedicel and crests).
FAN	Face Angle: angle formed by intersection of two corallum faces.
GCD	Greater Calicular Diameter.
GCD:H	Ratio of greater calicular diameter to height of corallum.
GCD:LCD	Ratio of greater calicular diameter to lesser calicular diameter.
LCD	Lesser Calicular Diameter.
LEL	Lateral Edge Length: linear measure taken from junction of lateral edge of calice to point of greatest angular inflection associated with pedicel; average of two edges.
LEL:H	Ratio of lateral edge length to height of corallum.
SEM	Scanning elctron microscopy.
SSI	Septal Sinuosity Index: ratio of amplitude of lower inner edges of a major septum to thickness of that septum (see Cairns, in press b).
S_x, C_x, P_x	Septa, costae, or pali (respectively) of cycle designated by numerical subscript.

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I would like to thank the following people who have generously loaned me specimens used in this study: H. Zibrowius (SME), P.F.S. Cornelius and B.R. Rosen (BM), R.W.M. van Soest (ZMA), M. Borel-Best (specimens from RGM), D. Doumenc (MNHNP), K. Mori (TIUS), D.H.H. Kühlmann (ZMB), E. Kritscher (NMW), K.W. Petersen (ZMC), S. Parker (South Australian Museum, Adelaide), R. Springthorpe (AM), and G. Bakus (AHF).

The scanning electron micrographs were taken in the SEM Laboratory, NMNH. Molly Ryan, NMNH illustrator, executed the three line drawings depicting micrabaciid costal and septal insertion patterns.

Historical Resume

The following historical resume pertains only to species previously reported from the Philippine Islands that belong to the families and subfamily covered in this revision; however, because most accounts of deep-water corals are of a general nature, most of the references to Philippine deep-water corals are included in the following discussion.

The earliest reports of ahermatypic Scleractinia from the Philippines were those of Milne Edwards and Haime (1848, 1857), who reported nine new species of flabellids having type localities of the Philippines: *Flabellum aculeatum, F. debile (= F. aculeatum), F. cumingii, F. elongatum* (see discussion of *Truncatoflabellum*), *F. crassum, F. stokesii, F. owenii (= T. stokesi), Placotrochus laevis,* and *Blastotrochus nutrix*. Their species of *Flabellum* have all been transferred to *Truncatoflabellum* herein, and three species have been synonymized. Regrettably, Milne Edwards and Haime did not give specific localities or depths of capture for their specimens. Their type specimens were deposited at the MNHNP and BM; however, some appear to be lost.

Holdsworth (1862) described *Flabellum campanulatum* from the Philippines, again without specific depth or geographic data. The types are unavailable for study (stated by Gardiner (1929:304) to be lost, and confirmed not to be at the BM in 1988 (S. Moore, pers. comm.)). Holdsworth's illustrations do not allow discrimination of *F. campanulatum* from any of several other species of *Truncatoflabellum* that have their anthocyathus stage still attached to the anthocaulus, an observation made earlier by Squires (1963:15). Because of the uncertainty of the identity of this species, it is not considered further in the species or distribution accounts.

In a largely physiological account of polyp growth and a description of "alternation of generations" in Scleractinia, Semper (1872) reported numerous shallow-water ahermatypes from off Bohol, Philippines, including four species included in this revision: *Blastotrochus nutrix, Flabellum irregulare, F. variable (= F. aculeatum),* and *Placotrochus laevis*. Because he reported two species previously described by Milne Edwards and Haime, and a third is a junior synonym of yet another, only his new species, *F. irregulare*, was a new record for the Philippines. Semper's specimens are deposited at the NMW.

Only one species in the families under consideration was collected in the Philippines on the *Challenger* expedition: *Letepsammia formosissima* (Moseley, 1876) from station 209 off Cebu. Because these specimens are syntypes of the species, the Philippines constitute part of the type locality. They are deposited at the BM.

The most important single paper published on Philippine deep-water corals was Alcock's (1902a) report on the *Siboga* corals collected throughout Indonesia. He reported specimens collected directly from the Sulu Archipelago of the Philippines from four very productive *Siboga* stations (95, 98, 100, and 105) and reported many more species from throughout Indonesia that were later also found to occur in the Philippines. From the Sulu Archipelago he reported *Trochocyathus (= Tropidocyathus) pileus*, new species; *Citharocyathus (= Notocyathus) conicus*, new species; *Desmophyllum alabastrum*, new species (= *?Javania insignis* Duncan, 1876); *Flabellum latum* Studer, 1877 (= *Rhizotrochus flabelliformis*, new species described herein); *F. suluense*, new species (= *?F. magnificum* Marenzeller, 1904); *F. dens*, new species; *Bathyactis (= Fungiacyathus) symmetricus* Pourtalès, 1871 (= a variety of different species); *B. (= Fungiacyathus) sibogae*, new species; *B. (= Fungiacyathus) palifera*, new species; *Stephanophyllia fungulus*, new species; and *S. (= Letepsammia) formosissima*, Moseley, 1876: 11 species (6 of them new), including nine new records for the Philippines. The *Siboga* material is deposited at the ZMA (Van Soest, 1979).

Smith (1913) reported two species of *Flabellum* (*F. australe* Moseley, 1881, and *F.* sp.) from the Miocene to Pliocene of Masbate, Philippines. I have not examined these specimens, but, based on the illustrations, it is doubtful that these specimens can be identified as to species.

Faustino's (1927) monograph of the Philippine Scleractinia reviewed all literature and scleractinian specimens ever reported from the Philippine Islands. Although essentially a review paper that included uncritical synonymies, Faustino was the first to draw on the *Albatross* deep-water coral collection, reporting five species pertaining to this revision from 80 records: *Flabellum pavoninum* Lesson, 1831 (= seven species, none of which are *F. pavoninum*); *F. paripavoninum* (Alcock, 1894) (= three species, including *F. paripavoninum*); *F. japonicum*, Moseley, 1881; *F. deludens* Marenzeller, 1904 (= three species, including *F. deludens*); and *F. rubrum* (Quoy and Gaimard, 1833) (= five species, none of which are *F. rubrum*). All of Faustino's specimens are deposited at the NMNH and have been carefully reexamined; the synonymies and discussions in the species accounts explain my reidentifications. In all, Faustino added three valid new records to the Philippine fauna within the purview of this revision: *T. paripavoninum*, *F. japonicum*, and *F. deludens*.

Eguchi (1941a) reported *Citharocyathus (= Notocyathus) conicus* from the Pliocene of Mindoro, Philippines, a species previously reported from the Sulu Archipelago by Alcock (1902a).

In an analysis of the living position of *F. pavoninum*, Squires (1964a) cited 12 lots of *Albatross* Philippine specimens. These specimens, which are all deposited at the NMNH are herein reidentified as *F. lamellulosum* Alcock, 1902, and *F. magnificum* Marenzeller, 1904; *F. pavoninum*, as yet, is not known from the Philippines.

Wells (1983:236), in an annotated listing of Galápagos corals, briefly alluded to two *Albatross* Philippine lots of *Sphenotrochus*, which he compared to *S. intermedius* (Goldfuss, 1827). These specimens are deposited at the NMNH and are identified as *S. hancocki* Durham and Barnard, 1952, in this revision.

Zibrowius and Grygier (1985), in their study of ascothoracid hosts, mentioned *Peponocyathus orientalis* (Duncan, 1876) (= *P. australiensis* (Duncan, 1870)) from yet another Philippine *Albatross* station, also deposited at the NMNH.

The type specimens on which Owens (1986a) based her new genus, *Rhombopsammia*, and two new species, *R. squiresi* and *R. niphada*, also came from eight *Albatross* Philippine stations, and are deposited at the NMNH.

Finally, as an outgrowth of the current revision, I (Cairns, in press b) published a discriminant analysis of eight species of Indo-West Pacific *Flabellum (Flabellum)*, of which four species came from *Albatross* Philippine material: species 1 (= *F. politum*, new species); *F. magnificum; F. patens*, Moseley, 1881; and *F. lamellulosum* Alcock, 1902. Three of these are new records for the Philippines.

To summarize, since 1848, 13 papers have contributed directly to our knowledge of Philippine deep-water Scleractinia. Allowing for synonymy, a total of 26 species have been reported previously, the highest number of species in any of the papers (nine) being from Alcock's (1902a) account of the *Siboga* Indonesian expedition. A total of 59 species are reported in this revision, 53 of which are known from the Philippines, which therefore results in 27 new species records for the Philippines.

Material

This study is based on the examination of approximately 4400 specimens collected throughout the Philippine Islands and adjacent waters, including about 400 lots of new material collected at 178 stations (see Appendix: Station List). Most of these specimens originated from the *Albatross* Philippine expedition of 1907-1910, which made most of its collections throughout the Philippine Islands, with some stations just south of Philippine territorial waters off Darvel Bay, Sabah, and several stations in the South China Sea off Hong Kong (see Anonymous, 1910, for history and station list of *Albatross* Philippine expedition). For completeness of coverage of this expedition and because of zoogeographic similarity, these outlying stations are included in this revision. Reference material from the R/V *Anton Bruun* and from the three *MUSORSTOM* expeditions (cruises 1-3) was also examined; however, the bulk of the material from the latter expeditions will form the basis of a separate report by H. Zibrowius. The *MUSORSTOM* specimens cited in this revision will eventually be deposited at the MNHNP, NMNH, and other museums.

In addition to the new material, previously reported specimens of historical interest from the following museums were examined: AHF (Durham and Barnard, 1952), AM (Hoffmeister, 1933, in part), BM (Milne Edwards and Haime, 1848, in part; Duncan, 1864, 1870; Moseley, 1881; Gardiner, 1899, 1902a; Gardiner and Waugh, 1938, 1939), MNHNP (Lesson, 1831; Milne Edwards and Haime, 1848, in part;

Zibrowius and Grygier, 1985), NMW (Semper, 1872; Marenzeller, 1889), RGM (Gerth, 1921; Umbgrove, 1938, 1950), South Australian Museum (Dennant, 1906), TIUS (Yabe and Eguchi, 1942a,b), USNM (Dana, 1846; Vaughan, 1907; Faustino, 1927; Hoffmeister, 1933; Squires, 1958, 1962, 1964a,b; Wells, 1959, 1964, 1983, 1984; Owens, 1986a,b), ZMA (Alcock, 1902a; Van der Horst, 1921; Boschma, 1923), ZMB (Marenzeller, 1904), and ZMC (Squires, 1965). Comparative material of Keller's (1974, 1975, 1976, 1977) papers could not be obtained, despite repeated attempts.

Methods

TERMINOLOGY.—The basic morphological terminology used in this paper is explained in Wells (1956); however, some terms and meristic counts require further explanation. The term *epicenter* refers to the exact center of the base (Plate 5*e,f*) or calice of a solitary coral, and is usually its point of origin. A *septal system* is a one-sixth sector of a calice, comprised of an S_1 and all septa between it and an adjacent S_1. The *septal* or *costal formula* is an abbreviated indication of the relative exsertness and width of the cycles of septa and costae, respectively. Thus, $S_{1-2} >> S_3 > S_4$ implies that the six septa of the first cycle (the S_1) are the same size as the six septa (S_2) of the second cycle, which, in turn, are much larger than the 12 septa of the third cycle (S_3), which are larger than the 24 septa of the fourth cycle (S_4). A septal formula of $1° > 2° > 3°$ is used for coralla lacking hexameral symmetry, and implies that the primary septa are larger than the secondary septa, which are larger than the tertiary septa. A *half-system* is a one-twelfth sector of a calice, including an S_1 and all septa between it and an adjacent S_2.

In the fungiacyathids, the *trabecular count* includes the number of septal ridges or undulations on one side of an S_1, from epicenter to calice edge. If trabeculae alternate in position on the septal faces, an S_1 will have twice as many trabeculae as the trabecular count. *Synapticular plates*, ribbons of calcium carbonate linking adjacent fungiacyathid septa, are sometimes referred to as T-, Y-, or U-shaped. These structures, which first appear as vertical rods midway between septa, later bifurcate, the two ends fusing to adjacent septal faces (T- or Y-shaped, Plates 1*k*, 4*b,c*). Eventually the lower part becomes solidly fused, producing a U-shaped structure. These plates appear to be structurally different from typical synapticulae. A distinction is made between *trabecular spines* (Plate 3*j*) and *trabecular septal lobes* (Plate 3*g,h*); the former composed of exsert, individualized trabeculae, usually on the inner part of a fungiacyathid septum; the latter composed of numerous trabeculae united into a solid lobate structure, invariably on the periphery of a septum.

Micrabaciid septal numbering follows the scheme devised by Cairns (1982) whereby the S_3 are considered to repeatedly bifurcate (figs. 1–3). The *marginal shelf* is a low rim encircling the corallum and is composed of greatly reduced septa and costae or exsert costal spines (Plate 9*c,g*).

Conventional flabellid morphological terms are discussed and illustrated by Squires (1964a) and Cairns (in press b). In addition (borrowing from the terminology used in fungiid corals), the terms *anthocaulus* and *anthocyathus* are used to refer to the basal and distal parts, respectively, of a transversely dividing flabellid (e.g., *Truncatoflabellum, Blastotrochus, Truncatoguynia, Placotrochides*). The base of the anthocyathus is usually flat or V-shaped and is referred to as the *scar of attachment*. The two *principal septa* of a flabellid are those opposing S_1 aligned with the greater axis of the calicular ellipse. When symmetry is not hexameral, the group of largest septa (often 16–20 in number), are termed the *primary septa;* the group of second largest septa (equal in number to the primaries), are termed *secondary septa*, etc. The external theca associated with the principal septa (thecal edges) may be *crested* (Plates 27*j*, 29*d*), if a solid calcareous keel extends from it; *acute* (Plate 24*a*), if the two thecal faces meet in a sharp line; *subacute* (Plate 28*i,j*), if the two faces meet at a low angle but not in a sharp line; or *rounded* (Plate 31*g*). The upper, outer septal edges (edge adjacent to theca) of species of *Rhizotrochus* and, to a lesser degree, some species of *Flabellum (Flabellum)* are very attenuate but slightly lower in the fossa are inflected upward into an exsert septal lobe. The point of inflection corresponds to the *septal notch* (Plates 34*i*, 41*f,g*).

SPECIES ACCOUNTS.—Species synonymies are complete unless otherwise indicated. Efforts were made to verify most historical records by personal examination, but when specimens were not available for study and the published account was unclear, the synonymy entry and corresponding distribution record are queried. Generic synonymies include references to the major revisions of the Scleractinia (i.e., Milne Edwards and Haime, 1848, 1850, 1857; Duncan, 1885; Vaughan and Wells, 1943; Alloiteau, 1952; Wells, 1956; Chevalier, 1987) supplemented by special revisions of specific groups (e.g., Zibrowius, 1974; Chevalier, 1961), as well as the original authors of senior and junior synonyms.

In the "Material Examined" sections, the number of specimens examined per station is indicated in parentheses, followed by the abbreviation of the museum of deposition and catalog number, if one was assigned. Additional reference material examined, not conspecific with the species being discussed, follows.

Holotypes, neotypes, and paratypes of new species are deposited in the NMNH, except for the types of *Rhizotrochus flabelliformis* and *Gardineria musorstomica*, which were borrowed from other museums.

Bottom temperature ranges are given for as many species as possible in the "Distribution" sections and in Table 7; however, these data were available for only about half of the *Albatross* stations; H.M.S. *Challenger* (Moseley, 1881); Royal Indian Marine Survey Ship *Investigator* (Alcock, 1898, 1902b); H.E.M.S. *Mabahiss* (Gardiner and Waugh, 1938, 1939); and the *Sôyô-maru* (Yabe and Eguchi, 1942a,b).

The SEM was done by the author on a Cambridge Stereoscan 100.

Order SCLERACTINIA Bourne, 1900

Suborder FUNGIINA Verrill, 1865

Superfamily FUNGIICAE Dana, 1846

Family FUNGIACYATHIDAE Chevalier, 1987

DIAGNOSIS.—Corallum solitary, cupolate, free; septotheca horizontal to concave and usually quite fragile. Septa and costae in direct correspondence with one another, 48 or 96 of each. Costae usually thin and serrate but may be rounded and granular. Septa imperforate, composed of a single fan system of widely spaced compound trabeculae that often terminate in tall septal spines; septal faces usually carinate. Adjacent septa united by T- or Y-shaped synapticular plates that originate from the thecal base. Pali sometimes present; columella spongy. Dissepiments absent. Polyp completely invests corallum. Exclusively ahermatypic.

DISCUSSION.—Vaughan and Wells (1943) and Wells (1956) queried the placement of *Fungiacyathus* in the Fungiidae, probably because of its unusual synapticular plates and its very different ecological niche (i.e., deep water) compared to the other shallow-water fungiids. Subsequent revisions of the Fungiidae (Wells, 1966; Cairns, 1984b) expressly excluded *Fungiacyathus* from the family but did not suggest to which family it might belong. Recently, Chevalier (1987) created a new family, the Fungiacyathidae, for species of the genus *Fungiacyathus*, according to him one of 14 families in the suborder Fungiina. It is distinguished from the Fungiidae by the following characters: (1) adjacent septa of Fungiacyathidae are laterally joined by T- or Y-shaped plates that originate from the inner thecal base and subsequently extend to adjacent septa (adjacent septa of Fungiidae are joined by stout transverse compound trabeculae); (2) the septa of Fungiacyathidae are composed of relatively few broad, compound trabeculae that often terminate in tall septal spines, the lateral faces of which are carinate; septa of Fungiidae are composed of numerous compound trabeculae that result in low septal teeth, the lateral septal faces being granular; (3) the septa of Fungiacyathidae are imperforate even at a young stage; the septa of Fungiidae are usually perforate at a young stage and often remain so in the adult; and (4) the wall of Fungiacyathidae is originally septothecate; the wall of the Fungiidae is primarily synapticulothecate and only secondarily septothecate. Ecologically, the two families are quite different: the Fungiacyathidae are all solitary, deep-water (99–6328 m), azooxanthellate corals with a worldwide distribution, including the Antarctic; the Fungiidae are solitary or colonial, shallow-water, zooxanthellate corals (except for some deep-water (475 m) ahermatypic *Diaseris*) restricted to the Indo-Pacific tropics.

Only one genus, *Fungiacyathus*, is included in the family.

DISTRIBUTION.—*Eocene:* Tonga, South Australia, Barbados. *Miocene:* South Australia. *Pleistocene:* Japan. *Recent:* Worldwide, including Antarctic; 99–6328 m (deepest record of any scleractinian coral).

Fungiacyathus Sars, 1872

Diaseris.—Pourtalès, 1868:139 [in part].
Fungia.—Pourtalès, 1871:46 [in part].
Fungiacyathus Sars, 1872:58.—Duncan, 1885:31.—Vaughan and Wells, 1943:144.—Alloiteau, 1952:674.—Wells, 1956:F390.—Keller, 1976:31.—Cairns, 1979:30.—Zibrowius, 1980:22.—Cairns, 1982:5–7.—Chevalier, 1987:705, fig. 405, 3a–b.
Bathyactis Moseley, 1881:185–186.—Duncan, 1885:151.—Yabe and Eguchi, 1942b:137.
Bathytrochus Gravier, 1915:8–9.

DIAGNOSIS.—Having the characters of the family.

DISCUSSION.—Species of *Fungiacyathus* described before the establishment of this genus were placed by Pourtalès (1868, 1871) in the genera *Fungia* and *Diaseris*. *Fungiacyathus* was described by Sars (1872) for *F. fragilis*, a five-septal-cycle species from the North Atlantic. *Bathyactis* was described by Moseley (1881) for *B. symmetricus* (Pourtalès, 1871), a four-septal-cycle species with an apparent cosmopolitan distribution. Moseley explained that the only difference between *Bathyactis* and *Fungiacyathus* was that the latter did not have synapticulae, and implied that upon reanalysis, they might prove to be the same genus. Duncan (1885) accepted the distinction of the two genera and even assigned them to different suborders: *Fungiacyathus* to Fungiidae and *Bathyactis* to Caryophylliidae. This distinction continued through 1942 (e.g., Gardiner and Waugh, 1939; Yabe and Eguchi, 1942b), until Vaughan and Wells (1943) synonymized the two genera, realizing that *F. fragilis* does, in fact, have synapticulae. *Bathyactis* is, however, retained herein as a subgenus of *Fungiacyathus* for those species having four cycles of septa.

The 22 valid species of *Fungiacyathus* can be conveniently divided into three groups: those with four cycles of septa, those with five cycles of septa, and those that are fissiparous, the latter of which are probably four-cycle derivatives. Because the fifth cycle of septa occurs early in the ontogeny of those species that have it (calicular diameter 7–8 mm), it is a reliable and easily recognized character and is herein employed to divide the genus into two subgenera: the nominate subgenus having species with five cycles of septa, and *F. (Bathyactis)*, having species with four cycles of septa. The nominate subgenus, typified by *F. fragilis*, contains five species; subgenus *Bathyactis*, typified by *F. symmetricus*, contains 15 species and two additional fissiparous species.

The taxonomy of species of *Fungiacyathus* has been confused for over a century, dating back to Moseley's (1881) misconception that *F. symmetricus* was a juvenile stage of a larger species having a cosmopolitan distribution and a great depth range. It was subsequently shown (Cairns, 1979, 1982) that *F. symmetricus* is endemic to the western Atlantic (183–1644 m) and rarely exceeds 14 mm in calicular diameter. Prior to that, *F. symmetricus* had been reported from Indonesia and the Indian Ocean (Wood-Mason and Alcock, 1891a; Alcock, 1898, 1902a; Gardiner and Waugh, 1939; Marenzeller, 1904), South Australia (Dennant, 1906), off Japan (Yabe and Eguchi, 1942b; Utinomi, 1965), and Antarctica (Wells, 1958;

Eguchi, 1965; Squires, 1969), which is only a partial listing. Most of these identifications were based on the excellent description and figures of *B. symmetricus* reported by Moseley (1881), based on specimens from 19 *Challenger* stations. Specimens from 15 of these 19 stations have been examined, most of which are four-septal-cycle species: four lots are *F. symmetricus*, nine lots are *F. marenzelleri*, one lot is the five-septal-cycle *F. fragilis* (*Challenger* 218), and another is the five-septal-cycle *F. stephanus* (*Challenger* 194). Moseley's illustrations, upon which most of the subsequent identifications were made, were based on specimens of *F. marenzelleri*. Likewise, Alcock (1902a) included five different species among his seven reported lots of *B. symmetrica* collected by the *Siboga*, including four lots of five-septal-cycle species, even though he keyed *B. symmetrica* as having only four septal cycles. Keller (1976) added to the confusion by describing three new subspecies of *F. symmetricus* from the Indo-West Pacific and North Atlantic, all of which appear to be very similar to *F. marenzelleri*, a species that she does not acknowledge in her paper. One of the subspecies, *F. symmetricus fragilis*, is a junior primary homonym of *F. fragilis* Sars, 1872, the type species of the genus. Keller had many specimens at her disposal and used the following characters to distinguish among species and subspecies: calicular diameter, GCD:H, corallum robustness, shape of base, nature of costae, presence or absence of columella, septal shape, and number of synapticular rows. Although I agree with the value of most of her criteria, I do not agree with her ultimate taxonomic decisions.

The characters used in this revision to distinguish species (Table 1), listed in order of relative importance, are as follows: number of septa, nature of septa (i.e., shape, number of trabecular spines, paliform lobes), nature of costae, adult calicular diameter, nature of synapticulae (i.e., height, shape), and nature of septal canopies. Characteristics of columella shape and shape of base were found to be quite variable and of little discriminating value.

TYPE SPECIES.—*Fungiacyathus fragilis* Sars, 1872, by monotypy.

DISTRIBUTION.—Same as for the family.

Key 1: The Six Species of *Fungiacyathus* Known from the Philippine Islands

1. Five cycles of septa (96 septa) (*F. (Fungiacyathus)*) 2
   Four cycles of septa (48 septa) (*F. (Bathyactis)*) 3
2. Costae thin ridges with fine serration; corallum large, up to 50 mm in calicular diameter; 12–15 T-shaped synapticular plates per S_1; septa corrugated . . . . ***F. stephanus***
   Costae rounded and granular; corallum of medium size, up to 21 mm in calicular diameter; 8–9 solid synapticular plates per S_1; septa planar . . . . . ***F. paliferus***
3. Costae rounded and granular 4
   Costae thin, serrate ridges 5
4. Intercostal furrows deep peripherally; basal epicenter smooth; calicular diameter less than 11 mm; septal spines compound, peripheral septal lobes small . . . . ***F. turbinolioides*, new species**
   Intercostal furrows shallow; basal epicenter costate; calicular diameter up to 23 mm; septal spines simple, peripheral septal lobes large . . . . ***F. granulosus*, new species**
5. S_{1-2} brown; septal canopies high and well developed . . . . ***F. variegatus*, new species**
   Septa white; septal canopies porous and rudimentary . . . . ***F. sibogae***

Subgenus *Fungiacyathus (Fungiacyathus)* Sars, 1872, new rank

Diaseris.—Pourtalès, 1868:139 [in part].

Fungiacyathus Sars, 1872:58.—Duncan, 1885:31.—Vaughan and Wells, 1943:144 [in part].—Alloiteau, 1952:674 [in part].—Wells, 1956:F390 [in part].—Keller, 1976:31 [in part].—Cairns, 1979:30 [in part].—Zibrowius, 1980:22 [in part].—Cairns, 1982:5–7 [in part].—Chevalier, 1987:705 [in part].

Bathyactis.—Yabe and Eguchi, 1942b:137 [in part].

DIAGNOSIS.—*Fungiacyathus* with five cycles of septa.

DISCUSSION.—Five species, including one fossil species, belong in this subgenus: *F. pusillus* (Pourtalès, 1868); *F. fragilis* Sars, 1872 (= *F. hawaiiensis* Vaughan, 1907); *F. stephanus* (Alcock, 1893); *F. paliferus* (Alcock, 1902) (= ?*F. kikaiensis* (Yabe and Eguchi, 1942)); and *F. euaensis* Wells, 1977 (Eocene of Tonga). Another species, *F. eocaenica* (Gerth, 1921) was described from the Eocene of Java, but Wells (1977) doubted its placement in *Fungiacyathus*.

TYPE SPECIES.—*Fungiacyathus fragilis* Sars, 1872, by monotypy.

DISTRIBUTION.—*Eocene:* Tonga. *Pleistocene:* Japan. *Recent:* Worldwide, but not Antarctic; 99–2200 m.

TABLE 1.—Comparisons of six species of *Fungiacyathus* known from the Philippine Islands.

Characters	*F. stephanus* (Alcock, 1893)	*F. paliferus* (Alcock, 1902)	*F. sibogae* (Alcock, 1902)	*F. granulosus*, new species	*F. variegatus*, new species	*F. turbinolioides*, new species
Maximum calicular diameter (mm); density	50 (?57); very fragile	20.9; robust	14.5; intermediate density	23; robust	8; intermediate density	10.3; robust
Shape of base	very concave to flat	flat to slightly concave	flat to slightly convex	flat to slightly convex	flat to slightly concave	flat to slightly concave
Nature of costae	thin, finely serrate ridges	rounded, unequal in width; granular	thin, serrate ridges	rounded, unequal in width; granular	C_{1-2} thin, serrate ridges	rounded, equal in width; granular; deep intercostal furrows
Number of septal cycles	5	5	4	4	4	4
Nature of S_1: trabeculae per septum; shape; granulation	20–23; septa corrugated; septal undulations bear very fine granules	15–20; septal planar; septal faces bear low, coarsely dentate ridges	14–19; septa planar; septal faces bear continuous dentate ridges	21–24; septa planar; septal faces bear low, coarsely dentate ridges	15–17; septa planar; septal faces bear low, dentate ridges	20–25; septa planar; septal faces bear low, serrate ridges with clavate granules
S_1 synapticulae: number, height, and shape	12–15; 5–7th highest; T-shaped	9–14; 4–7th highest; solid	~6; 5th tallest; T- or Y-shaped	6–9; 4–7th tallest; Y- or YY-shaped	3; 2nd highest; solid	3–4; 2nd highest but still low; T-shaped to solid
Nature of septal canopies	porous, rudimentary	porous, rudimentary	slightly porous, rudimentary	porous, well developed	solid, well developed, at 45°–55° angle	absent
Paliform lobes or spines	small P_2 usually present	well-developed P_2; P_3 in larger coralla	individualized, tall, slender trabecular spines on S_{1-4}; no paliform lobes	individualized, tall, slender trabecular spines on S_{1-4}; no paliform lobes	second and third trabecular spines of S_2 broad and recurved	robust, compound trabecular spines; no paliform lobes
Columella	crispate, flat	crispate, rudimentary	crispate, low, round, spiny	well developed, tuberculate	rudimentary	well developed, tuberculate
Other characters	S_{1-2} septal lobes quite high; marginal shelf present in concave specimens				S_{1-2} light brown	

1. *Fungiacyathus (Fungiacyathus) stephanus* (Alcock, 1893)

PLATES 1*a–k*, 2*a*,*b*

Bathyactis symmetricus.—Moseley, 1881:189 [in part: *Challenger* 194].—?Wood-Mason and Alcock, 1891a:8.—?Alcock, 1898:28; 1902a:37 [in part: *Siboga* 12, 18].

Bathyactis stephanus Alcock, 1893a:149, pl. 5: figs. 12, 12a.

Bathyactis stephana.—Alcock, 1898:28–29, pl. 3: figs. 5, 5a; 1902a:38; 1902b, fig. 93.—Gardiner and Waugh, 1939:232.

?*Bathyactis sibogae* Alcock, 1902a:38 [in part: specimen 57 mm in calicular diameter, *Siboga* 95 or 159].

Bathyactis symmetrica.—Gardiner and Waugh, 1939:230–231.

Fungiacyathus stephana.—Wells, 1977:7.

?*Fungiacyathus sibogae*.—Van Soest, 1979:109 [in part: probably *Siboga* 95 or 159].

Not *Fungiacyathus* sp. cf. *F. stephanus*.—Wells, 1984:207, pl. 1: figs. 3, 4 [= *F. paliferus*].

DESCRIPTION.—The study material contains specimens representing two morphological forms: one with a concave base and very exsert septa, referred to as the typical form; the other with a flat base and less prominent septa, referred to as the flat-based form.

Corallum of typical form up to 39 mm in diameter and 18 mm tall, often with an extremely concave base. Flat-based form up to 50 mm in diameter and 14 mm tall, with a perfectly flat base. Coralla of both forms extremely fragile, but corallum porosity not evident in well-preserved coralla. Costae consist of thin (0.8–1.0 mm wide), finely serrate ridges, which become more prominent (up to 0.75 mm tall) and slightly sinuous toward calicular edge. Costal dentition fine, each tooth roughly cylindrical, about 51 µm in diameter and 0.10 mm tall. Intercostal area about 0.75 mm wide and smooth peripherally, somewhat granular near epicenter. C_5 originates about 6 mm from epicenter, corresponding to inception of S_5 on basal plate.

Septa hexamerally arranged in five complete cycles. Six S_1 largest septa, each forming a very tall internal lobe, which decreases in size abruptly, often having a vertical outer edge but continuing to the calicular edge as a low ridge. S_1 of typical form composed of 20-23 trabeculae that steadily increase in size from the columella to the 10th or 11th trabeculum and then rapidly decrease in size peripherally. In contrast, in the larger corallum and longer septa of the flat-based form there are fewer trabeculae, e.g., 14-19, the tallest trabeculae occurring in the 7th to 9th positions. S_2 only slightly smaller than S_1, but more obliquely inclined from the fossa and therefore having a septal apex farther from the fossa and slightly lower than that of the S_1. S_3 inclined even farther, with a crown of 12 septal lobes positioned lower and more peripheral than those of the S_2. Septal lobes of S_4 considerably smaller; S_5 lack septal lobes. All septa are highly corrugated, corresponding to the underlying trabeculae, each crest bearing a row of fine triangular teeth, each tooth about 0.11 mm tall and spaced about 0.28 mm apart; however, in well-preserved specimens it is clear that the corrugations attenuate at the upper septal edges forming smooth, straight, continuous upper septal borders. S_1 independent, united to adjacent septa only by synapticular plates; septa of all other cycles joined to one another by porous triangular canopies. Canopies linking S_3 to S_2 occupy about $^1/_5$ of calicular radius, those linking S_4 to S_3 about $^1/_3$ of calicular radius, and those linking S_5 to S_4 occupy about $^2/_3$ of calicular radius and are the lowest and best developed of the canopies. Canopies uniting the larger septa are better developed in the flat-based form. Each S_1 of the typical form has 10-13 T-shaped synapticular plates gradually increasing in size from the columella to the 6th or 7th position, and then decreasing in size peripherally. Probably because of its larger size, the flat-based form has 13-15 synapticular plates per S_1, with the largest in the 7th to 9th position. In both forms, the tallest synapticular plate is equal in height to an adjacent S_4. Synapticulae do not form rings; they are rarely continuous across a septum. Both septal trabeculae and synapticular plates are obliquely inclined away from the fossa, but the former more so, such that in the typical form it is not unusual for the 6th synapticular plate to reinforce and obliquely intersect the 11th trabeculum at the height of the septal lobe. In well-preserved coralla, which are rare in this fragile species, a marginal shelf is present beyond the outer edges of the outer septal lobes. The shelf is about 5 mm wide, composed of the outer edges of the 96 septa, all of which are about 1.5 mm tall at this radius.

Frequently there is a crown of six acute P_2 near the columella originating from the S_2-S_3 canopies. A ring of 12 P_3 is also sometimes present near the S_3-S_4 canopies; however, there is great variation in both size and presence of paliform lobes. If present, the P_2 are about 1.0 mm broad; the P_3, 2.5-3.0 mm broad. Columella a low, loose fusion of inner septa about 4.5 mm in diameter.

DISCUSSION.—Wood-Mason and Alcock (1891a) and Alcock (1898) reported two lots of *B. symmetrica* from *Investigator* stations 102 and 150. Although not illustrated or well described, their comments imply a flat-based species with five cycles of septa and a calicular diameter of 20 mm. These specimens have not been examined, but based on the range of variation of the *Albatross* specimens and the geographic and bathymetric data of the *Investigator* specimens, they are tentatively placed in synonymy with the flat-based form of *F. stephanus.*

Likewise, although not examined, the 57 mm calicular diameter specimen reported by Alcock (1902a) as *B. sibogae,* also having five cycles of septa and a flat base (*Siboga* 95 or 159), is assumed to be the flat-based form of *F. stephanus.* As discussed in detail in the discussion of *F. sibogae,* although the description of *F. sibogae* was based on a large five-cycle specimen, the lectotype of *F. sibogae* was chosen from *Siboga* 175, a smaller four-septal-cycle specimen, which preserves the name *F. sibogae* for a different valid species instead of submerging the name as a junior synonym of *F. stephanus.*

Fungiacyathus stephanus is very similar to *F. fragilis,* the only other large five-septal-cycle species; in fact, damaged specimens are often difficult to distinguish. The major differences between the two are that *F. stephanus* usually has small P_2, its S_{1-2} septal lobes are much higher (GCD:H of *F. stephanus* is 1.8-2.8 compared to 5.0 for *F. fragilis*), and concave-based specimens have a marginal shelf. A brief comparison of these species is made by Vaughan (1907:146) and Zibrowius (1980:24).

The shape of the base of *Fungiacyathus* species, i.e., concave, convex, flat, is usually of diagnostic value at the species level, but in *F. stephanus* great variation is present, the base ranging from extremely concave to flat. The species was originally based on a specimen with an extremely concave base, but specimens subsequently collected show intergrading variation in degree of concavity. For this reason, and because the flat-based form is identical in all other respects to typical *F. stephanus,* the two forms are assumed to be the same species, the different base shapes probably caused by different environmental (?substrate) factors.

MATERIAL EXAMINED.—ALB-5110 (5) USNM 81768, AM G15240; ALB-5198 (1) USNM 81777; ALB-5348 (2) USNM 81776; ALB-5349 (1) USNM 81781; ALB-5425 (1) USNM 81780; ALB-5445 (1) USNM 81778; ALB-5510 (1) USNM 81779; ALB-5582 (11) USNM 81783; ALB-5587 (1) USNM 81775; ALB-5605 (3) USNM 81782; ALB-5618 (1) USNM 81774; ALB-5619 (1) USNM 81773; ALB-5630 (3) USNM 81771; ALB-5648 (2) USNM 81772; ALB-5668 (1) USNM 81770; ALB-5670 (1) USNM 81769; *Challenger* 194 (1) BM 1880.11.25.125 (Moseley, 1881); *Siboga* 12 (1) ZMA 707a, Plate 1*f*; *Siboga* 18 (6) ZMA 570 (*B. symmetrica* of Alcock, 1902a); *Siboga* 88 (1) ZMA 705 (Alcock, 1902a) Plate 1*i*; off Natal (1) BM 1939.7.20.121 (Gardiner and Waugh, 1939) Plate 1*g*; JM 185 (7) BM 1939.7.13.75-76 (Gardiner and Waugh, 1939).

TYPES.—The holotype of *B. stephanus* is presumed to be deposited at the Calcutta Museum, India. *Type Locality: Investigator* 133, 15°43′30″N, 81°19′30″E (off Kistna Delta, Bay of Bengal), 1240 m.

DISTRIBUTION.—*Recent:* Throughout Philippines; Indonesia (off Sabah, Celebes Sea; Makassar Strait; Halmahera Sea; Banda Sea (Moseley, 1881); Java Sea); Bay of Bengal (Alcock, 1893a); Gulf of Aden (Gardiner and Waugh, 1939); off Natal, South Africa (Gardiner and Waugh, 1939); 245-1977 m; 3.5°-15.0°C.

2. *Fungiacyathus (Fungiacyathus) paliferus* (Alcock, 1902)

PLATES 2*c*-*i*, 3*a*-*c*

Bathyactis palifera Alcock, 1902a:38, pl. 5: figs. 34, 34a.—Van der Horst, 1921:38.—Faustino, 1927:214, pl. 71: figs. 1, 2.—?Hoffmeister, 1933:14, pl. 4: fig. 6.—Yabe and Eguchi, 1942b:137, pl. 12: figs. 5b,c.

Bathyactis symmetrica.—Alcock, 1902a:37 [in part: *Siboga* 95].—Faustino, 1927:213 [in part: *Siboga* 95].

?Bathyactis kikaiensis Yabe and Eguchi, 1932b:443 [nomen nudum]; 1942b:155-156, pl. 12: figs. 6, 7.

Fungiacyathus palifera.—?Keller, 1976:33-34, pl. 1: figs. 1, 2.—Wells, 1977:G7.—Van Soest, 1979:109.

?Fungiacyathus kikaiensis.—Wells, 1977:7.

Fungiacyathus sp. cf. *F. stephanus*.—Wells, 1984:207, pl. 1: figs. 3, 4.

Fungiacyathus paliferus.—Cairns, 1982:7.

Fungiacyathus sp. Zibrowius and Grygier, 1985:119-120, figs. 6, 7.

DESCRIPTION.—Largest corallum (*Marion Dufresne* 32-128) 20.9 mm in calicular diameter and 5.8 mm high. Corallum base solid and sturdy, flat to slightly concave. Costae rounded and unequal in thickness and height according to the formula: $C_{1-2}>C_3>C_4>C_5$. C_1 about 0.3 mm wide with rounded edges; C_3-C_4 about 0.2 mm wide and virtually flat. Costae and base uniformly covered with low, rounded granules 80-100 µm in diameter and 50-60 µm tall.

Septa hexamerally arranged in five complete cycles in mature coralla. Coralla less than 1.8 mm in calicular diameter have only three septal cycles; between 1.8-4.5 mm in calicular diameter, four cycles; and above 4.5 mm calicular diameter, a full five cycles. S_1 composed of 4 or 5 trabecular spines adjacent to the columella that project up to 0.5 mm above septum, followed by a high peripheral septal lobe. Approximately 16 trabeculae (including the inner trabecular spines) compose an S_1, although trabeculae are sometimes difficult to count because the granules are not always perfectly aligned. S_2 composed of 5 or 6 projecting inner trabecular spines, the third and fourth of which are very robust and tall, which in large coralla fuse together forming a paliform lobe up to 0.8 mm wide and as tall as the S_2. Peripheral to the trabecular spines is a small septal lobe. S_3 composed of 2 or 3 inner trabecular spines, followed by a low, broad paliform lobe, which may have 1 or 2 spines on its outer edge. Peripheral to the P_3 is a low septal lobe. S_4 composed of a series of 5-15 (depending on corallum size) tall trabecular spines. S_5 composed of a lesser number of smaller trabecular spines. All septa planar (not corrugated) and covered with triangular (occasionally bifid) teeth up to 0.12 mm tall and 0.06 mm in width, arranged in lines following the trabeculae. On the outer lobes of the S_{1-2}, these teeth are usually fused into short serrate ridges. Higher-cycle septa are joined to one another in typical fungiacyathid fashion, but canopies are not present; septal junctions are composed of individual digitiform processes. Eight or nine synapticular plates per S_1, the tallest (fourth or fifth from columella) in the region of the tall septal lobe. Synapticulae equal in height to adjacent S_4.

Columella feeble, composed of a small concave mass about 0.8 mm in diameter.

DISCUSSION.—Alcock (1902a) reported seven lots of *B. symmetrica* from Indonesia, one of which was *F. paliferus*. The other lots were a mixture of both four- and five-septal-cycle species referred to in later synonymies, including *F. stephanus*, *F. granulosus*, *F. fragilis*, and *F. sibogae*.

Hoffmeister's (1933) specimen of *B. palifera* from South Australia was not examined and is therefore queried (specimen deposited at AM). If correctly identified, this specimen would be the largest known, with a calicular diameter of 22.1 mm.

Although not examined, the description and figures of *B. kikaiensis* Yabe and Eguchi, 1942, correspond exactly to *F. paliferus*, not *F. fragilis* as suggested by Wells (1984). The costae of *F. fragilis* are sinuous serrate ridges; those of *F. paliferus* and *F. kikaiensis* are straight, granular, and rounded.

Keller (1976) reported three lots of *F. paliferus* near the Kurile Trench in the northwest Pacific Basin from 3175-4110 m, which, unfortunately, are not available for comparison. Her specimens are considerably larger than those from the Philippines (calicular diameters up to 37 mm) and have correspondingly higher numbers of trabeculae and synapticular plates. They were described as having the characteristic granular costae and 96 septa, but, oddly, Keller did not mention the presence of paliform lobes. Because of the greater size, much deeper bathymetric range, and inability to verify the identification of these specimens, I strongly query this distributional record.

Fungiacyathus paliferus is distinguished from other five-septal-cycle congeners by its granular, rounded costae; most species of *Fungiacyathus*, including the four-septal-cycle species, have thin, serrate ridges for costae (Table 1).

MATERIAL EXAMINED.—ALB-5153 (15) USNM 81756; ALB-5162 (4) USNM 81758; ALB-5178 (79) USNM 81759; ALB-5577 (1) USNM 81757; ALB-5579 (2) USNM 81760; *Siboga* 153 (3 syntypes) ZMA 1171; *Siboga* 95 (9) ZMA 707b (*B. symmetrica* of Alcock, 1902a); *Siboga* 204 (2) ZMA 1172 (*B. palifera* of Van der Horst, 1921); *Sôyô-maru* 412 (1) TIUS 58913 (Yabe and Eguchi, 1942b) Plate 2*e*; USGS 25715 (1) USNM 71838 (*F. stephanus* of Wells, 1984); *Marion Dufresne* 32-128 (10) MNHNP (*Fungiacyathus* sp. of Zibrowius and Grygier, 1985) Plates 2*f*,*h*-*i*, 3*c*.

TYPES.—Three syntypes of *B. palifera* are deposited at the ZMA (1171), collected from *Siboga* 153 (Plates 2*c*,*d*,*g*, 3*b*). The two syntypes from *Siboga* 98 are missing and presumed lost (Van Soest, 1979:109). *Type Locality:* Sulu Sea and off Moluccas, 141-350 m.

DISTRIBUTION.—*Pleistocene:* Vanuatu (Wells, 1977); ?Ryukyu Islands (Yabe and Eguchi, 1942b). *Re-*

cent: Philippines (off Mindoro, Sulu Archipelago); Indonesia (Halmahera Sea, off Celebes) (Alcock, 1902a; Van der Horst, 1921); ?Kurile Trench (Keller, 1976); ?Great Australian Bight (Hoffmeister, 1933); Reunion (Zibrowius and Grygier, 1985); 75-522 m (?3175-4110 m); 11.6°-13.7°C.

Fungiacyathus (Bathyactis) Moseley, 1881, new rank

Fungia.—Pourtalès, 1871:46 [in part].
Bathyactis Moseley, 1881:185-186.—Duncan, 1885:151.—Yabe and Eguchi, 1942b:137 [in part].
Bathytrochus Gravier, 1915:8-9.
Fungiacyathus.—Vaughan and Wells, 1943:144 [in part].—Alloiteau, 1952:674 [in part].—Wells, 1956:F390 [in part].—Keller, 1976:31 [in part].—Cairns, 1979:30 [in part].—Zibrowius, 1980:22 [in part].—Cairns, 1982:5-7 [in part].—Chevalier, 1987:705 [in part].

DIAGNOSIS.—*Fungiacyathus* with four cycles of septa, including fissiparous species.

DISCUSSION.—Fifteen species, including three fossil species, belong to this subgenus: *F. symmetricus* (Pourtalès, 1871); *F. sibogae* (Alcock, 1902); *F. excelsa* (Dennant, 1906) (Eocene of South Australia); *F. beaumariensis* (Dennant, 1906) (Miocene of South Australia); *F. marenzelleri* (Vaughan, 1906); *F. stabilis* (Gardiner and Waugh, 1939) (= *F. symmetricus* of Gardiner and Waugh, 1939); *F.* sp. of Wells, 1945 (Eocene of Barbados); *F. durus* Keller, 1976 (= *?F. marenzelleri*); *F. aleuticus* Keller, 1976 (= *?F. marenzelleri*); *F. pseudostephanus* Keller, 1976; *F. fragilis* Keller, 1976 (junior primary homonym of *F. fragilis* Sars, 1872); *F. pliciseptus* Keller, 1976; *F. variegatus*, new species; *F. granulosus*, new species; and *F. turbinolioides*, new species. Another two exclusively fissiparous species are also assigned to this subgenus: *F. crispus* (Pourtalès, 1871) and *F. fissilis* Cairns, 1984. Two other species, *Fungiacyathus nascornatus* Gardiner and Waugh, 1938, and *F. sarsi* Gardiner and Waugh, 1938, clearly do not pertain to this genus or family, both probably belonging in *Deltocyathus*.

TYPE SPECIES.—*Fungia symmetrica* Pourtalès, 1871, by monotypy.

DISTRIBUTION.—*Eocene:* Barbados, South Australia. *Recent:* Worldwide, including Antarctica; 183-6328 m.

3. *Fungiacyathus (Bathyactis) sibogae* (Alcock, 1902)

PLATES 3*d-k*, 4*a-c*

Bathyactis symmetrica.—Alcock, 1902a:37 [in part: *Siboga* 208].
Bathyactis sibogae Alcock, 1902a:38 [in part: *Siboga* 175].—Faustino, 1927:214 [in part: *Siboga* 175].—Van Soest, 1979:109 [in part: *Siboga* 175, ZMA 1173 (not 889)], pl. 2: figs. 1, 2.
Fungiacyathus sibogae.—Wells, 1977:7.

DESCRIPTION.—Corallum fragile, up to 14.5 mm in calicular diameter and 4.7 mm tall. Base flat to slightly convex, often with a slight epicentral boss. C_{1-2} ridged from epicenter to calice edge, C_{3-4} ridged only near calicular edge. Costae finely serrate, adorned with closely spaced, blunt cylindrical teeth about 0.10 mm tall and 0.09 mm in diameter. At a calicular diameter of about 6 mm a fifth cycle of rudimentary costae appears to form without correspondence to a fifth cycle of septa; however, these low ridges are simply junction lines of basal plate between costae.

Septa hexamerally arranged in four complete cycles. S_1 composed of 5 or 6 inner trabecular spines that gradually increase in size away from the columella, bordered peripherally by a tall septal lobe of 8-14 more trabeculae, resulting in a total of 14-19 trabeculae per S_1. S_2 composed of 4-6 inner trabecular spines, the third and fourth of which are the tallest and often curved inward toward the columella; a septal lobe occurs peripheral to the spines. S_3 composed of 4-7 inner trabecular spines, the fourth to sixth of which are very elongate and often strongly inwardly curved toward the columella; a septal lobe occurs peripheral to these spines. S_4 composed of 9 or 10 trabecular spines but no lobe. Trabecular spines simple, quite slender, elongate (extending up to 1.4 mm), and usually slightly recurved toward the columella, resulting in a very delicate calicular aspect. Septa planar, covered by straight, parallel, serrate ridges, each about 70 µm wide and spaced 0.25 mm apart. Ridges present even on innermost septal edges near columella, where, in most species, trabeculae are represented only by aligned granules. Septal ridges covered by broad-based, well-spaced, triangular teeth, each about 0.32 mm broad at the base and 90 µm tall. Canopies not extensive but fairly solid, only slightly porous. Synapticular plates T-shaped, about 6 per S_1, the fifth plate being the highest (i.e., rising to just below level of adjacent S_4). Marginal shelf absent.

Columella papillose and rounded, about 2.0 mm in diameter.

DISCUSSION.—Alcock's (1902a) original description of *B. sibogae* was unillustrated and consisted of little more than a brief comparison to two other species. Nonetheless, it is clear that he was describing a five-septal-cycle species of large calicular diameter. Although the species was based on four syntypes, only one corallum is now available for study (*Siboga* 175), which is a four-septal-cycle specimen of much smaller calicular diameter. The specimen from *Siboga* 175 is undoubtedly a different species from the larger, described specimen. The original description refers to a large specimen with 96 septa, probably either the flat-based form of *F. stephanus* or *F. fragilis*, both of which have nomenclatural priority; however, the smaller 48-septa syntype represents a valid species in need of a name. Therefore, the specimen from *Siboga* 175 (ZMA 1173), illustrated by Van Soest (1979, pl. 2: figs. 1, 2), is chosen as the lectotype.

Fungiacyathus sibogae is very similar to *F. granulosus* in general aspect, and both species are known from the Philippines. The most obvious discriminating character between them is that *F. sibogae* has costae composed of narrow serrate ridges, whereas those of *F. granulosus* are uniformly granulated and rounded (Table 1). *Fungiacyathus sibogae* also differs in having a smaller calicular diameter (and therefore a lesser number of trabecular and synapticular plates per septum); more delicate, simple trabecular spines; a slightly convex base; and slightly lower synapticular plates.

Based on calicular diameter and septal number another three species should be compared to *F. sibogae*: *F. symmetricus* (Pourtalès, 1871), *F. pliciseptus* Keller, 1981, and *F. excelsa* (Dennant, 1904). *Fungiacyathus sibogae* is distinguished from the often misidentified western Atlantic *F. symmetricus* by its easily diagnosed peripheral septal lobes; *F. symmetricus* has only trabecular spines. It is distinguished from the southeast Pacific *F. pliciseptus* and the Eocene species from Victoria, Australia, *F. excelsa*, by its serrate, ridged costae; the other two species have a granular base. Also, *F. pliciseptus* has highly corrugated septa, and *F. excelsa* has a concave base and thus a more exsert calice than *F. sibogae*.

MATERIAL EXAMINED.—ALB-5618 (2) USNM 81766; ALB-5619 (9) USNM 81767, (1) AM G15249; ALB-5648 (1) USNM 82092; *Siboga* 175 (1) lectotype, ZMA 1173; *Siboga* 297 (decalcified tissue) paralectotype, ZMA 889; *Siboga* 208 (1) ZMA 707d (*B. symmetrica* of Alcock, 1902a).

TYPES.—*Bathyactis sibogae* was based on four syntypes from four Siboga stations: the specimen from *Siboga* 159 is missing (Van Soest, 1979); the specimen from *Siboga* 297 (ZMA 889) consists only of decalcified tissue and is unidentifiable; the specimen from *Siboga* 95 is also missing (ZMA 5098); and the specimen from *Siboga* 175 (ZMA 1173, not 889 as indicated by Van Soest, 1979) is present at the ZMA. Based on the preceding discussion, the specimen from *Siboga* 175 is designated as the lectotype (Plate 3*d*), the other three as paralectotypes. *Type Locality:* 2°37.7′S, 130°33.4′E (Ceram Sea), 1914 m.

DISTRIBUTION.—*Recent:* Indonesia (Ceram Sea, Molucca Sea, Banda Sea) (Alcock, 1902a); unverified from Timor Sea (*Siboga* 297) and Sulu Archipelago (*Siboga* 95)(Alcock, 1902a); 411–522 m.

4. ***Fungiacyathus (Bathyactis) granulosus*, new species**

PLATE 4*d–i*

Bathyactis symmetrica.—Alcock, 1902a:37 [in part: *Siboga* 59].

DESCRIPTION.—Corallum robust, up to 23 mm in calicular diameter and 6.5 mm tall, which is considered to be close to the maximum size for this species. Base flat to slightly concave. Costae rounded, becoming carinate only near calicular edge. Costae unequal in width and height according to the formula: $C_{1-2}>C_3>C_4$, the C_1 about 0.9 mm wide, C_2–C_4 progressively narrower to 0.6 mm. Base, including tops and sides of costae and intercostal spaces, uniformly covered with low rounded granules 0.13–0.16 mm in diameter.

Septa hexamerally arranged in four complete cycles. S_1 composed of 3 or 4 inner trabecular spines, the spines gradually increasing in size away from the columella, followed by a large exsert septal lobe, composed of up to 18–20 closely spaced trabeculae, resulting in a total of 21–24 trabeculae per S_1. Each S_2 has 4–6 inner trabecular spines, the third or fourth of which is much taller and broader (often compound), approximating narrow paliform lobes. Peripheral to the trabecular spines is a septal lobe. S_3 composed of 8 or 9 trabecular spines, the sixth or seventh of which is the tallest and slightly inwardly curved toward the columella, followed by a small peripheral lobe. S_4 composed of 10 or 11 trabecular spines but no outer lobe. Septa planar and covered by relatively closely spaced (0.20 mm apart) parallel serrate ridges corresponding to the underlying trabeculae. Near columella ridges are replaced by aligned granules, which are often clavate or bifid. Canopies not extensive but fairly solid; only slightly porous. Synapticular plates Y-shaped or double Y-shaped, 6–9 per S_1, depending on corallum size, the 4th to 7th plate being the highest (i.e., attaining level of adjacent S_4 exclusive of trabecular spines).

Columella spongy and tuberculate, formed by the fusion of innermost clavate and ramified septal granules. Typical columella about 2.5 mm in diameter.

DISCUSSION.—*Fungiacyathus granulosus* is most similar to *F. sibogae* and is compared to that species in the discussion of the latter. A combination of its medium adult size (23 mm calicular diameter), granular base, and densely arranged trabeculae distinguish it from all other species of *Fungiacyathus* having 48 septa. In the Philippines, only one other species is known to have a granular base: *F. variegatus*. The granulation of this species is restricted to the central area of the base. *Fungiacyathus granulosus* differs from the cosmopolitan *F. marenzelleri* by its more robust corallum, smaller canopies, more numerous trabeculae, and different septal spination.

ETYMOLOGY.—The species name is from the Latin *granulosus* (granular) and refers to the granular nature of the corallum base.

MATERIAL EXAMINED.—*Types:* *Siboga* 59 (1) ZMA 707c (*B. symmetrica* of Alcock, 1902a).

TYPES.—*Holotype:* ALB-5590, USNM 81751, Plate 4*d,e*. *Paratypes:* ALB-5260 (1) USNM 81755; ALB-5282 (1) USNM MO 230047; ALB-5283 (3) USNM 81752; ALB-5589 (4) USNM 81754; ALB-5592 (6) USNM 81753, (1) AM G15256. *Type Locality:* 4°10′50″N, 118°39′35″E (off Sabah, Celebes Sea), 567 m.

DISTRIBUTION.—*Recent:* Philippines (off Luzon, Mindoro, Panay, Sulu Archipelago); 390–567 m; 6.1°–10.8°C.

5. ***Fungiacyathus (Bathyactis) variegatus*, new species**

PLATE 5*a–h*

Fungiacyathus fragilis.—Wells, 1984:205–207 [in part: USGS 24918], pl. 1: figs. 1, 2.

DESCRIPTION.—Largest corallum (holotype) 8.0 mm in calicular diameter and 4.5 mm tall, which is assumed to be near the maximum size for the species. Base flat to concave with a small epicentral boss. Boss bears large, low, rounded granules up to 0.11 mm in diameter, rapidly decreasing to 0.07 mm in diameter near calicular edge. C_{1-2} ridged from boss to calicular edge, the rounded granules yielding to a unilinear row of slender pointed spines up to 0.09 mm tall. C_3 ridged only near calicular edge; C_4 rudimentary. Forty-eight radiating light brown stripes correspond to the 48 costae.

Septa hexamerally arranged in four complete cycles. S_1 consist of 15-17 trabeculae, the innermost 4 or 5 projecting inward as tall (up to 0.5 mm), thick (0.11 mm in diameter) trabecular spines; the remaining trabeculae form a tall peripheral septal lobe. Innermost portion of S_2 consists of 6 or 7 projecting trabecular spines, the second or third of which (in the vicinity of the S_{2-3} canopy) is very robust, taller than all others, and slightly inwardly curved toward the columella. The remainder of the S_2 comprise a septal lobe smaller than that of the S_1. S_3 composed of 8 or 9 projecting trabecular spines; S_4, of 7 or 8 projecting spines. S_{3-4} lack peripheral septal lobes. Outer edges of all septa extend around the calicular edge, being continuous with the underlying costae; there is no marginal shelf. Lower half of S_{1-2} pigmented light brown in well-preserved coralla, a color that is often missing from specimens that were dead when collected. All septa planar and bear low, continuous serrate ridges; the teeth on the ridges quite small (up to 0.14 mm) and widely spaced, occasionally bifid. Septal ridges spaced about 0.2 mm apart. Canopies solid and high, obliquely oriented at a 45°-55° angle. Synapticular plates solid and U-shaped, usually three to an S_1. Innermost S_1 synapticular plate links the S_{3-4} canopy to an adjacent S_1. Intermediate synapticular plate, which is the highest, rises above level of adjacent S_4.

Columella rudimentary, sometimes absent; composed of inner S_{1-2} junctions or simply the six inner edges of the S_1. Paliform lobes absent.

DISCUSSION.—One lot of 17 specimens (USGS 24918) reported by Wells (1984) from the Pleistocene of Vanuatu is *F. variegatus*. The other 7 specimens reported by Wells from USGS 25718 are larger specimens of five septal cycles, which appear to be a species of *Diaseris*.

Fungiacyathus variegatus is distinguished from the other Philippine species by its small size; pigmented corallum; very high, solid septal canopies; and very few synapticular rings (Table 1). Worldwide, no other species of *Fungiacyathus* has a pigmented corallum, and few other species have such a small adult calicular diameter.

ETYMOLOGY.—The species name is from the Latin *variegatus* (many different colors) and refers to the streaked light-brown pigmentation on an otherwise white corallum.

MATERIAL EXAMINED.—*Types:* USGS 24918 (17) USNM 71837 and 73977 (*F. fragilis* of Wells, 1984). *Reference Material:* USGS 25718 (7) USNM 73957 (*F. fragilis* of Wells, 1984).

TYPES.—*Holotype:* ALB-5113, USNM 81761, Plate 5*a*-*c*. *Paratypes:* ALB-5113 (9) USNM 81762, (1) AM G15254; ALB-5278 (11) USNM 81763; ALB-5314 (58) USNM 81764; ALB-5403 (54) USNM 81765. *Type Locality:* 13°52'N, 120°51'E (Verde Island Passage, Luzon), 291 m.

DISTRIBUTION.—*Pleistocene:* Vanuatu (Wells, 1984). *Recent:* Off Hong Kong, South China Sea; Philippines (western Luzon, Visayan Sea); 187-333 m; 13.1°-15.3°C.

6. *Fungiacyathus (Bathyactis) turbinolioides*, new species

PLATE 6*a*-*g*

DESCRIPTION.—Corallum robust, up to 10.3 mm in calicular diameter; holotype (best-preserved specimen) 8.1 mm in calicular diameter. Base flat to slightly convex, the central 1/2 to 3/4 of base relatively smooth. Peripherally, starting at a well-defined boundary, the base bears rounded equal costae 0.25-0.30 mm in width, separated by deep intercostal furrows about 0.20 mm wide. The costae bear low, rounded granules (0.1 mm in diameter) adjacent to the boundary area; taller and more slender cylindrical granules up to 0.07 mm tall near calicular edge (Plate 6*e*). In the central, relatively smooth area of the base, septal granules are somewhat masked.

Septa hexamerally arranged in four complete cycles. S_1 composed of 5-8 tall, robust, compound trabecular spines, bordered by a low peripheral lobe of 5-9 smaller simple trabeculae. Each compound spine composed of 2 or 3 trabeculae, the third or fourth spine from the columella being the tallest. Compound trabecular spines about 0.35 mm broad project about 0.65 mm beyond septal edge. S_2 shaped like the S_1 except that the second or third trabecular spine is curved inward toward the columella. S_3 also composed of 5 or 6 large, compound trabecular spines, bordered peripherally by a small septal lobe. The second to third S_3 spine at the S_{3-4} junction are usually the tallest of all septal spines. S_4 composed of 5-9 simple trabecular spines, equivalent in position and shape to the outer septal lobes of the lower-cycle septa. Septa planar, the septal spines, and upper septal edges covered by low parallel serrate ridges, which degenerate into discontinuous ridges and individualized clavate spines lower on septal face. Septal teeth triangular to cylindrical, often bifid, about 0.06 mm tall. Septal canopies not present, the higher-cycle septa joined to lower-cycle septa by thin digitiform processes. Synapticular plates T-shaped to solid, 3 or 4 per S_1, the tallest one being the second from the columella and only half as high as the adjacent S_4.

Fossa slightly concave, containing a robust columella composed of a low, solid fusion of 5-10 papillae.

DISCUSSION.—*Fungiacyathus turbinolioides* is distinguished from the other Philippine congeners (Table 1 and Key 1) as well as from all other species of *Flabellum (Bathyactis)* by its deep intercostal furrows, which appear to be turbinoliid in character. Other distinctive characters are its robust compound septal spines; relatively smooth central basal region; and relatively few, low synapticular plates.

ETYMOLOGY.—The species name *turbinolioides* is given to this species because of its resemblance to corals of the subfamily Turbinoliinae.

MATERIAL EXAMINED.—Types.

TYPES.—*Holotype:* ALB-5586, USNM 81750, Plate 6*a*.

Paratypes: ALB-5586 (62) USNM 81748, (2) AM G15253; ALB-5318 (3) USNM 81749. *Type Locality:* 4°06′50″N, 118°47′20″E (off Sabah, Celebes Sea), 635 m.

DISTRIBUTION.—*Recent:* Off Sabah, Celebes Sea; Formosa Strait, China; 622–635 m.

Family MICRABACIIDAE Vaughan, 1905

DIAGNOSIS.—Corallum solitary, cupolate, free; synapticulothecate wall horizontal or convex. Costae and septa alternate in position. Costae achieve full complement by repeated bifurcation of original 6 C_1. Septa achieve equivalent complement (48, 72, 96, 120, or 144) by combination of first two cycles of septa followed by multiple bifurcations of S_3. Septa attached to costae by regularly spaced simple synapticulae, which results in a series of intercostal pores. Septa composed of one fan system of simple trabeculae. Septa often perforate, with highly dentate margins; pali absent. Synapticulae usually present between lower, outer septal edges. Dissepiments absent. Columella spongy or papillose. Polyp completely invests corallum. Exclusively ahermatypic.

DISCUSSION.—Throughout the nineteenth century (e.g., Milne Edwards and Haime, 1857; Duncan, 1885), genera now assigned to the Micrabaciidae were divided between the Fungiidae (i.e., *Micrabacia*) and Eupsammidae (= Dendrophylliidae) (i.e., *Stephanophyllia, Leptopenus*), probably because both families contain species with porous coralla and a Pourtalès-like septal plan. This arrangement was accepted by both Vaughan (1905), who erected the family Micrabaciidae but did not include *Stephanophyllia* in it, and Yabe and Eguchi (1932c), who divided *Stephanophyllia* into four subgenera but included it in the Dendrophylliidae. Wells (1933) redefined the family to include genera having alternating costae and septa, which excluded three disparate genera originally included by Vaughan (1905), and united *Micrabacia* and *Stephanophyllia* in the same family within the superfamily Fungiicae. This classification has been followed to the present day, except for Chevalier (1987), who, once again, placed the family in the suborder Dendrophylliina. The earlier tendency to group *Stephanophyllia* with the dendrophylliids was based on the superficial similarity in septal arrangement between the two taxa, which was even acknowledged by Wells (1933); however, when carefully compared, the ontogeny and final septal arrangement of the dendrophylliid Pourtalès plan is quite different from that of the micrabaciid S_3 multiple bifurcations. Although the higher classification of the Micrabaciidae has been stable since 1933, significant contributions to the knowledge of this family have been made by Kühn (1967), Squires (1967, ms), and Owens (1984a,b, 1986a,b). Micrabaciidae was incorrectly synonymized as Stephanophyliidae by Yabe and Eguchi (1934 and 1942b).

Three characters distinguish the Micrabaciidae: the unique bifurcation pattern of both septa and costae, the alternation of septal and costal insertion, and the marginal shelf. Of these characters, the alternation of septa and costae is shared with two other taxa: the turbinoliid *Idiotrochus* and *Dunocyathus;* however, both of these genera have only three cycles of septa. Also, some fungiacyathids have a marginal shelf, but never as well developed as in the micrabaciids.

Five genera are assigned to the Micrabaciidae (see Key 2), with *Stephanopsammia* Yabe and Eguchi, 1932c, considered as a Lower Tertiary subgenus of *Micrabacia.* Approximately 44 species pertain to this family, most (29) attributed to *Micrabacia* (see Squires, ms). Thirty of the 44 species are known exclusively as fossils.

DISTRIBUTION.—*Lower Cretaceous to Recent* (but not yet known from Oligocene): Worldwide; 15–5000 m.

Key 2: The Genera of Micrabaciidae

(adapted from Squires, ms)

1. Septa rudimentary, composed primarily of tall septal spines . . . . . . ***Leptopenus***
   Septa lamellar 2
2. Septa perforate 3
   Septa imperforate 4
3. All septa highly perforate with complex dentition; costae spinose ridges, thinner than intercostal space, producing a highly porous base; marginal shelf present . . . . ***Letepsammia***
   Septa perforate basally, with simple dentition; costae granular and rounded, equal to or thicker than intercostal space, producing a less porous, more robust base; marginal shelf narrow or absent . . . . ***Stephanophyllia***
4. Corallum small (rarely exceeding 10 mm in calicular diameter); base narrow, thick, flat to concave; synapticulae well developed; marginal shelf narrow; known only from Cretaceous to Eocene . . . . ***Micrabacia***
   Corallum large (calicular diameter up to 41 mm); base fragile, convex; synapticulae reduced; marginal shelf broad; known only from Recent . . . ***Rhombopsammia***

Leptopenus Moseley, 1881

Leptopenus Moseley, 1881:204-205.—Duncan, 1885:174.—Wells, 1933:233.—Vaughan and Wells, 1943:146.—Alloiteau, 1952:675.—Wells, 1956:F390.—Kühn, 1967:323.—Squires, 1967:505.—Keller, 1977:37, 42.—Cairns, 1982:9.—Chevalier, 1987:697, fig. 402,3.

DIAGNOSIS.—Corallum extremely fragile. Costae thin dentate ridges individually extending far beyond calice to form a delicate marginal shelf. Intercostal spaces much broader than costae, penetrated by large pores. Septa rudimentary, composed primarily of a series of tall spines; no synapticulae between "septa." Columella spiny.

DISCUSSION.—*Leptopenus* is distinguished from other micrabaciid genera by its highly reduced septa and its very fragile and porous corallum (Key 2). It is most similar to *Letepsammia*, another genus with highly porous septa and base, but one that has well-developed septa. Yabe and Eguchi (1932c) and Kühn (1967) suggested that *Letepsammia* was most closely related and in transition to *Leptopenus*. Vaughan and Wells (1943) considered *Leptopenus* to be a "deep-water facies of *Stephanophyllia*" (= *Letepsammia*). Keller (1977) suggested that *Letepsammia* and *Leptopenus* were so similar that they might be considered as congeneric. *Leptopenus* is often considered to represent the end point of an evolutionary trend within the Micrabaciidae, representing a migration from shallow (Cretaceous *Micrabacia*) to deep water (Recent genera, including *Leptopenus*) with concomitant decreases in skeletal weight, number of septal trabeculae, and thickness of basal plate, and an increase in corallum porosity. This theme has been discussed by Steinmann (1908), Squires (1967), Kühn (1967), Keller (1977), and Owens (1984a,b). Keller (1977) suggested that the reduction in the corallum was a progressive neotenic development that is also seen in other deep-water species of *Fungiacyathus* and *Flabellum*. Owens (1984a), on the other hand, presented the intriguing idea that the lightening of the corallum may have been a preadaptation inherited from shallow-water ancestors that acquired a low-density corallum to facilitate automobility. Regardless of the evolutionary pathway or reasons for it, species of *Leptopenus* have the most fragile, porous coralla of all Scleractinia and occur at very great depths (to 5000 m), second only to the depth limit of *Fungiacyathus* (6328 m).

Six species of *Leptopenus* are known: *L. discus* Moseley, 1881 (southern Indian Ocean, off Argentina, Cuba, 2842-3566 m); *L. hypocoelus* Moseley, 1881 (eastern Pacific, ?Makassar Strait, ?2000-3949 m); *L. irinae* Keller, 1977 (North Pacific, 3175-5000 m); *L. solidus* Keller, 1977 (North Pacific, 3175-3250 m); *L. antarcticus*, new species (Antarctic, 2035-2384 m); and *L.* sp. A (Philippines, 871 m). Characters most useful in distinguishing species include: GCD:H ratio, development of septal canopies, development of webbing between septal spines, and exsertness of septal spines.

TYPE SPECIES.—*Leptopenus discus* Moseley, 1881, by subsequent designation (Wells, 1936).

DISTRIBUTION.—*Recent:* Worldwide, including Antarctic. 871-5000 m.

7. *Leptopenus* species A

PLATE 7*a-f*

DESCRIPTION OF SPECIMEN FROM ALB-5585.—Corallum extremely delicate. Maximum calicular diameter 28.5 mm; however, peripheral marginal shelf (spines) and outer septa all broken away. Corallum quite low in profile, with a virtually flat base and a maximum height of 3 mm (GCD:H = 9.4+). Central 1.8 mm of base solid and very slightly convex. Costae very thin ridges about 0.03 mm wide and 0.12 mm tall, bearing small (0.08 mm tall), widely spaced (every 0.5 mm) spines. Intercostal width increases with distance from epicenter: about 0.10 mm wide near epicenter and about 0.90 mm wide near calicular edge. Intercostal space traversed by thin trabeculae 0.10–0.13 mm in diameter at regular but increasingly greater intervals from the epicenter to edge, occurring about every 0.36 mm near epicenter and every 0.55 mm near calicular edge. Peripheral widening of the intercostal space and the gradual increase in distance between synapticulae produce elliptical intercostal pores of graduated size: about 0.26×0.10 mm near epicenter and 0.45×0.36 mm near calicular edge. Occasionally some larger peripheral pores are bisected by a downward projecting spine that originates from the under surface of the flanked septum. In all, a very porous, lightweight base results.

Septa arranged in typical micrabaciid fashion: S_{1-2} nonbifurcate, S_3 having multiple bifurcations in a consistent fashion, as illustrated and described for *Stephanophyllia fungulus* (Figure 3), resulting in 96 septa. S_1 composed of 10–12 slender (0.10 mm in basal diameter) inwardly curved spines, the sixth or seventh from the columella being the largest, about 0.8 mm tall. Spines widely spaced, about 0.70 mm apart, and not united basally. S_2 similar in morphology to S_1; however, inner edges slightly obscured by fusion with adjacent S_3. S_3 extremely short, obscured by the columellar fusion. $S_{3'}$ about 2.5 mm long, consisting of 4 or 5 tall, robust (0.15 mm in diameter) inwardly curved spines, the tips of which constitute the highest points of the corallum. Because septa are completely reduced to spines there is no facial ornamentation. Discrete septal canopies not present at S_2–S_3 or S_3–$S_{3'}$ junctions, but individual synapticulae form a very porous connection among the inner edges of the $S_{3'}$ and S_2 in some systems. Aside from the synapticulae that unite septa to costae, and the pseudocanopies, there are no additional synapticulae that unite adjacent septa.

Columella round, 1.5 mm in diameter, composed of a loose crispate mass of spines, surrounded by the inner edges of the $S_{3'}$–S_2 junctions.

DISCUSSION.—The specimen from ALB-5585 cannot be identified as any of the previously described species of *Leptopenus*, but, because only one incomplete specimen is at hand and no comparative specimens of Keller's (1977) North Pacific species are available, I choose not to formally designate a new species for this specimen. The *Albatross* specimen is most similar to *L. discus* in size and GCD:H ratio (>9.4 vs. 12.5 for *L. discus*); however, it differs in having 96 septa instead of 72; septal canopies rudimentary or absent vs. discrete canopies in *L. discus;* and slender, inwardly curved septal spines vs. outward-curved projecting spines that are united at their bases by a low calcareous web in *L. discus.*

Although collected relatively nearby, the central disc of a *Leptopenus* reported by Squires (1965) from Makassar Strait (Plate 6*h,i*) differs from the *Albatross* specimen in having a low septal webbing between spines, and massive S_2 spines, similar to those of *L. hypocoelus.* Unfortunately, Squires' *Galathea* specimen is too small to properly compare. *Leptopenus hypocoelus* itself is easily distinguished from other species by its very high S_2 septal spines and correspondingly low GCD:H ratio of 2.2; massive, solid canopies; and having only 48 septa.

Although no specimens are available for study, it would appear that the North Pacific *L. irinae* Keller, 1977, differs from the *Albatross* specimen in having a lower GCD:H ratio (as low as 5.0); 72 septa; long outward projecting septal spines; and a very pronounced spinose marginal shelf. Likewise, *L. solidus* is distinguished by having a relatively low GCD:H ratio of 6 and a compact corallum with a robust columella.

MATERIAL EXAMINED.—ALB-5585 (1) USNM 81747. *Reference Material:* Syntypes of *L. discus,* BM 1880.11.25.159; holotype of *L. hypocoelus,* BM; types of *L. antarcticus,* new species (see below); *Galathea* 453 (1) ZMC (Squires, 1965).

DISTRIBUTION.—Off Sabah, Celebes Sea; 871 m; 5.1°C. This record constitutes the shallowest depth at which a specimen of *Leptopenus* has been collected and yet the corallum of this species is the most fragile of any species of *Leptopenus* collected thus far.

Leptopenus antarcticus, new species

Leptopenus sp. cf. *L. discus.*—Cairns, 1982:9–10, fig. 1, pl. 2: figs. 1–3 [complete description].

DIAGNOSIS.—Corallum discoidal and extremely fragile. Largest specimen 18.0 mm in diameter. Base flat to slightly concave; corallum relatively high in profile with a GCD : H of about 5. Costae alternate in position with septa, joined to one another by thin synapticular bridges. Individual costae extend up to 1.6 mm beyond synapticular zone (or 17%–20% calicular radius) forming a delicate marginal shelf.

Septa hexamerally arranged in typical micrabaciid fashion (see Cairns, 1982, fig. 1), usually resulting in 72 septa. S_{1-2} independent; S_3 repeatedly bifurcate to form the characteristic number of septa per half system. S_1 composed of 8 or 9 long, robust, inwardly curved spines. S_2 also consist of 5 or 6 robust, curved spines, including the tallest of the corallum. Septa low and solid, produced by a low calcareous "webbing" between adjacent spines. Septal canopies rudimentary. Columella a spiny mound in center of calice.

DISCUSSION.—*Leptopenus antarcticus* differs from the previously described *Leptopenus* species A by having a slightly concave base; a much lower GCD : H; robust septal spines; 72 septa; and a solid webbing between septal spines. It differs from *L. discus* in having a much lower GCD : H (i.e., a taller corallum); a concave base; inwardly curved septal spines; and rudimentary or absent septal canopies.

MATERIAL EXAMINED.—Types.

TYPES.—*Holotype: Eltanin* 2002, USNM 47483 (72°18'S, 177°35'E, Ross Sea, 2032–2035 m). *Paratypes: Eltanin* 598 (1) USNM 47480; *Eltanin* 1545 (2) USNM 47481; *Eltanin* 1926 (1) USNM 47479; *Eltanin* 2002 (2) USNM 81746; and *Eltanin* 2108 (37) USNM 47482.

Letepsammia Yabe and Eguchi, 1932

Stephanophyllia.—Moseley, 1881:198 [in part].—Duncan, 1885:173–174 [in part].—Wells, 1933:233 [in part].—Vaughan and Wells, 1943:145 [in part].—Wells, 1956:F390 [in part].—Chevalier, 1961:433 [in part].

Stephanophyllia (Letepsammia) Yabe and Eguchi, 1932c:58.

Letepsammia.—Squires, 1967:505.—Owens, 1986b:486–488.

DIAGNOSIS.—Costae thin, dentate ridges; broad marginal shelf present. Intercostal spaces much broader than costae and penetrated by large pores. Septa lamellar but highly porous, with complex dentition; usually 120 septa per corallum. Small simple synapticulae present uniting lower, outer edges of all septa. Columella spongy.

DISCUSSION.—The two species currently placed in *Letepsammia* were previously assigned to *Stephanophyllia,* albeit sometimes as a separate subgenus. As early as 1964, Squires (1964b) used the name *Letepsammia* as a genus name, and subsequent authors (e.g., Squires, 1965; Keller, 1977; Cairns, 1982, 1984a; Owens, 1984a,b, 1986a) also considered *Letepsammia* a separate genus. Owens (1986b), however, was the first to formally elevate *Letepsammia* to generic status.

According to Kühn (1967) and Keller (1977), *Letepsammia* is a morphological intermediate between *Leptopenus* and *Stephanophyllia.* Comparisons to *Leptopenus* and *Rhombopsammia* are made in the accounts of these genera (see also Key 2), and comparisons to *Stephanophyllia* are summarized by Owens (1986b). To reiterate, *Letepsammia* has a larger corallum, more highly perforate septa, more complex septal dentition, a thinner base, and a larger marginal shelf than *Stephanophyllia. Letepsammia* also has a porous columella and costae that are thinner than the intercostae.

Only one species is currently assinged to *Letepsammia: L. formosissima* (Moseley, 1876). A second, undescribed species, alluded to by Squires (1967) and Owens (1986b), occurs in the western Indian Ocean.

TYPE SPECIES.—*Stephanophyllia formosissima* Moseley, 1876, by original designation.

DISTRIBUTION.—*Pliocene-Pleistocene:* Japan. *Recent:* Indo-West Pacific; 128–828 m.

8. *Letepsammia formosissima* (Moseley, 1876)

FIGURE 1; PLATES 6*j*, 7*g–i*, 8*a–d*,

Stephanophyllia formosissima Moseley, 1876:561–562; 1881:201–204, pl. 4: fig. 11, pl. 13: figs. 6, 7, pl. 16: figs. 8–9.—Fowler, 1888:418–419, figs. 4–6.—Alcock, 1902a:39.—Vaughan, 1907:146–147, pl. 44: figs 2, 2a; 1919, pl. 14: figs. 4, 4a.—Boschma, 1923:144–145, pl. 10: fig. 31.—

Faustino, 1927:244–245, pl. 77: figs. 7, 8.—?Wells, 1958:263, pl. 1: figs. 1, 2.—Ralph and Squires, 1962:16.—Utinomi, 1965:249.

Stephanophyllia superstes Ortmann, 1888:160–161, pl. 6: fig. 5.—Owens, 1986b:487.

Not *Stephanophyllia formosissima* var.—Alcock, 1902a:39–40 [= *Rhombopsammia squiresi*].

Stephanophyllia complicata.—Alcock, 1902a:40 [in part: 2 of 3 specimens from *Siboga* 59].

?*Leptopenus discus*.—Dennant, 1906:162.

Not *Stephanophyllia formosissima*.—Van der Horst, 1927:7 [= undescribed species of *Letepsammia*].—Gardiner and Waugh, 1939:234 [= undescribed species of *Letepsammia*].—Boshoff, 1981:24 [= undescribed species of *Letepsammia*].—Zibrowius and Grygier, 1985:120.

Stephanophyllia (Letepsammia) formosissima.—Yabe and Eguchi, 1932c:58, 61–63, pl. 8: figs. 7, 8; 1942b:138–139.—Eguchi, 1968:C16–17, pl. C6: figs. 7–11, pl. C25: figs. 10–13, pl. C27: figs. 2, 3.

Stephanophyllia (Letepsammia) japonica Yabe and Eguchi, 1934:280–281, figs. 1–3; 1942b:156–157, pl. 12: figs. 8a–c.

?*Letepsammia* sp.—Squires, 1964b:3.—Squires and Keyes, 1967:21, pl. 4: fig. 1.

Letepsammia formosissima.—Squires, 1967:505.—Cairns, 1984a:6–7.—Owens, 1986b:486–487.

DESCRIPTION.—Corallum fragile, up to 38 mm in calicular diameter (largest syntype), with GCD:H ratios of 3.5–3.8. Base flat to slightly convex, with slightly upturned peripheral edges. Costae thin ridges, each 0.12–0.15 mm wide and 0.25–0.30 mm tall, bearing a roughly unilinear row of close-set cylindrical granules. Granules each about 0.11 mm tall and 0.09 mm in diameter, producing finely serrate costal edges. Twelve pairs of costae unite at epicenter, each pair corresponding to one half-system and meeting in a V, the apex of which is directed toward the epicenter. The costal arm of the V adjacent to the S_2 bifurcates three times, producing 4 terminal costae; the costal arm adjacent to the S_1 bifurcates five times, producing 6 terminal costae. These costal bifurcations correspond in origin to the overlaying septal pattern, such that every newly formed septum is flanked by costae (see Figure 1). Intercostal spaces broad, 0.50–0.55 mm near calicular edge of a large corallum, between which the bases of the septa can be seen. Transverse synapticulae about 0.10 mm in diameter unite the costae to their adjacent septa at regular intervals, producing elliptical pores about 0.10×0.15 mm in diameter in a paired or sometimes alternating arrangement across either side of a septum. The result is a very porous and lightweight corallum.

Septa arranged in typical micrabaciid fashion: the first two cycles of septa straight and nonbifurcate, the S_3 leading to multiple bifurcations. S_1 smallest of the septa and entirely independent, except for simple synapticulae uniting their lower, outer edges to adjacent $S_{3^{\mathrm{III}}}$. Because adjacent $S_{3^{\mathrm{II}}}$ and $S_{3^{\mathrm{III}}}$ slope away from the S_1, an open space is produced, which isolates the S_1 from other septa and produces the 6-rayed stellate pattern characteristic of this and most other micrabaciid genera. Inner part of S_1 extremely fragile and usually missing, even in well-preserved coralla, but, when intact, has a relatively vertical inner edge and an upper right-angle shoulder. Upper, inner S_1 septal edges have broad, lobulate septal teeth, which anastomose to adjacent septal lobes on the same septum via thin lateral processes (Plate 8*b*), resulting in the porous septal structure characteristic of the genus. Upper, outer S_1 septal edges have finer individualized septal spines. S_1 highly perforate but with increasing size they become more solid on their upper, inner edges. S_2 taller than S_1, bisecting a delta formed by flanking S_3 near the columella. Near the delta, S_2 bear 1 or 2 tall, slender, inwardly curved spines about 1.4 mm tall and 0.6 mm in diameter; S_2 highly perforate, with upper edges much like those of the S_1. S_3 bifurcate in a rather complex but consistent pattern (Figure 1). An S_3, before its first bifurcation, is horizontally short (2–3 mm long) but vertically quite tall, bearing 1–3 tall inwardly curved spines. Following the first bifurcation, the resultant $S_{3^{\mathrm{I}}}$ adjacent to the S_2 bifurcates three more times, resulting in 4 septa. The other $S_{3^{\mathrm{I}}}$, adjacent to the S_1, bifurcates four times resulting in 5 septa. The final composition of a half-system is thus: S_1, $S_{3^{\mathrm{III}}}$, $S_{3^{\mathrm{IV}}}$, $S_{3^{\mathrm{IV}}}$, $S_{3^{\mathrm{III}}}$, $S_{3^{\mathrm{III}}}$, $S_{3^{\mathrm{II}}}$, $S_{3^{\mathrm{IV}}}$, $S_{3^{\mathrm{IV}}}$, $S_{3^{\mathrm{III}}}$, S_2, which results in a corallum with 120 septa. Only one specimen, the largest examined (a syntype), had more septa (144). The 120-septa stage is usually attained at a calicular diameter of 16–17 mm. Simple synapticulae join the lower edges of all terminal S_3. Interestingly, $S_{3^{\mathrm{I}}}$ adjacent to S_1 are often shorter than their complement within the half-system, which, teleologically speaking, allows it more space to achieve its additional bifurcation. All septa highly porous, increasingly so in the higher cycle S_3. Septal faces sparsely granulated with low rounded elements 0.06–0.15 mm in diameter, not aligned in rows and most common on the lobulate septal teeth. In fully intact coralla, all septa extend a full 2 mm beyond their outer septal lobes in a very reduced fashion, the septa and alternating costae forming a thin marginal shelf around the calice. The costae project an additional 0.5 mm beyond the septal edges as a marginal shelf.

The columella ils a large, elongate, spongy mass, joined to the inner edges of the S_1 and S_2–S_3 deltas.

Aspects of septal trabecular structure and notes on soft parts of this species can be found in Owens (1986b), Moseley (1881), and Fowler (1888).

DISCUSSION.—Specimens of *L. formosissima* reported from the western Indian Ocean (Van der Horst, 1927; Boshoff, 1981) and the Red Sea (Gardiner and Waugh, 1939) are most likely the undescribed species alluded to by Squires (1967) and Owens (1986b). Three of Van der Horst's (1927) specimens of *S. formosissima* (USNM 82091) have been compared to the undescribed species, showing them to be identical. The undescribed species, specimens of which are also deposited at the NMNH, differs from *L. formosissima* in having a papillose columella, a more robust corallum, larger and coarser septal teeth, and more solid S_1.

Squires (1964b) implied that specimens of *Stephanophyllia* and *Letepsammia* reported from Tasmania (Wells, 1958) and New Zealand (Wells, 1958; Ralph and Squires, 1962), several of which were later figured (Squires and Keyes, 1967), represent a species distinct from *L. formosissima*. Some of the specimens Squires reported in 1964 (Squires, 1964b) are

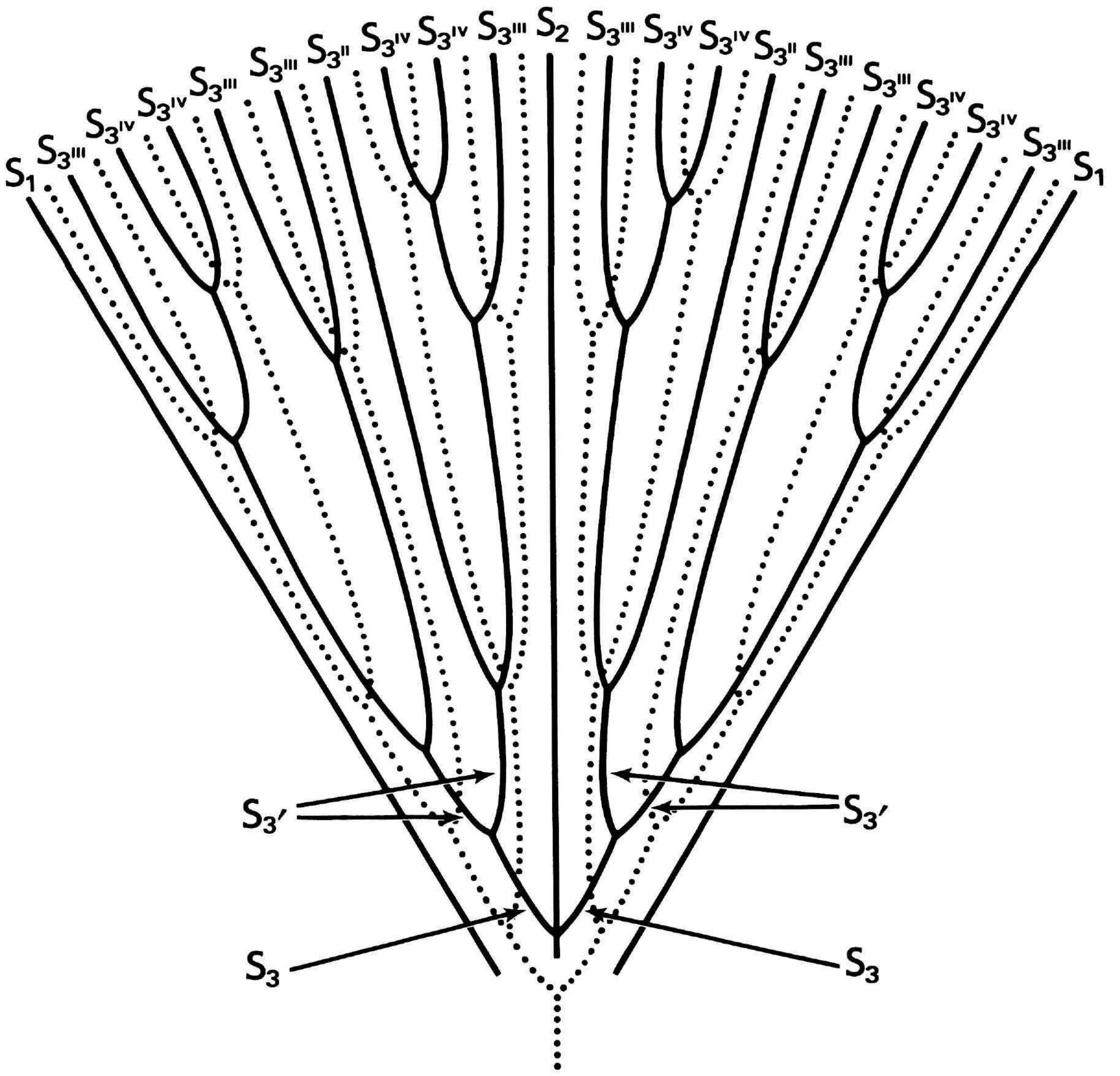

FIGURE 1.—Diagrammatic representation of one system of *Letepsammia formosissima*, a micrabaciid with 120 septa. (Solid lines represent septa; dotted lines, costae. Septa designated as explained in text.)

cataloged at the NMNH (USNM 81868, 81869) under a manuscript name. This fragmentary material, however, cannot be distinguished from small specimens of *L. formosissima*. Although not examined, Dennant's (1906) *Leptopenus discus* reported from off South Australia (165–457 m) is probably also *L. formosissima* (see Wells, 1958). Its bathymetric and geographic range and brief description suggest a stronger affinity to *Letepsammia* than to *Leptopenus*.

Although I have not personally examined the holotype of *S. superstes* Ortmann, 1888, Zibrowius (pers. comm.) has and suggested that it is a juvenile *L. formosissima*. Owens (1986b) also made the synonymy of *L. japonica* Yabe and Eguchi, 1934, with *S. superstes*, apparently based on the unpublished manuscript of Squires. If all three nominal species are synonymous, as implied above, then *L. formosissima* is the only valid species in the genus, having a relatively widespread distribution and known from the Pliocene to the Recent.

MATERIAL EXAMINED.—ALB-5178 (16) USNM 81884; ALB-5217 (2) USNM 81885; ALB-5278 (7) USNM 81882; ALB-5369 (45), USNM 81881, (2) AM G15244; ALB-5371 (14) USNM 81880; ALB-5376 (1) USNM 81883; ALB-5398 (1) USNM 81886; MUSORSTOM 3-96 (24) USNM 81879;

MUSORSTOM 3-108 (21) USNM 818877; MUSORSTOM 3-109 (17) USNM 81876; MUSORSTOM 3-143 (27) USNM 81878; syntypes of *S. formosissima* (5) BM; *Siboga* 95 (5) ZMA 1452a (*S. formosissima* of Alcock, 1902a); specimens reported by Vaughan (1907) and Cairns (1984a) from Hawaiian Islands, USNM. *Reference Material:* *Siboga* 284 (1) ZMA 1863 (*S. formosissima* var. of Alcock, 1902a); *S. formosissima* of Van der Horst (1927) (3) USNM 82091; *Letepsammia* n. sp. of Squires (1967) and Owens (1986b), USNM; *Ikatare* B-26 (fragments) USNM 81868 (*Letepsammia* sp. of Squires, 1964b).

TYPES.—*Stephanophyllia formosissima* is based on five syntypes deposited at the BM: 3 from *Challenger* 192 (BM 1880.11.25.155, 157) (Plate 7*g,h*), and 2 from *Challenger* 209 (BM 1880.11.25.156) (Plate 6*j*). *Type Locality:* Philippines and Indonesia, 174-236 m.

The holotype of *S. superstes* is deposited at the Strasbourg Zoological Museum. *Type Locality:* Sagami Bay, Japan, 183-366 m.

The "numerous" syntypes of *S. japonica* are presumably deposited at the TIUS. *Type Locality:* RyuKyu limestone of Kikai-jima, RyuKyu Islands, Plio-Pleistocene.

DISTRIBUTION.—*Plio-Pleistocene:* Japan (Yabe and Eguchi, 1934). *Recent:* Southern Japan (Yabe and Eguchi, 1942b); Philippines; Indonesia (Banda Sea, Timor Sea, Flores Sea (Alcock, 1902a)); ?New Zealand (Ralph and Squires, 1962); ?Australia (Dennant, 1906); ?Tasmania (Wells, 1958); Hawaiian Islands (Cairns, 1984a); 97-470 (?828) m; 9.3°-21.7°C.

Rhombopsammia Owens, 1986

"Undescribed genus."—Squires, 1967:505.
New Genus A.—Owens, 1984a:521.
Rhombopsammia.—Squires, ms:9 [unpublished].
Rhombopsammia Owens, 1986a:249-250.

DIAGNOSIS.—Costae thin, dentate ridges; intercostal spaces broader than costae, penetrated by large pores. Septa lamellar and imperforate; 96-144 in number. Small simple synapticulae unite lower, outer edges of septa. Marginal shelf broad. Columella spongy.

DISCUSSION.—Specimens of *Rhombopsammia* were first recognized by Squires (1967), but the genus was not formally described until 1986 (Owens, 1986a). Owens suggested that *Rhombopsammia* was morphologically, but not necessarily evolutionarily, intermediate between *Letepsammia* and *Stephanophyllia*, with a stronger affinity to *Letepsammia*. Both *Rhombopsammia* and *Letepsammia* have thin bases with narrow, dentate costae; broad intercostal spaces; prominent marginal shelves; and a spongy columella. They differ primarily in the degree of septal porosity: *Rhombopsammia* having virtually solid septa, *Stephanophyllia* having basally perforate septa (see Key 2).

Only two species of *Rhombopsammia* have been described: *R. squiresi* Owens, 1986a, and *R. niphada* Owens, 1986a; however, Squires (1967) alluded to a third species from the Pliocene of Italy, specimens of which have not been located. Characters used to distinguish the two species include number of septa, structure of the marginal shelf, and shape of corallum base.

TYPE SPECIES.—*Rhombopsammia squiresi* Owens, 1986, by original designation.

DISTRIBUTION.—*?Pliocene:* Italy. *Recent:* China and Philippine Sea; 424-1401 m.

9. *Rhombopsammia squiresi* Owens, 1986

PLATES 8*e-j*, 9*a-c*

Stephanophyllia formosissima var.—Alcock, 1902a:39-40.
"Undescribed genus."—Squires, 1967:505 [in part].
Rhombopsammia waldmanae.—Squires, ms:13 [not published].
Rhombopsammia squiresi Owens, 1986a:250-252, figs. 1 a-d, 2a.

DESCRIPTION.—Corallum robust, up to 30.6 mm in calicular diameter (ALB-5513), with GCD:H ratios of 2.25-2.41. Base convex, basal angle as low as 127°. Costae of variable width depending on distance from epicenter and recency of origin. Central 6-8 mm of major costae bear a medial, unilinear series of coarse, rounded granules, each 0.08-0.10 mm in diameter (equivalent to the costal width). Beyond 8 mm from epicenter, costal granules become staggered or random in arrangement, and at the calicular edge (in the vicinity of the marginal shelf) the costae become poorly defined and rather porous. Costal arrangement and bifurcations similar to that of *Stephanophyllia fungulus* (Figure 3): 6 C_1 originate at epicenter and eventually divide into 96 terminal costae. Intercostal width much greater than that of costae, 0.32-0.41 mm, and regularly traversed by synapticulae about 0.11 mm in diameter, producing a series of elliptical pores 0.15-0.25 mm in greater diameter.

Septa arranged in typical micrabaciid fashion: S_{1-2} nonbifurcate, S_3 having multiple bifurcations in a consistent pattern similar to that of *S. fungulus* (Figure 3), resulting in 96 septa. S_1 composed of up to 60 fine, closely spaced trabeculae alternating in expression on each side of the septum, the alternation giving the septum a sinuous margin. Inner edges of S_1 vertical; upper edges rounded; outer edges vertical to slightly undercut, producing a sharp boundary with marginal shelf. The 2 principal S_1 are slightly smaller than 4 lateral S_1. S_2 similar in shape to S_1, sometimes extending inward from the delta as a short lamella or series of 3 or 4 coarse spines. S_3 very short, less than 1 mm, serving mainly as a point of origin for the S_3'. S_3' about 2.5 mm long and are the tallest of the septa, originating relatively close to the S_2-S_3 delta. Septal faces covered by low triangular granules (8-10 µm in height) aligned in discontinuous, slightly elevated rows following the trabeculae. All septal edges are entire, without septal spines. Synapticulae extremely reduced, only visible in a broken corallum at the lower, outer septal edges of the terminal S_3 bifurcations. Septal perforations present but rare and not arranged in a regular manner, occurring only at septal bifurcations and at the bases of higher order S_3. Marginal shelf well developed, extending up to 3.5 mm beyond the lamellar septa. On marginal shelf, each septum, regardless of cycle, transforms from a thin lamella, about 0.10 mm thick, to a broad, flat, spongy mass about 0.75 mm wide, separated from one another by narrow septal furrows 0.22-0.25 mm wide.

Fossa deep, formed by the vertical inner edges of the S_1 and S_2-S_3 deltas. Columella elongate in alignment with the 2 principal S_1, composed of a mass of fused trabeculae.

DISCUSSION.—*Rhombopsammia squiresi* is easily distinguished from the only other species in the genus, *R. niphada*, by its broader costae; maximum number of 96 septa per corallum; well-developed marginal shelf with broadened and flattened marginal septa (unique); and strongly convex base. It is also considerably more robust than *R. niphada*.

MATERIAL EXAMINED.—Types; *Siboga* 284 (1 specimen preserved in alcohol) *S. formosissima* var. of Alcock (1902a), ZMA 1863, Plate 8*h*.

TYPES.—*Holotype:* ALB-5423, USNM 72797. *Paratypes:* ALB-5424 (1 embedded specimen and 1 thin section) USNM 72798; ALB-5425 (3 fragments) USNM 72800; ALB-5513 (1) USNM 72799. *Type Locality:* 9°38′30″N, 121°11′E (off Cagayan Island, Philippines), 929 m.

DISTRIBUTION.—*Recent:* Philippines (off Cagayan Island, Sulu Sea; Iligan Bay, Mindanao); Timor Sea (Alcock, 1902a); 622-1401 m; 9.7°-11.6°C.

In the original description, Owens (1986a) reported a paratype from ALB-5427. The original label for this specimen is worn and ambiguous, being equally well deciphered as ALB-5427 or ALB-5429. Because ALB-5429 represents a depth of capture of 1401 m (considerably more consistent with the range of the other specimens (906-930 m) than that of ALB-5427, which was made at 68 m), it is suggested, based on this circumstantial evidence, that the correct station for Owens's paratype from ALB-5427 is actually ALB-5429. The shallowest record for this species is thus changed from 68 to 622 m.

10. *Rhombopsammia niphada* Owens, 1986

FIGURE 2; PLATES 9*d–i*, 10*a,b*

"Undescribed genus."—Squires, 1967:505 [in part].
New Genus A.—Owens, 1986a:521, fig. 3.
Rhombopsammia niphada.—Squires, ms:13 [unpublished].
Rhombopsammia niphada Owens, 1986a:252–255, figs. 2b, 3a–d.

DESCRIPTION.—Corallum fragile, up to 41 mm in calicular diameter (USNM 72805), with GCD:H ratios of 2.8–4.0. Base usually flat, but may be slightly concave or convex. Costae and intercostal architecture very similar to that of *R. squiresi*. Costae tall (0.15-0.20 mm), thin (0.06-0.07 mm) ridges, each bearing a unilinear row of coarse rounded teeth about 0.08 mm in height and 0.06 mm in diameter, producing a finely serrate costal edge. Six pairs of costae unite at epicenter, each pair corresponding to one system and meeting in a V, the apex of which is directed toward the epicenter. Each arm of the V bifurcates 11 times, resulting in 12 costae per half-system (Figure 2). Following the first bifurcation of an arm, the segment nearest the S_2 bifurcates three more times, whereas the segment adjacent to the S_1 bifurcates seven times. This is slightly different from the pattern illustrated by Owens (1986a, fig. 2b). A total of 144 costae result, 24 per system. Intercostal width considerably greater than costal width, about 0.44 mm, and, as in *R. squiresi*, each intercostal space is bisected by a septal base. Septal bases resemble costae in thickness and arrangement but are easily distinguished by their recessed position and nonserrate margin. Slender cylindrical synapticulae about 0.10 mm in diameter join costae to adjacent septal bases, producing a double series of intercostal pores. These pores are round to elliptical in shape, 0.10–0.40 mm long and about 0.10 mm wide, producing a very porous, lightweight corallum base.

Septa arranged in typical micrabaciid fashion, attaining a full complement of 144 septa at a calicular diameter of 27-29 mm. S_1-$S_{3'}$ are very similar in size and shape to those of *R. squiresi*, except that the outer edges of all septa slope gradually toward the marginal shelf, not meeting the base at a sharp boundary. There is variation regarding septal face granulation. The septal faces of the holotype and paratypes from ALB-4911 all bear tall, blunt or Y-shaped granules that are not arranged in linear sequence. Septal faces of all other specimens examined are relatively smooth, bearing lines of very fine granules (7-9 µm in diameter) corresponding to the septal trabeculae. Upper, outer edges of larger septa, inward from the marginal shelf, bear a series of short, coarse trabecular spines, extending about 0.10 mm above the septum and covered by granules 35-40 µm in diameter (Plate 10*b*). S_3 bifurcate in a complex but consistent pattern (Figure 2). Following the first bifurcation of an S_3, the resultant $S_{3'}$ adjacent to an S_2 is slightly longer than its counterpart adjacent to the S_1 and bifurcates three times resulting in 4 septa. The shorter $S_{3'}$ adjacent to the S_1 bifurcates six times, resulting in 7 septa. The final composition of a half-system is thus: S_1, $S_{3^{\mathrm{III}}}$, $S_{3^{\mathrm{IV}}}$, $S_{3^{\mathrm{IV}}}$, $S_{3^{\mathrm{III}}}$, $S_{3^{\mathrm{V}}}$, $S_{3^{\mathrm{V}}}$,$S_{3^{\mathrm{IV}}}$, $S_{3^{\mathrm{II}}}$, $S_{3^{\mathrm{IV}}}$, $S_{3^{\mathrm{IV}}}$, S_2, and the mirror image of this order for the complementary half-system in a system (Figure 2). Synapticulae are simple and, in an undamaged corallum, can usually be seen uniting the lower, outer septal edges, including those of the S_1. Septal perforations occur sparingly at septal bifurcations and at bases of higher-order S_3. Marginal shelf up to 3 mm wide but very delicate and often broken from corallum. All septa extend over the marginal shelf at a reduced height of about 0.6 mm but of the same septal width (i.e., about 0.12 mm thick).

Fossa deep, as in *R. squiresi*, enclosing an elongate, spongy columella aligned with the two principal S_1. In some specimens (e.g., holotype; specimen from Mi Sake), the columella is a more solid fusion with several solid trabeculae aligned on the axis of the principal septa.

DISCUSSION.—Comparisons to *R. squiresi* are made in the account of that species; however, additional comparisons are

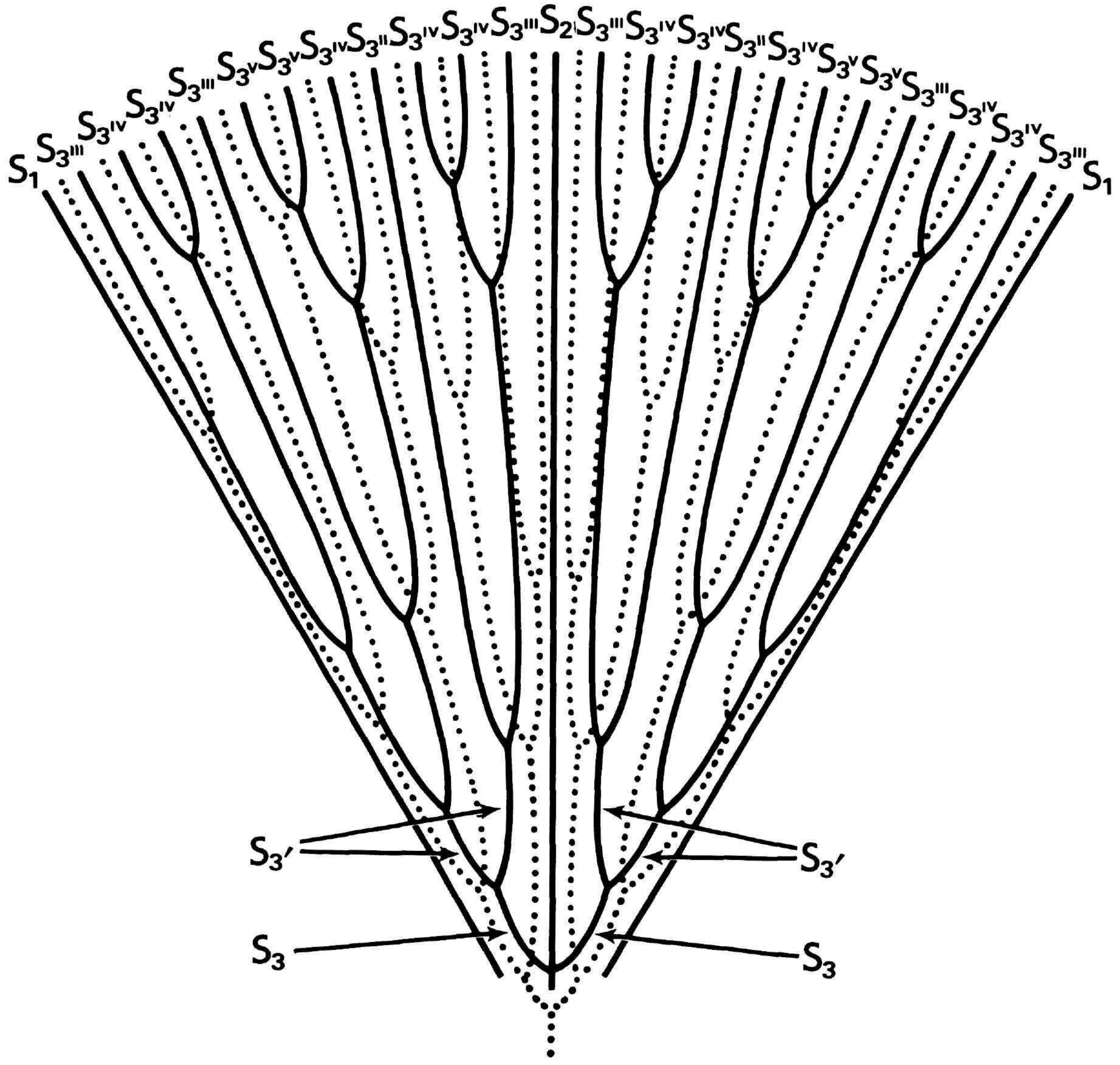

FIGURE 2.—Diagrammatic representation of one system of *Rhombopsammia niphada*, a micrabaciid with 144 septa. (Solid lines represent septa; dotted lines, costae. Septa designated as explained in text.)

appropriate to *L. formosissima*. As Owens (1986a) noted, *L. formosissima* and *R. niphada* have many similarities, including virtually identical costal and intercostal architecture; similar marginal shelf and columella; similar corallum fragility; and tendency to attain 144 septa in large specimens. The main differences are that *L. formosissima* has highly perforate septa and tall septal spines, both considered to be generic level differences. Nonetheless, based on the similarities of the two species, Owens suggested that *R. niphada* might be viewed as a morphological intermediate between *Letepsammia* and *Rhombopsammia*, the latter epitomized by the type species *R. squiresi*.

MATERIAL EXAMINED.—Types; Mi Sake, Japan (2) USNM 81867.

TYPES.—*Holotype:* ALB-4911, USNM 72802, Plate 9*d,e*. *Paratypes:* ALB-4911 (3) USNM 72801; ALB-5283 (3) USNM 72804; ALB-5348 (3) USNM 72803; unknown ALB sta (3) USNM 72805. *Type Locality:* 31°38′30″N, 129°19′E (East China Sea, off Kyūshū, Japan), 715 m.

DISTRIBUTION.—*Recent:* Southern Kyūshū, Japan (Owens, 1986a); Philippines (off Manila, Luzon; Sulu Archipelago); 424–715 m; 8.2°–11.9°C.

Stephanophyllia Michelin, 1841

Stephanophyllia Michelin, 1841:484; 1841-1843:32 [in part: not *S. italicus* (= *Deltocyathus*)].—Milne Edwards and Haime, 1848:92 [in part]; 1857:108-109 [in part].—Duncan, 1885:173-174 [in part].—Wells, 1933:233.—Vaughan and Wells, 1943:145-146 [in part: not *Letepsammia* or *Stephanopsammia*].—Alloiteau, 1952:675 [in part].—Wells, 1956:F390 [in part: not *Letepsammia* or *Stephanopsammia*].—Chevalier, 1961:433-434; 1987:696, fig. 402, 2a-b.

Stephanophyllia (Stephanopsammia) Yabe and Eguchi, 1932c:58 [in part: *S. neglecta*].

Stephanophyllia (Stephanophyllia).—Yabe and Eguchi, 1932c: 58.

Micrabacia.—Vaughan and Wells, 1943:145 [in part: Recent record of *S. fungulus*].—Wells, 1956:F390 [in part: Recent records].

DIAGNOSIS.—Costae granular, equal to or thicker than intercostal spaces; base thick; marginal shelf narrow. Septa lamellar, perforate only at base; 96 septa. Synapticulae large and compound, firmly uniting outer edges of septa. Columella solid, compact, and often lenticular.

DISCUSSION.—The generic synonymy of *Stephanophyllia* is complicated by the persistent inclusion of *Micrabacia, Letepsammia, Stephanopsammia,* and even *Deltocyathus* in this genus. However, with the elevation of the subgenus *Letepsammia* to generic rank (Owens, 1986a), the attribution of all Cretaceous to Eocene micrabaciid species to either *Micrabacia* or *Stephanopsammia* (Squires, 1967), and the synonymy of all Miocene to Pliocene European species (e.g., *S. imperialis, S. nysti*) as *S. elegans* (see Chevalier, 1964), the number of valid species of *Stephanophyllia* reduces to four: *S. elegans* (Bronn, 1837); *S. complicata* Moseley, 1876; *S. fungulus* Alcock, 1902; and *S. neglecta* Boschma, 1923 (Table 2). Characters of diagnostic value in distinguishing species include shape of columella; size and shape (GCD:H) of corallum; shape, spination, and granulation of septa; and, to a lesser degree, costal ornamentation and presence of a marginal shelf.

Stephanophyllia is similar to both *Letepsammia* and *Rhombopsammia*, as discussed in the accounts of those genera and in Key 2. To reiterate, *Stephanophyllia* differs from *Letepsammia* in having less perforate septa; a compact, solid columella; and broader, granular costae. It differs from *Rhombopsammia* in having fenestrate septal bases; a very narrow marginal shelf; and costae that are greater than or equal to the thickness of the intercostal space.

TYPE SPECIES.—*Fungia elegans* Bronn, 1837, by original designation.

DISTRIBUTION.—*Miocene to Pliocene:* Northern Europe, Mediterranean. *Pleistocene:* Japan. *Recent:* Indo-West Pacific; 15-635 m.

Wells (1956) cited the Cretaceous to Recent as the stratigraphic range for *Micrabacia* because he considered *S. fungulus* to belong to *Micrabacia* (see Wells, 1933). Removing *S. fungulus* from *Micrabacia* restricts the stratigraphic range of *Micrabacia* from the Cretaceous to the Eocene.

11. *Stephanophyllia fungulus* Alcock, 1902

FIGURE 3; PLATES 10*c-k*, 11*a,b*

Stephanophyllia fungulus Alcock, 1902a:40, pl. 5: figs. 35 a,b.—Faustino, 1927:245-246, pl. 77: figs. 9-11.—Yabe and Eguchi, 1932b:443; 1932c:58, 60-61, pl. 8: figs. 1-6, pl. 9: figs. 1-8; 1934:278.—Gardiner and Waugh, 1939:234.—Yabe and Eguchi, 1942b:138.—Squires, 1967:506.—Van Soest, 1979:109.

Stephanophyllia complicata.—Alcock, 1902a:40 [in part: 1 of 3 specimens from *Siboga* 59].

Micrabacia fungulus.—Vaughan and Wells, 1943:312, pl. 20: figs. 1a,b.—Uchida, 1963:17-21, pl. 2: figs. 1-3.

DESCRIPTION.—Corallum robust, up to 15.6 mm in calicular diameter (ALB-5586), with GCD:H ratios of 2.1-2.6. Base variable in shape, ranging from flat to slightly concave or

TABLE 2.—Comparisons of the four known species of *Stephanophyllia*.

Characters	*S. fungulus* Alcock, 1902	*S. neglecta* Boschma, 1923	*S. complicata* Moseley, 1876	*S. elegans* (Bronn, 1837)
Maximum calicular diameter (mm); D : H	15.6; 2.1-2.6	11.2; 2.8-3.2	17.0; 2.7	33.0; 1.5-1.7
Shape of base; thickness	flat, slightly concave or convex; thick	flat, slightly concave to very convex (138° basal angle); thin	flat; thin	flat to slightly concave; thin
Costal ornamentation	large medial granules yield to two rows of smaller lateral granules	same as for *S. fungulus*	same as for *S. fungulus*	unilinear row of granules
Septal edges	straight	straight	sinuous	sinuous
Septal face granulation	wide-based, equilateral-triangle-shaped granules	blunt to clavate cylindrical granules	narrow-based, isosceles-triangle-shaped granules; spiny	faces ridged; granules, if any, too worn to distinguish
Synapticulae	elongate	variable: round, elliptical, or quite elongate	round to elliptical in cross section	round to elliptical in cross section
Marginal shelf	absent	absent	narrow	narrow
Columella	lenticular to rectangular in cross section; massive	variable: usually papillose, sometimes lamellar	thin lamella	papillose or aligned trabeculae
Distribution	Pleistocene: Japan. Recent: Indo-West Pacific; 15-635 m	Recent: Indonesia; 49-555 m	Recent: Indonesia and Saya de Malha, Indian Ocean; 229-397 m	Miocene to Pliocene: Europe

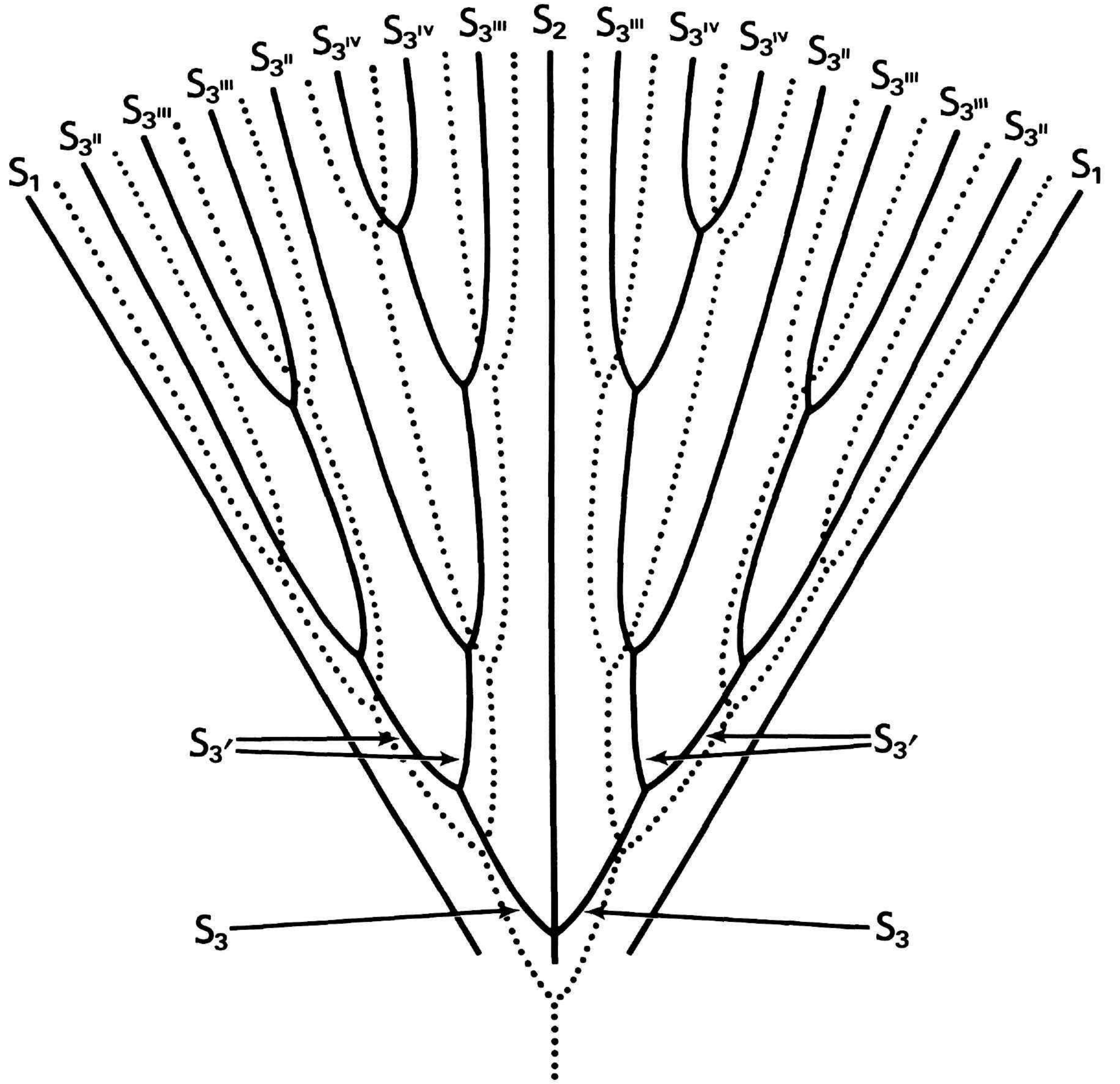

FIGURE 3.—Diagrammatic representation of one system of *Stephanophyllia fungulus*, a micrabaciid with 98 septa. (Solid lines represent septa; dotted lines, costae. Septa designated as explained in text.)

convex, but the peripheral edges are always slightly upturned. Costae equal in width (0.14–0.21 mm near calicular edge), having rounded edges. Costal ornamentation complex, the proximal 3.2–3.7 mm of each costa covered by a medial series of low, closely spaced granules, each about 0.14 mm in diameter and corresponding to the intersection of each costa and transverse synapticulae. These coarse granules are flanked on both sides by a row of much smaller slender granules about 0.02 mm in diameter and 0.03 mm tall. With increasing distance from the epicenter, the coarse granules of the medial row diminish in size and the lateral slender granules increase in size until, at a calicular radius of about 3.5 mm, the middle part of the costa is flat and the lateral edges bear spines about 0.04 mm in diameter and 0.10 mm tall. This ornamentation persists to the calicular edge. Costae (base) robust, increasing in thickness toward calicular edge, where it may be up to 1.0 mm vertical thickness. Six costae originate at the epicenter and quickly bifurcate twice, resulting in four costae per system. Each of these four costae also bifurcates twice at different but consistent distances from the epicenter, complementing the adjacent septal bifurcations above, resulting in 16 terminal costae per system (Figure 3). Intercostal spaces narrow, 0.10 mm wide near calicular edge of a larger corallum, and traversed in a regular manner by massive synapticulae 0.18–0.25 mm wide and as tall as the costae that it joins. Parallel transverse synapticulae spaced such that a single series of round pores about 0.18 mm in diameter are formed along an intercostal area.

Septa arranged in typical micrabaciid fashion: the first two cycles of septa straight and nonbifurcate, the S_3 having multiple bifurcations and meandering to calicular edge. S_1 smallest of septa, entirely independent of other septa, except for synapticulae. S_1 composed of 14-16 trabeculae (depending on calicular diameter), each trabeculum projecting up to 0.3 mm as a tall, transversely flattened spine, the innermost spines the largest and inclined toward the columella. At the S_3-S_2 delta stands one massive incurved septal spine. The S_2 and all S_3 also bear slender septal spines on their upper, inner margins. S_3 bifurcate in a complex but consistent pattern (Figure 3). Within a half-system, an S_3 splits into two equal length S_3^{I}: the S_3^{I} adjacent to the S_2 bifurcates three more times, resulting in 4 septa; the S_3^{I} adjacent to the S_1 bifurcates only twice, resulting in 3 septa. The bifurcations occur in a definite sequence resulting in arms of differential lengths, and a typical half-system composed of: S_1, S_3^{II}, S_3^{III}, S_3^{III}, S_3^{II}, S_3^{IV}, S_3^{IV}, S_3^{III}, S_2, and a corallum of 96 septa. The 96-septum stage is usually attained at a calicular diameter of 8-10 mm. Massive, elongate compound synapticulae up to 1.0 mm long and 0.3 mm wide unite all adjacent septa, often extending to the upper septal edges. Synapticulae aligned in rows corresponding to trabeculae on the outer half of each septal face, and, along with the thick base, produce a very solid corallum. Aligned, elongate septal granules (= vepreculae), similar to synapticulae in size and orientation, occur on the inner septal faces. Septa perforate on lower edges and at points of bifurcation (Plate 11*b*), visible only in a damaged corallum. Marginal shelf not present; however, costae project about 0.2 mm beyond the septal outer edges.

Fossa shallow, containing a prominent, solid columella, lenticular to rectangular in cross section and aligned with the two principal S_1.

DISCUSSION.—*Stephanophyllia fungulus* is similar to *S. neglecta* in costal ornamentation, septal arrangement, septal spination, and in lacking a marginal shelf, but can be distinguished by its massive, lenticular columella, thick corallum base, and broad, triangular septal granules (Table 2). It also attains a larger size and has a lower GCD:H ratio than *S. neglecta.*

MATERIAL EXAMINED.—ALB-5311 (5) USNM 81855; ALB-5312 (5) USNM 81857; ALB-5586 (3) USNM 81856; near Kamikatetsu, Kikai-jima, Ryukyu Islands (Pleistocene) (3) USNM 81858; syntypes (5) ZMA, Plate 10*c-f; Siboga* 59 (1) ZMA 1453b (*S. complicata* of Alcock, 1902a), Plate 10*i-k;* JM 149 (1) BM 1939.7.13.94 (Gardiner and Waugh, 1939); off Natal (1) BM 1939.7.20.408, Plate 10*h*.

TYPES.—Five syntypes, all collected from *Siboga* 100, are deposited at the ZMA (1321) (Van Soest, 1979). *Type Locality:* 6°11'N, 120°37.5'E (Sulu Archipelago), 450 m.

DISTRIBUTION.—*Pleistocene:* Ryukyu Islands, Japan (Yabe and Eguchi, 1932b). *Recent:* East China Sea off southwest Kyūshū (Yabe and Eguchi, 1942b); South China Sea off Hong Kong; Philippines (Sulu Archipelago); Celebes Sea off Sabah; Chagos Archipelago (Gardiner and Waugh, 1939); off Natal, South Africa; 15-635 m; 6.7°-21.2°C.

12. *Stephanophyllia neglecta* Boschma, 1923

PLATE 11*c-j*

Fungia patella.—Van der Horst, 1921:57 [in part: *Siboga* 260].
Stephanophyllia neglecta Boschma, 1923:144-145, pl. 10: figs. 28-30.—Yabe and Eguchi, 1932c:58.—Squires, 1967:505, 506 (90-140 m).—Van Soest, 1979:109.

DESCRIPTION.—Corallum moderately robust, up to 11.2 mm in calicular diameter (ALB-5213), with GCD:H ratios of 2.8-3.2. Base usually flat but may range from slightly concave to convex (see "Discussion"); peripheral edges not upturned. Costae equal in width (about 0.17 mm wide near calicular edge) with squared-off edges. Costal ornamentation and arrangement similar to that of *S. fungulus*. Intercostal spaces narrow, about 0.10 mm wide near calicular edge, traversed in a regular manner by synapticulae about 0.18 mm wide, producing a series of elliptical pores about 0.14 mm in greater diameter.

Septa arranged in typical micrabaciid fashion: the first two cycles (S_{1-2}) straight and nonbifurcate, the S_3 having multiple bifurcations in a well-defined sequence identical to that of *S. fungulus* (Figure 3), resulting in 96 septa at a calicular diameter of ≥6.8-7.0 mm. S_1 composed of 16-18 trabeculae, each trabeculum projecting as a tall spine up to 0.5 mm above the septal edge, the innermost spines the tallest and inclined toward the columella. Spines of all septa strongly flattened in a plane perpendicular to septal plane. S_2 composed of 15-16 trabeculae, and similar in size and shape to the S_1, the third or fourth trabecular spine (in the vicinity of the S_{2-3} delta) always the tallest. S_3, proper, quite short, bearing only 2 tall septal spines; S_3^{I} bears about 3 septal spines. Septa and septal spines of all septal cycles are approximately the same size and shape at equivalent distances from the columella, the inner edges of S_{1-2} gently sloping toward the columella. Upper, inner septal faces, as well as septal spines, of all septa bear tall slender granules up to 0.21 mm tall. Synapticulae round to slightly elliptical in cross section (see "Discussion"), about 0.21 mm in diameter, and unite all adjacent septa, and are particularly apparent between: the S_1 and their adjacent S_3^{I} and S_3^{II}, and the S_2 and their adjacent S_3^{III}. Septa imperforate except for the lines of junction of bifurcating septa and where the lower septal faces meet the costae. Marginal shelf absent; however, costae project about 0.2 mm beyond septal edges.

Fossa moderately deep, containing a columella of variable structure. Usually the columella is composed of an elliptical field of twisted, fused trabeculae; however, in small specimens (e.g., calicular diameters less than 4 mm) it is often lamellar, and even in larger specimens it may be composed of several aligned trabeculae that fuse into a lamellar structure.

DISCUSSION.—*Stephanophyllia neglecta* is compared to *S. fungulus* in the account of the latter species and in Table 2. To reiterate, *S. neglecta* has a smaller, more delicate corallum with a less massive base, the peripheral edges of which are not upturned. Its columella is papillose instead of lamellar and it has more finely spinose septal edges. *Stephanophyllia neglecta* differs from *S. complicata* (see Plate 12*a,b*) in having a smaller corallum, a papillose columella (vs. lamellar), and relatively straight septa (not sinuous, as in *S. complicata*). Although both species have 96 septa, the sinuosity of the higer order S_3 of *S. complicata* is such that the branching pattern is usually obscure (complicated) and difficult to trace.

Forty-seven specimens from two MUSORSTOM stations (3-91, 3-102) are consistently different from the other specimens in two characters: their bases are convex (basal angle as low as 138°) and their synapticulae are massive and elongate, up to 1 mm long and 0.2 mm wide. Some of these synapticulae, which parallel the trabeculae, are almost continuous from the septal edge to the base, producing a firm, robust corallum. At first considered a new species, I now regard them as an ecological variation of *S. neglecta*, all other characters being identical.

MATERIAL EXAMINED.—ALB-5178 (19) USNM 81860; ALB-5213 (186) USNM 81863; ALB-5426 (3) USNM 81861; ALB-5569 (1) USNM 81862; MUSORSTOM 2-33 (1) USNM 81866; MUSORSTOM 3-102 (10) USNM 81859, (36) MNHNP; MUSORSTOM 3-91 (1) USNM 81865; MUSORSTOM 3-131 (1) USNM 81864; syntypes of *S. neglecta* (3) ZMA. *Reference Specimens:* Syntypes of *S. complicata* (2) BM 1880.11.25.155a-b (Plate 12*a,b*); USGS 24918 (2) USNM 71839 (*S. japonica* of Wells, 1984, = *?S. complicata*).

TYPES.—Three syntypes of *S. neglecta*, all collected at *Siboga* 260 (Plate 11*c-e*), are deposited at the ZMA (1102). *Type Locality:* 5°36.5′S, 132°55.2′E (north point of Nehu Jaan, Kei Islands), 90 m.

DISTRIBUTION.—*Recent:* Philippines (off Luzon, Sibuyan Sea, Sulu Archipelago, off Palawan); Kei Island, Moluccas (Boschma, 1923); 49–555 m.

Suborder CARYOPHYLLIINA Vaughan and Wells, 1943

Superfamily CARYOPHYLLIICAE Dana, 1846

DIAGNOSIS.—Caryophylliina with septothecal wall.

Family CARYOPHYLIIDAE Dana, 1846

DIAGNOSIS.—Mostly solitary, ahermatypic corals. Columella trabecular, spongy, or absent, rarely lamellar. Stereome not heavy.

Subfamily TURBINOLIINAE Milne Edwards and Haime, 1848

DIAGNOSIS.—Corallum small, solitary, and free, being completely invested by polyp. Corallum trochoid, cuneiform, or conical. Intercostal grooves deeply incised from point of origin to calice. Thecal pores present in some genera. Septa moderately to highly exsert. Endotheca absent. Ahermatypic, usually found at continental shelf and slope depths (50–400 m).

DISCUSSION.—Milne Edwards and Haime (1848:235) established the subfamily Turbinoliinae for a polyphyletic assemblage of 11 genera, distinguished from the only other subfamily in the Turbinoliidae by lacking pali. Some of the genera originally included in this subfamily have been transferred to the Flabellidae, Desmophyllinae, and Caryophylliinae, only three still remaining in the Turbinoliinae. Duncan (1885), in his unique classification of the Scleractinia, considered the Turbinoliidae to be composed of three subfamilies. One of these, the "Turbinoliidae simplices" contained seven alliances (?equivalent to supergenera), two of which, the Placotrochoida and Turbinolida, contained what are now considered to be the Turbinoliinae. He did not consider the presence or absence of pali as an important character at the subfamily level. Vaughan and Wells (1943) redefined the subfamily to include those genera having their corallum entirely covered by the polyp, which results in deep, continuous intercostal grooves. They included 14 genera in the subfamily, their generic key employing characters such as columella type and presence or absence of pali as key discriminating characters. Alloiteau (1952) elevated the subfamily back to family status and created two subfamilies, Turbinoliinae and Conocyathinae, the former lacking pali, the latter having pali, reiterating the criterion used by Milne Edwards and Haime (1848) for the division of the taxon. Wells (1956), in a revision of the turbinoliid genera, followed the classification of Vaughan and Wells (1943) but included 16 genera in the subfamily. Three new Tertiary genera were subsequently described by Alloiteau and Tessier (1958); one new Cretaceous genus, *Wellsotrochus*, by Squires (1960b); and one new Recent genus, *Oryzotrochus*, by Wells (1959), the latter including a key to seven of the genera. Chevalier (1987) listed 16 genera and one subgenus in the family. Cairns (1988) described another new genus, *Cryptotrochus*, and two more are proposed herein. A key to the 23 valid turbinoliid genera is provided (Key 3). The key emphasizes the distinction between those genera with perforate and imperforate theca, this character being proposed as a more conservative phylogenetic division among the genera than the presence or absence of pali. Other characters used to distinguish genera include presence or absence of pali, arrangement of pali and paliform lobes, and corallum shape.

Species of the subfamily Turbinoliinae are common in moderately deep-water Tertiary deposits, especially those from the Miocene of South Australia, the Eocene of the United States, and the Eocene to Oligocene of Europe. Of the 23 genera, 8 are exclusively fossil, and most of the other genera have fossil representatives. Of the approximately 122 valid species, 92 are exclusively fossil, some of the Recent species also having extensive fossil records. Although the average number of described species per genus is about five, most of the genera have less than that number, 9 genera being monotypic. Only three genera have high species diversities: *Sphenotrochus*—33 species, *Turbinolia*—20+ species, and *Platytrochus*—15 species.

The genera of the subfamily can be further subdivided into three groups: (1) those genera with imperforate theca and pali or paliform lobes present (10 genera): *Tropidocyathus* Milne Edwards and Haime, 1848; *Dunocyathus* Tenison-Woods, 1878; *Notocyathus* Tenison-Woods, 1880; *Kionotrochus* Dennant, 1902; *Peponocyathus* Gravier, 1915; *Idiotrochus* Wells, 1935; *Coronocyathus* Alloiteau and Tessier, 1958; *Monticyathus* Alloiteau and Tessier, 1958; *Cryptotrochus* Cairns, 1988; and *Thrypticotrochus*, new genus, (2) those genera with imperforate theca and no pali (8 genera): *Sphenotrochus* Milne Edwards and Haime, 1848; *Platytrochus* Milne Edwards and Haime, 1848; *Koilotrochus* Tenison-Woods, 1878; *Holcotrochus* Dennant, 1902; *Dominicotrochus* Wells, 1937; *Sphenotrochopsis* Alloiteau and Tessier, 1958; *Oryzotrochus* Wells, 1959; and *Wellsotrochus* Squires, 1960, and (3) those genera with perforate theca (5 genera): *Turbinolia* Lamarck, 1816; *Conocyathus* d'Orbigny, 1849: *Trematotrochus* Tenison-Woods, 1879; and *Bothrophoria* Felix, 1909; to which is provisionally added *Endocyathopora*, new genus. If the Caryophylliinae is considered to be the outgroup for the Turbinoliinae, then an imperforate theca (groups 1 and 2) would be the plesiomorphic character state, the 4-5 genera with perforate theca (group 2) considered the derived state.

DISTRIBUTION.—*Upper Cretaceous to Recent:* Worldwide, including Antarctica; 9-835 m.

Key 3: The Genera of Turbinoliinae

(† = an exclusively fossil genus)

1. Corallum perforate 2
Corallum imperforate 5
2. Pali (P_2) present 3
Pali absent 4
3. Costae hispid or granular; P_2 small . . . . ***Trematotrochus*** Tenison-Woods, 1879
(= *Batotrochus* Wells, 1937)
Costae smooth; P_2 large . . . . ***Conocyathus*** d'Orbigny, 1849
4. Columella spongy . . . . **†*Bothrophoria*** Felix, 1909
Columella styliform . . . . **†*Turbinolia*** Lamarck, 1816
5. Theca internally pitted . . . . ***Endocyathopora*,** new genus
Theca not internally pitted 6
6. Columella absent . . . . **†*Dominicotrochus*** Wells, 1937
Columella present 7
7. Pali and paliform lobes absent 8
Pali or paliform lobes present 14
8. Adult corallum with less than 12 septa . . . . ***Holcotrochus*** Dennant, 1902
Adult corallum with 12 septa or more 9
9. Columella lamellar 10
Columella papillose or styliform 11
10. Corallum cuneiform . . . . . . ***Sphenotrochus*** Milne Edwards and Haime, 1848
Corallum turbinate, curved . . . . **†*Sphenotrochopsis*** Alloiteau and Tessier, 1958
11. Columella styliform; corallum bowl-shaped or rice grain shaped 12
Columella papillose; corallum cuneiform 13
12. Corallum bowl shaped; 5-8 mm in calicular diameter . . . .
. . . . **†*Wellsotrochus*** Squires, 1960
Corallum has shape and size of rice grain (calicular diameter less than 2 mm)
. . . . ***Oryzotrochus*** Wells, 1959
13. Thickened alate primary costae . . . .
. . . . ***Platytrochus*** Milne Edwards and Haime, 1848
Normal principal costae . . . . **†*Koilotrochus*** Tenison-Woods, 1878
(probably junior synonym of *Platytrochus*)
14. Multiple paliform lobes present (P_{1-3}) . . . . ***Thrypticotrochus*,** new genus
Discrete pali present 15

15. Only P_2 present 16
    P_1 and P_2 present 17
    Pali before all but last septal cycle (usually P_{1-3}), but P_{1-2} often suppressed in adult
    Notocyathus 19
16. P_2 obscure and fused to columella; corallum bowl-shaped with rounded base
    . . . . **Kionotrochus** Dennant, 1906
    P_2 prominent and independent; corallum conical with pointed base
    . . . . **Cryptotrochus** Cairns, 1988
17. Septa correspond to costae; transverse division lacking . . . .
    . . . . †**Coronocyathus** Alloiteau and Tessier, 1958
    Septa alternate with costae; transverse division present 18
18. Corallum discoidal; pali in one crown of 12 elements; columella spongy
    . . . . **Dunocyathus** Tenison-Woods, 1878
    Corallum cuneiform; pali in two crowns of 10–12 elements; columella papillose
    . . . . **Idiotrochus** Wells, 1935
19. Eighteen primary septa . . . . †**Monticyathus** Alloiteau and Tessier, 1958
    Typical hexameral symmetry ($S_1 \geq S_2 > S_3 > S_4$) 20
20. Pairs of P_3 fused to one another in V-shaped structures; P_2 usually suppressed in adult; septa independent; corallum conical with pointed base . . . .
    . . . . **Notocyathus** Tenison-Woods, 1880
    P_3 fused to intermediate P_2; P_2 well developed; higher-cycle septa fuse with lower-cycle septa; corallum of variable shape but lacking a pointed base . . . 21
21. Corallum large (adult calicular diameter >10 mm); corallum cuneiform; P_1 well developed . . . . **Tropidocyathus** Milne Edwards and Haime, 1848
    Corallum small (adult calicular diameter <8 mm); corallum variable in shape (e.g., cylindrical, hemispherical); P_1 often poorly developed . . . .
    . . . . **Peponocyathus** Gravier, 1915
    (= *Cylindrophyllia* Yabe and Eguchi, 1937)

Notocyathus Tenison-Woods, 1880

Caryophyllia.—Duncan, 1864:162 [in part: *C. viola*].
Notocyathus Tenison-Woods, 1880a:9 [in part: *N. viola*].—Vaughan and Wells, 1943:214.—Yabe and Eguchi, 1946:6–8.—Squires, 1962:147.—Chevalier, 1987:748, fig. 417,8.
Nototrochus Duncan, 1885:17.
Citharocyathus Alcock, 1902a:21.—Yabe and Eguchi, 1942b:122.—Alloiteau, 1952:646.—Wells, 1984:214.
Deltocyathus.—Dennant, 1902:4 [in part: *D. subviola*].
Sphenotrochus.—Gerth, 1921:393 [in part: *S. viola*].
Notocyathus (Notocyathus).—Wells, 1956:F425 [in part: not *Paradeltocyathus*].—Squires, 1958:54 [in part: not *Notocyathus (Paradeltocyathus)*].
Citharocyathus (Citharocyathus).—Vaughan and Wells, 1943:210–211.

DIAGNOSIS.—Corallum cylindrico-conical or cuneiform, with a pointed base; transverse division lacking. Wall imperforate; costae serrate, corresponding to septa. Four cycles of highly exsert septa. Pali before all but last cycle of septa, but P_{1-2} suppressed in adult; pairs of P_3 united in V-shaped structures in one crown. Columella papillose.

DISCUSSION.—When originally described, Tenison-Woods (1880a) compared *Notocyathus* to both *Conocyathus* and *Deltocyathus*, the former a turbinoliid and the latter now considered to be a caryophylliid. Duncan (1885) unnecessarily synonymized *Notocyathus* with his new genus *Nototrochus*, but correctly placed it in alliance with other turbinoliid genera, as did Alcock (1902a), under the name *Citharocyathus*. Yabe and Eguchi (1946) correctly recognized the synonymy of *Citharocyathus*—known only from deep-sea Recent specimens—with *Notocyathus*, previously known only from Miocene fossil specimens, although the name *Citharocyathus* continued to be used by some (Vaughan and Wells, 1943; Alloiteau, 1952; Wells, 1984; but not Wells, 1956). Wells divided *Notocyathus* into two subgenera: the nominate subgenus and *N. (Paradeltocyathus)*, the latter now considered to be a junior synonym of *Peponocyathus*.

Regardless of how Tenison-Woods (1880a) originally described *Notocyathus* (e.g., as lacking a columella), and which six species he included in the genus, *Notocyathus* must be characterized by its type species, *Caryophyllia viola* Duncan, 1864, as subsequently designated by Felix (1927). Therefore, contrary to the original generic account, *Notocyathus* does indeed have a columella, and only one of the six originally assigned species pertain to this genus: the type species, the other five having been reassigned to other turbinoliid genera.

Of the 10 imperforate paliferous turbinoliid genera (Key 3), only three have pali before all but the last cycle: *Notocyathus*, *Tropidocyathus*, and *Peponocyathus*, these three genera forming a closely related genus complex. In fact, *Notocyathus* and *Peponocyathus* were considered to be so similar that Vaughan and Wells (1943) and Wells (1956) considered *Paradeltocyathus* (= *Peponocyathus*) as a subgenus of *Citharocyathus* (= *Notocyathus*). *Notocyathus* is distinguished from the other two genera by its conical corallum, independent higher-cycle septa, and presence of only P_3 in the adult corallum, which fuse together before the S_2 in a distinctive V-shaped structure. Only in small coralla of *Notocyathus* (e.g., ≤3 mm calicular diameter) are P_{1-2} developed (Plate 13*e*); as the corallum increases in size, they become indistinguishably incorporated into the columella. Therefore, at a small size *Notocyathus* specimens pass through an ontogenetic stage having distinct P_{1-2}, equivalent to adult *Tropidocyathus*. Slightly later in ontogeny, the P_1 merge with the columella, resulting in coralla with P_2 and P_3, equivalent to adult *Peponocyathus*. Finally, the P_2 are also incorporated into the columella and only V-shaped pairs of P_3 remain, characteristic of adult *Notocyathus*.

Five species are assigned to *Notocyathus: N. viola* (Duncan, 1864) (Miocene of Australia); *N. subviola* (Dennant, 1902) (Eocene to Miocene of Australia); *N. conicus* (Alcock, 1902); *N. venustus* (Alcock, 1902a); and *N. euconicus* Squires, 1958 (Oligocene to Miocene of New Zealand). Characters of diagnostic value include corallum shape, relative septal exsertness, and degree of expression of P_{1-2}.

TYPE SPECIES.—*Caryophyllia viola* Duncan, 1864, by subsequent designation (Felix, 1927).

DISTRIBUTION.—*Eocene to Miocene:* Australia. *Recent:* Western Pacific; 34–923 m.

13. *Notocyathus venustus* (Alcock, 1902), new combination

PLATE 12*c–h*

Citharocyathus venustus Alcock, 1902a:22, pl. 3: figs. 19, 19a.
Not *Citharocyathus venustus*.—Yabe and Eguchi, 1932b:443, 444 [= *N. conicus*].
Citharocyathus conicus.—Yabe and Eguchi, 1941b:212, figs. 4a,b.
?*Citharocyathus conicus* form *venustus*.—Wells, 1984:214, pl. 4: figs. 2–5.

DESCRIPTION.—Corallum cylindrico-conical, with a pointed base, the basal angle being 40°–70°; at a height of 3.5–4.0 mm the corallum becomes a constant-diameter cylinder. Largest specimen examined 6.7×6.5 mm in calicular diameter and 9.2 mm tall (syntype). Calice almost perfectly circular, the GCD:LCD being a narrow range of 1.02–1.05. Costae of different cycles are of different widths: C_{1-2} about 0.22 mm wide, C_4 only 0.14–0.15 mm wide. Costae separated by intercostal furrows about 0.12 mm wide and 0.30–0.35 mm deep at calicular edge. Each costa bears a unilinear row of prominent, slightly tapered, outward-projecting cylindrical teeth up to 0.14 mm tall, as well as slightly smaller (0.09 mm tall) granules on the lateral costal surface, the latter obscuring the intercostal furrow. Costae symmetrically arranged on base, only the 12 C_{1-2} meeting at epicenter. Each C_2 bifurcates into two C_3 only 0.15–0.20 mm from epicenter, each C_3 subsequently bifurcating into two C_4 about 1.5 mm from the base.

Septa hexamerally arranged in four cycles according to the formula: $S_1>S_2>S_3>>S_4$. S_1 highly exsert, up to 2.4 mm above the calicular edge in large specimens, with rounded upper edges and straight, vertical inner edges that extend about $^3/_4$ of the distance to columella. At the level of the calice the inner edges of S_1 fuse with the columella. S_2 also highly exsert (e.g., 1.3 mm), have rounded upper edges, and extend about half the distance to the columella, where they fuse basally to the P_3. S_3 slightly less exsert than S_2 (e.g., 1.1 mm), with flat upper edges, extending about 0.4 distance to columella, where each is bordered by a prominent P_3. S_4 much less exsert than S_3 (e.g., 0.4 mm, or 35% of S_3), independent, and extend only about 0.2 distance to columella. Septal and palar faces relatively smooth, bearing very small, sparse granules that are most prominent along inner septal edges. Small P_1 and P_2 present in specimens of small calicular diameter, e.g., 2.0–2.8 mm, but as the corallum grows they become incorporated into the columella. Early in ontogeny of the P_3 (e.g., 3.0 mm calicular diameter) the S_3 pair in each system becomes fused basally. With growth, each pair becomes more solidly fused along its entire inner margin, eventually forming a lamellar to V-shaped structure before the S_2. Even in large specimens, however, it is clear that this structure is not a P_2, rather two fused P_3. P_3 as exsert as S_2, their lower, inner edges fusing to the columella above the calicular level.

Fossa lacking, the upper edges of the columella and pali rising well above the calicular edge. Columella linear, composed of a solid fusion of 8–12 elements aligned along the greater calicular diameter.

DISCUSSION.—Wells' (1984) Pleistocene *C. conicus* form *venustus* from Vanuatu are too small to definitively identify and are therefore only tentatively assigned to *N. venustus*. Some of his specimens (Wells, 1984, pl. 4: figs. 2–5) were so small that only P_2 were developed, no P_3 having formed yet. Other larger unillustrated specimens showed the typical fused P_3 configuration of *Notocyathus*.

Notocyathus venustus is very similar to *N. conicus*, some authors having synonymized them in the past (Yabe and Eguchi, 1946; Squires, 1958; Wells, 1984); however, I support Alcock's (1902a) original separation of the two species. Characters in which *N. venustus* differs consistently include (1) having a slender cylindrico-conical corallum; that of *N. conicus* is conical, (2) having very small S_4, less than half as exsert as the S_3; S_4 of *N. conicus* are over half as large as the S_3, (3) having relatively smooth septal faces; septal faces of *N. conicus* are highly granular, (4) having an exsert columella and no fossa; *N. conicus* has a shallow fossa, (5) having P_3 that extend well above the calicular edge; P_3 of *N. conicus*, because of originating in a shallow fossa, rarely extend above the calicular edge, (6) having, in general, more exsert S_{1-3}, and (7) having a calice more closely approximating a circle (GCD:LCD = 1.02–1.05 vs. 1.05–1.22 for *N. conicus*). Even with these guidelines, small and/or damaged specimens are often difficult to distinguish.

MATERIAL EXAMINED.—ALB-5133 (2) USNM 81787;

ALB-5311 (3) USNM 81789; ALB-5312 (4) USNM 304173; ALB-5380 (2) USNM 81791; ALB-5567 (13) USNM 81784; ALB-5569 (8) USNM 81786; ALB-5576 (1) USNM 81785; ALB-5579 (1) USNM 81790; 3 syntypes of *C. venustus*, ZMA, Plate 12*c–d;* USGS 24918 (9) USNM 73968 (*C. c. venustus* of Wells, 1984).

TYPES.—Three of the four syntypes from *Siboga* 59 are deposited at the ZMA (1244) (Van Soest, 1979). *Type Locality:* 10°22.7′N, 123°16.5′E (Savu Sea, Indonesia), 390 m.

DISTRIBUTION.—*Pleistocene:* Ryukyu Islands (Yabe and Eguchi, 1942b); ?Vanuatu (Wells, 1984). *Recent:* Philippines (Sibuyan Sea, Sulu Archipelago); South China Sea near Hong Kong; off Sabah, Celebes Sea; Savu Sea, Indonesia; 70–555 m; 11.1°–14.1°C.

14. *Notocyathus conicus* (Alcock, 1902)

PLATE 13*a–i*

Citharocyathus conicus Alcock, 1902a:22, pl. 3: figs. 18, 18a.—Faustino, 1927:78, pl. 6: figs. 6, 7.—Wells, 1936:103–104 [designated as type species of genus].—?Yabe and Eguchi, 1941a:414; 1942b:122, pl. 10, figs. 17, 18.

Sphenotrochus viola.—Gerth, 1921:393, pl. 57: figs. 10, 11.

Citharocyathus venustus.—Yabe and Eguchi, 1932b:443, 444.

Not *Citharocyathus conicus.*—Yabe and Eguchi, 1941b:212 [= *N. venustus*].

Notocyathus conicus.—Yabe and Eguchi, 1946:7, figs. 1, 2.—Eguchi, 1965:289, 2 figs.

Not *Notocyathus conicus.*—Squires, 1958:54–55, pl. 9: figs. 12–14 [= *N. euconicus* and *Peponocyathus* sp.]; 1962:147 [= *Peponocyathus* sp.].

DESCRIPTION.—Corallum conical, constantly increasing in diameter with height; basal angle 40°–70°. Largest specimen examined 7.0×6.9 mm in calicular diameter and 8.1 mm tall (Plate 13*a,b*, larger syntype). Calice elliptical, the GCD:LCD ranging from 1.01–1.22, with an average of 1.15. Costal size, ornamentation, and arrangement as in *N. venustus;* however, in larger specimens (e.g., larger syntype) costal granules near the calicular edge are staggered, no longer arranged in unilinear fashion. Width of theca about 0.15 mm.

Septa hexamerally arranged in four cycles according to the formula: $S_1>S_2>S_3>S_4$. S_1 exsert, up to 1.3 mm in large specimens, with straight, vertical inner edges extending to the columella. S_2 slightly less exsert (e.g., 1.1 mm) and extend about 0.6 distance to columella, where they fuse basally to the fused P_3. S_3 progressively less exsert (e.g., 1.0 mm) and extend about halfway to columella, where each is bordered by a prominent P_3. Because P_3 originate from the bottom of a shallow fossa, their upper thecal edges rarely extend above the calicular edge. S_4 slightly less exsert (e.g., 0.8 mm, or 0.8 height of S_3), independent, and extend about 0.4 distance to columella. Upper edges of all septa rounded. Septal and palar faces covered by prominent elongate to spiniform granules up to 0.18 mm tall on septa (0.22 mm tall on pali), which are often aligned in rows reflecting the underlying trabeculae. As in *N. venustus*, small P_1 and P_2 are usually present in small coralla but rarely retain their individual identities in larger coralla. The fusion of the paired P_3 is also similar to that of *N. venustus*.

Fossa usually present as a shallow depression. Columella linear, composed of a loose fusion of 8–12 elements aligned along greater calicular diameter.

DISCUSSION.—As previously noted, *N. conicus* is extremely similar to *N. venustus*, but, in general, can be distinguished based on seven characters enumerated in the discussion of the latter species.

Notocyathus viola (Duncan, 1864) (see Plate 14*a–c*), known only from the Miocene of South Australia, is distinguished from *N. conicus* by its compressed corallum (GCD:LCD = 1.28–1.39, based on six lots of topotypic specimens deposited at the NMNH and the holotype) and its greater tendency to preserve P_1 and sometimes even P_2 in the adult corallum.

It is difficult to compare *N. conicus* to *N. euconicus* Squires, 1962, known from the Oligocene to Miocene of New Zealand, based on the original description and two specimens available to me (USNM 67904, 67935); however, *N. euconicus* appears to differ in having a more circular calice and a nonlinear columella.

MATERIAL EXAMINED.—ALB-5152 (5) USNM 81793; ALB-5162 (2) USNM 81794; ALB-5178 (26) USNM 81792, (2) AM 15247; ALB-5272 (2) USNM 81795; ALB-5277 (1) USNM 81796; ALB-5403 (1) USNM 81797; ALB-5513 (1) USNM 81798; ALB-5586 (1) USNM 81799; MUSORSTOM 2-11 (1) MNHNP; MUSORSTOM 2-33 (10) USNM 81801, (39) MNHNP; MUSORSTOM 3-102 (6) MNHNP; *Corindon* 2-235 (3) MNHNP; 2 syntypes, ZMA. *Reference Material:* Holotype of *C. viola*, BM R29281; 23 topotypes of *N. viola* mentioned in "Discussion" (USNM 44306, 67976, 67982, 77062, 77067, 353588); NZGS 9487 (1) USNM 67935 (*N. euconicus* of Squires, 1962); NZGS 4578 (1) USNM 67904 (*N. euconicus* of Squires, 1962).

TYPES.—The two syntypes of *Citharocyathus conicus*, collected at *Siboga* 95, are deposited at the ZMA 1185 (Van Soest, 1979) (Plate 13*a–e*). *Type Locality:* 5°43.5′N, 119°40′E (Sulu Sea, Sulu Archipelago), 522 m.

DISTRIBUTION.—*Miocene:* Java (Gerth, 1921). *Pliocene:* Mindoro, Philippines (Yabe and Eguchi, 1941a). *Pleistocene:* Ryukyu Islands (Yabe and Eguchi, 1942b). *Recent:* Kyūshū, Japan (Yabe and Eguchi, 1942b); Philippines (off Luzon; Sibuyan Sea; Visayan Sea; Bohol Sea; Sulu Archipelago); Makassar Strait; Sabah, Indonesia; 34–923 m; 6.7°–17.5°C.

Peponocyathus Gravier, 1915

Stephanophyllia.—Pourtalès, 1868:139 [in part].

Leptocyathus.—Pourtalès, 1871:12 [in part].

Paracyathus.—Pourtalès, 1871:11 [in part].

?Discotrochus.—Reuss, 1872:225.

Deltocyathus.—Duncan, 1870:297; 1876:431.—Alcock, 1902a:19 [in part].—Gardiner and Waugh, 1938:198 [in part].

Peponocyathus Gravier, 1915:5.—Yabe and Eguchi, 1932b:444.—Wells, 1956:F426.—Cairns, 1979:113.—Zibrowius, 1980:111–113.—Chevalier, 1987:739–740.

?Deltocyathoides Yabe and Eguchi, 1932a:389.—Vaughan and Wells, 1943:207.—Wells, 1956:F424.—Zibrowius, 1980:112.—Chevalier, 1987:740–741.
Deltocyathus (Paradeltocyathus) Yabe and Eguchi, 1937:130.
Discotrochus (Cylindrophyllia) Yabe and Eguchi, 1937:142.
Trochocyathus (Peponocyathus).—Vaughan and Wells, 1943:205.
Citharocyathus (Paradeltocyathus).—Vaughan and Wells, 1943:211.—Alloiteau, 1952:646.
Kionotrochus.—Vaughan and Wells, 1943:213 [in part: *Cylindrophyllia*].
Cytharocyathus (Cytharocyathus).—Alloiteau, 1952:646.
Cylindrophyllia.—Wells, 1956:F426.—Mori and Minoura, 1983:185.
Notocyathus (Paradeltocyathus).—Wells, 1956:F425.
Kionotrochus (Cylindrophyllia).—Squires, 1960a:287.
Notocyathus.—Lewis, 1965:1062.
Paradeltocyathus.—Eguchi, 1965:289.

DIAGNOSIS.—Corallum variable in shape, including bowl-shaped, cylindrical, and globose with a flattened base; transverse division lacking. Theca imperforate; costae serrate, corresponding to septa. Three or four cycles of highly exsert septa. Pali present before all but last cycle of septa in two crowns; P_1 often suppressed or merged with columella of adult. Columella papillose.

DISCUSSION.—As evidenced by its synonymy, species of *Peponocyathus* have been assigned to many different genera. Much of this confusion has resulted because the genus was based on an Atlantic species, and not until recently (Yabe and Eguchi, 1932b, but particularly Zibrowius, 1980) have the Pacific specimens been considered congeneric. Therefore, the Pacific species had been assigned to several genera and subgenera, a number of which were described as new taxa. One of these new subgenera, *Cylindrophyllia* Yabe and Eguchi, 1937, was based on immature stages of *Peponocyathus*, this name being widely used for the Pacific specimens.

Long before its recognition as a distinct turbinoliid genus, species now placed in *Peponocyathus* had been assigned to *Stephanophyllia*, *Leptocyathus*, *Discotrochus*, and *Deltocyathus*. Even after 1915, some authors (e.g., Gardiner and Waugh, 1938; Yabe and Eguchi, 1937; Mori, 1964; Chevalier, 1987) continued to assign Pacific specimens to *Deltocyathus*, and Yabe and Eguchi (1937) even created a new subgenus, *Paradeltocyathus*, for those species with unusual (turbinoliid) costae. *Paradeltocyathus* was based on Duncan's (1876) *D. orientalis*, a species I consider to be a junior synonym of *P. australiensis*. The turbinoliid nature of *Peponocyathus* and its affinities to *Notocyathus* were recognized by Vaughan and Wells (1943), who considered *Paradeltocyathus* a subgenus of *Citharocyathus* (= *Notocyathus*); Wells (1956) later placed it as a subgenus of *Notocyathus;* Eguchi (1965), however, established it as a separate genus. As an ironic reversal of the previous trend, some authors (e.g., Lewis, 1965; Keller, 1975) used the names attributed to Pacific species (e.g., *Notocyathus*, *Paradeltocyathus*) for Atlantic species, from whence *Peponocyathus* had originally been described.

Another genus described for Pacific peponocyathid species was *Deltocyathoides* Yabe and Eguchi, 1932a, which was based on one regenerated corallum. Although Yabe and Eguchi (1937) compared the type species to two species of *Peponocyathus*, the genus was subsequently classified (Vaughan and Wells, 1943) within the Caryophylliinae, with affinities to *Deltocyathus* and *Paracyathus*. Nevertheless, the original description and figures clearly indicate the characteristic corallum shape and costae of *P. australiensis* (see Zibrowius, 1980:100, as *P. orientalis*).

As previously mentioned, *Peponocyathus* was also linked to the genus *Cylindrophyllia* Yabe and Eguchi, 1937, which is based on the type species *Discotrochus (Cylindrophyllia) minima* Yabe and Eguchi, 1937 (Neogene to Recent of Japan). Vaughan and Wells (1943) considered *Cylindrophyllia* to be a junior synonym of *Kionotrochus*, but Wells (1956) later separated the two taxa into discrete genera: *Cylindrophyllia*, possessing P_2, and *Kionotrochus*, lacking pali. Squires (1960a) relegated *Cylindrophyllia* to a subgenus of *Kionotrochus* and made the important observation that *Kionotrochus (K.) suteri* has indistinct, rod-like P_2. He therefore distinguished the two subgenera based on corallum shape and degree of P_2 expression: *K. (K.)* having a conical corallum with indistinct P_2, *K. (C.)* having a subcylindrical corallum with broad P_2. In 1964, Squires (1964b) added the observation that *K. (K.) suteri* divides asexually by transverse fission, the attached polycyclic anthocaulus having well-developed P_2, like *Cylindrophyllia*. This lead to Zibrowius's (1980:113) salient observation that in Madeira he had seen similar polycyclic anthocauli, which were probably young stages of *Peponocyathus*, *Kionotrochus* not being known from the Atlantic. His conclusion was that the young attached stages of both *Peponocyathus* and *Kionotrochus* are indistinguishable and probably represent a common type of development within the subfamily. At this early stage of development there are only three cycles of septa and 6 P_2, the P_1 of *Peponocyathus* often being suppressed. This would explain why *Cylindrophyllia*, based on small, juvenile specimens, would be confused with *Kionotrochus* or *Peponocyathus*.

Ten species have been assigned to *Kionotrochus*. Two species described by Durham and Barnard (1952) from the Galápagos are *Cyathoceras;* four species described by Alloiteau and Tessier (1958) from the Tertiary of the Alps do not appear to be congeneric, based on their descriptions and figures; *K. lecomptei* Wells, 1937, and *K. duncani* (Reuss, 1871), both Miocene European species, have been assigned to *Cylindrophyllia* (= *Peponocyathus*) by Squires (1960a) and Mori and Minoura (1983), and to *Peponocyathus* by Zibrowius (1980). The remaining two species are *K. suteri* Dennant, 1906, type species of the genus and endemic to New Zealand (Recent: 48–241 m); and *C. minima* Yabe and Eguchi, 1937, type species of *Cylindrophyllia*. In a thorough study of 792 specimens from the type locality of *P. orientalis*, Mori and Minoura (1983) synonymized *C. minima* with *Peponocyathus orientalis* Yabe and Eguchi, 1932. They found two varieties of the species, one with 20–*24*–28 septa, originally described as *Cylindrophyllia minima*, and another variety with 30–*36*–48 septa, originally described as *P. orientalis* Yabe and Eguchi, 1932. Although I agree with their results, it is unfortunate that they chose to retain the generic name *Cylindrophyllia* instead of *Peponocyathus*. They did this based on a comparison of their specimens to the type species of *Peponocyathus*, *P. variabilis* (= *P. folliculus*), which, according to them, had a gourd-shaped corallum and pali before S_2 and S_3 (even if S_4 were not present). But, both of these points of difference are groundless (Cairns, 1979; Zibrowius, 1980): *P. variabilis* was so named because of its variation in corallum shape, which easily includes that of *C. orientalis*, and *P. variabilis* does not have P_3 unless the corresponding S_3 is flanked by S_4, just as in *C. orientalis*. Mori and Minoura's (1983) specimens of *Cylindrophyllia orientalis*, and thus *C. minima*, are most certainly *Peponocyathus*.

The transfer of *C. minima* to *Peponocyathus* results in *Kionotrochus* being a monotypic genus endemic to New Zealand, whereas *Peponocyathus* is widespread in the Atlantic, Indian, and Pacific oceans with eight Recent and fossil species. As previously mentioned, the young stages of *Kionotrochus* and *Peponocyathus* ("*Cylindrophyllia*" stage) are indistinguishable, but, because *Kionotrochus* is endemic to New Zealand, it is only logical to assume that all such young stages found outside New Zealand are probably *Peponocyathus*.

Peponocyathus is most closely related to *Tropidocyathus* and *Notocyathus*, the other two imperforate turbinoliid genera having pali before all but the last cycle of septa. As previously noted in the discussion of *Notocyathus*, both Vaughan and Wells (1943) and Wells (1956) considered *Peponocyathus* a subgenus of *Notocyathus*. Comparisons to those two genera are made in the discussions of those genera and in Key 3. To reiterate, *Peponocyathus* is distinguished by the suppression of its P_1, its bowl-shaped to cylindrical corallum, and its relatively small coralla.

Eight valid species are provisionally assigned to *Peponocyathus*: two Recent and seven exclusively fossil species. The two Recent species, each of which has three to five junior synonyms, are discussed in this paper; both have fossil records also. The remaining fossil species, in chronological order are *P. cylindricus* (Sismondi, 1871) Miocene, Italy; *P. duncani* (Reuss, 1872) Miocene, Europe; *P. pedicellatus* (Tenison-Woods, 1880) Oligocene, New Zealand; *P. lecomptei* (Wells, 1937) Miocene, Belgium; *P. minutus* (Vašiček, 1946)(junior secondary homonym of *D. minutus* Gardiner and Waugh, 1938), Miocene, Italy; and *P. cuspidatus* (Squires, 1958) Oligocene, New Zealand. Characters used to distinguish species within the genus include corallum shape and costal ornamentaion.

TYPE SPECIES.—*Peponocyathus variabilis* Gravier, 1915 (= *P. folliculus* (Pourtalès, 1868)), by original designation.

DISTRIBUTION.—*Oligocene to Miocene:* Australia, New Zealand, Europe. *Recent:* Atlantic, Indo-West Pacific; 44–635 m.

15. *Peponocyathus australiensis* (Duncan, 1870), new combination

PLATES 14*d–j*, 15*a–d*

Deltocyathus italicus var. *australiensis* Duncan, 1870:297, pl. 19: fig. 4.

Leptocyathus stimpsonii Pourtalès, 1871:12, pl. 3: figs. 1–3.

Deltocyathus orientalis Duncan, 1876:431, pl. 38: figs. 4–7.—Eguchi, 1941b:418–419, figs. 1–3.—Yabe and Eguchi, 1942b:125–126.—Mori, 1964:314, pl. 46: figs. 1, 2.

Deltocyathus lens Alcock, 1902a:19–20, pl. 2: fig. 16 [in part: not *Siboga* 275].—Gravier, 1920: 36–37, pl. 3: figs. 47–54, pl. 13: figs. 200, 201.—Umbgrove, 1925:4, pl. 1: figs. 8–10.—Faustino, 1927:75–76, pl. 6: figs. 1, 2.

Not *Peponocyathus orientalis* Yabe and Eguchi, 1932b:444–445 [= *P. folliculus*].

Deltocyathoides japonicus Yabe and Eguchi, 1932a:389, fig. 3; 1937:140–141, pl. 20: figs. 23a–c.—Eguchi, 1968:C35, 36.

Deltocyathus (Paradeltocyathus) orientalis Duncan, 1876.—Yabe and Eguchi, 1937:131–137, pl. 20: figs. 1–10.

Not *Deltocyathus lens*.—Gardiner and Waugh, 1938:198, fig. 4 [= *Deltocyathus* sp.].

Deltocyathus minutus Gardiner and Waugh, 1938:198, fig. 15.—Scheer and Pillai, 1983:165.

Deltocyathoides japonicum.—Yabe and Eguchi, 1942b:126.

Citharocyathus (Paradeltocyathus) orientalis (Duncan, 1876).—Vaughan and Wells, 1943:211.

Notocyathus (Paradeltocyathus) orientalis (Duncan, 1876).—Wells, 1956:F425.—Squires, 1958:55, pl. 9: figs. 19–22.—Squires and Keyes, 1967:24, pl. 3: figs. 1–7.—Eguchi, 1968:C40, 41.—Hamada, 1969:253, 254, pl. 2: figs. 4a–c.—Wells, 1977:G9, pl. 3: figs. 1–3.—Cairns, 1979:116.—Omura et al., 1984:31, fig. 1b.

Paradeltocyathus orientalis (Duncan, 1876).—Eguchi, 1965:289, 2 figs.—Kikuchi, 1968:11.—Zibrowius, 1980:112.

Peponocyathus stimpsonii.—Lewis, 1965:1063.—Cairns, 1979:115–117, pl. 22: figs. 5–7, not pl. 20: fig. 11 [description and synonymy of Atlantic records].—Zibrowius, 1980:115–116, pl. 60: figs. A–M [description and synonymy of Atlantic records].

Deltocyathus sp. Eguchi, 1974, pl. 70: figs. 6–11.

Peponocyathus orientalis (Duncan, 1876).—Cairns, 1979, pl. 40: figs. 8, 9.—Zibrowius, 1980:112.—Cairns, 1984a:19–20, pl. 4: fig. A.—Wells, 1984:214.—Zibrowius and Grygier, 1985:121, fig. 13.—Veron, 1986:608.

DESCRIPTION.—Corallum variable in shape, usually hemispherical with a rounded base, but also cylindrical with a flat base, or a slightly tapered cylinder with a flat base. Regardless, even cylindrical coralla are greater in calicular diameter than in height. Asexual regeneration from corallum fragments as small as three septa is known but not common. Largest corallum examined 7.9 mm in calicular diameter and 5.0 mm tall (ALB-5312), a hemispherical form; however, Yabe and Eguchi (1937) reported specimens up to 11 mm in calicular diameter. Costae equal in width (0.18–0.22 mm), separated by very deep (0.70 mm) and narrow (0.10 mm) intercostal furrows. Each costa bordered peripherally by a uniserial row of blunt, cylindrical (0.06–0.08 mm tall and 0.04 mm in diameter) granules, as well as bearing equal-sized granules laterally, up to 5 deep on the deep edges of a costa (Plate 15*a*). Costae symmetrically arranged on base, the C_1 and C_2 extending independently to the granular epicenter, itself about 0.85 mm in diameter. At a calicular radius of about 1.1 mm, or about 0.7 mm from the edge of the granular base, each C_3 bifurcates to form a pair of C_4. A new C_3 originates at the point of bifurcation and sometimes fuses with one of the adjacent C_4. Thecal wall about 0.28 mm thick.

Septa hexamerally arranged in 4 cycles, the fourth cycle appearing at the relatively small calicular diameter of 2.2–2.8 mm. Septa formula: $S_1>S_2>S_3\leq S_4$, however, Yabe and Eguchi (1937) reported specimens with 52 septa. S_1 highly exsert, reaching their highest point near the fossa; inner edges straight and vertical. Occasionally small paliform lobes (P_1) appear on the lower, inner edges of the S_1 and are virtually indistinguishable from the columellar elements. S_2 less exsert, each bearing a thick, spiny palus (P_2) on its inner edge, which also merges with the columella. S_3 less exsert than S_2, each usually bearing a more slender but longer and taller palus, the inner edges of which are loosely fused at a lower level in fossa to the outer edges of the P_2. Sometimes, more often in large specimens, the P_3 become indistinguishably incorporated with the S_3 that it borders. S_4 equal in exsertness to S_3, extending an equal or sometimes slightly farther distance toward columella than S_3, their inner edges fusing with the P_3. Tall (40 μm high), pointed granules, often arranged in serrate ridges, cover the septal faces paralleling the trabecular structure, giving the septa a very spiny appearance. Pali bear more prominent granules than those of septa, up to 50 μm tall and 0.07×0.14 mm in cross section, aligned vertically on each palus.

Fossa variable in depth, depending on size and shape of corallum. In large hemispherical coralla, the fossa is moderately deep; in small, cylindrical specimens, the fossa may be absent; the septa, pali, and columella all rising well above the calicular edge. Columella papillose, varying from 0–12 tuberculate papillae, each of which may be independent or all of which may be strongly fused together.

DISCUSSION.—The synonymy of *P. australiensis* is complex for essentially the same reasons that the generic synonymy is. Not only was the species described under six different names but these names have been assigned to seven different genera. To add to this confusion, the Atlantic and Pacific specimens were generally considered to comprise two different species.

Cairns (1979) noted the extreme similarity of *Peponocyathus orientalis* (Duncan, 1876) to *P. stimpsonii* and suggested they might be synonymous. A year later, Zibrowius (1980:112, 116) suggested that the difference between the Atlantic and Indo-West Pacific species concerned slight differences in the septal face granulation: the granules of *P. orientalis* being pointed and shorter, producing more apparent space between septa. After having examined over 950 Indo-West Pacific specimens, most from the Philippines and Hawaii, and approximately 150 specimens from the Atlantic (Cairns, 1979; Zibrowius, 1980), I conclude that the Atlantic and Pacific specimens are the same species. This widespread distribution was previously implied by Gravier (1920) under the name *Deltocyathus lens*, and by Yabe and Eguchi (1937) and Wells (1977) as *Deltocyathus (Paradeltocyathus) orientalis*. Wells (1977) also suggested an Oligocene to Recent stratigraphic range for the species and remarked that *D. italicus* var. *australiensis* Duncan, 1870, from the Miocene of Australia was also very similar. The holotype of this variety was examined and found to be identical to the widespread species under consideration. According to the *International Code of Zoological Nomenclature* (1985), article 45g, a variety proposed before 1961 must be treated as a subspecies. Since *D. italicus* var. *australiensis* is clearly not a subspecies of *D. italicus* (Michelotti, 1838), it is treated as a species of the genus *Peponocyathus* and, as such, has a one-year priority over *P. stimpsonii* (Pourtalès, 1871).

To summarize, *P. australiensis* has one of the broadest distributions of any coral species known, both geographically and stratigraphically, undoubtedly leading to its having been independently described six times. Its earliest description, however, appears to have been based on a Miocene fossil from South Australia, described in 1870 as a variety of a species originally placed in a different subfamily, and based on a specimen that has probably not been reexamined since its original description.

MATERIAL EXAMINED.—ALB-5133 (3) USNM 81813; ALB-5146 (1) USNM 81832; ALB-5152 (4) USNM 81811; ALB-5162 (3) USNM 81809; ALB-5172 (1) USNM 81812; ALB-5178 (29) USNM 81814; ALB-5213 (3) USNM 81807; ALB-5217 (24) USNM 81810; ALB-5268 (9) USNM 81805; ALB-5277 (4) USNM 81806; ALB-5282 (1) USNM 81803; ALB-5311 (41) USNM 81819; ALB-5312 (62) USNM 304174; ALB-5313 (149) USNM 81833; ALB-5314 (22) USNM 81830; ALB-5315 (11) USNM 81817; ALB-5317 (13) USNM 81826; ALB-5318 (1) USNM 81804; ALB-5381 (1) USNM 81808; ALB-5392 (56) USNM 81825, (2) AM G15246; ALB-5393 (1) USNM 81822; ALB-5398 (182) USNM 81831; ALB-5403 (8) USNM 81824; ALB-5541 (1) USNM 81815; ALB-5565 (2) USNM 81823; ALB-5567 (10) USNM 81829; ALB-5569 (25) USNM 81821; ALB-5577 (2) USNM 81834; ALB-5584 (17) USNM 81816; ALB-5586 (3) USNM 81818; ALB-5592 (1) USNM 81820; MUSORSTOM 2-33 (10) USNM 81836, (132) MNHNP; Atlantic specimens reported by Cairns (1979) USNM and Zibrowius (1980) MNHNP; Hawaiian specimens reported by Cairns (1984a) Bishop Museum and USNM; Miocene specimens of Squires (1958) from New Zealand (USNM 68391, 67913, 649156): NZOI A-910 (4) USNM 81802, Squires and Keyes (1967); USGS 24686 (4) USNM 208323 (*N. (Paradeltocyathus) orientalis* of Wells, 1977); USGS 24918 (12) USNM 73973 (*Peponocyathus orientalis* of Wells, 1984); 30 syntypes of *Deltocyathus minutus* Gardiner and Waugh, 1938, BM; syntypes of *Deltocyathus lens* Alcock, 1902, from *Siboga* 256 (1) and 275 (3), ZMA. *Reference Material: N. (P.) pedicellatus* Squires, 1958 (USNM 67902, 67940, 67948, 68396); *JM* 126 (1) BM 1950.1.9.1189 (*D. lens* of Gardiner and Waugh, 1938, = *Deltocyathus* sp.).

TYPES.—The holotype of *Deltocyathus italicus* var. *australiensis* is deposited at the BM (R29255) Plate 14*d,e*. *Type*

Locality: 1.5 miles west of Cape Otway, Victoria, Australia (Miocene: Janjukian).

Four syntypes of *Leptocyathus stimpsonii* Pourtalès, 1871, are deposited at the MCZ (5572) and 1 syntype is deposited at the Yale Peabody Museum (4766). *Type Locality:* Off Florida Keys, 110–293 m.

The holotype of *Deltocyathus orientalis* Duncan, 1876, appears to be lost from the BM (Zibrowius, 1980). *Type Locality:* 34°12'N, 136°20'E (off Owase, southeastern Honshū, Japan), 95 m.

Seven of the nine original syntypes of *Deltocyathus lens* Alcock, 1902, are deposited at the ZMA (Van Soest, 1979). Two are from *Siboga* 95 (5444); 2 are from *Siboga* 275 (5445) Plate 14*h;* 1 is from *Siboga* 256 (1191); and 2, from *Siboga* 59, are lost. *Type Locality:* Indonesia, 390–522 m.

The holotype of *Deltocyathoides japonicus* Yabe and Eguchi, 1932, is presumed to be deposited at the TIUS. *Type Locality:* Off Japan, depth unknown.

Fifty-eight syntypes of *Deltocyathus minutus* Gardiner and Waugh, 1938, are deposited at the BM: 29 syntypes from *JM* 206 are numbered BM 1950.1.9.1190–1219, Plate 14*f;* 1 syntype from *JM* 209 is numbered BM 1950.1.9.1237A. *Type Locality:* Southern Red Sea and off Kenya, 101–366 m.

DISTRIBUTION.—*Eocene:* Tonga (Wells, 1977). *Oligocene-Miocene:* New Zealand (Squires, 1958). *Miocene:* South Australia (Duncan, 1870). *Miocene to Pliocene:* Japan. *Pliocene:* Ceram (Umbgrove, 1925). *Pleistocene:* Vanuatu, Ryukyu Islands (Wells, 1984; Yabe and Eguchi, 1942b). *Recent:* Indo-West Pacific: Hawaii (Cairns, 1984a); Japan (Yabe and Eguchi, 1942b); off Hong Kong and Formosa Strait; throughout Philippines; Indonesia; New Zealand (Squires and Keyes, 1967); Australia (Veron, 1986); Red Sea and off Kenya (Gardiner and Waugh, 1938); Atlantic: Florida to Brazil (Cairns, 1979); Madeira and Azores (Zibrowius, 1980); 44–635 m; 6.2°–17.3°C.

16. *Peponocyathus folliculus* (Pourtalès, 1868)

PLATES 15*e–h*, 16*a–c*

Stephanophyllia folliculus Pourtalès, 1868:139.

Peponocyathus variabilis Gravier, 1915:5, figs. 1, 2.

Peponocyathus orientalis Yabe and Eguchi, 1932b:444–445, 1 fig. [junior secondary homonym of *D. orientalis* Duncan, 1876].—Eguchi, 1974, pl. 70: figs. 17, 18.

Discotrochus (Cylindrophyllia) minimus Yabe and Eguchi, 1937:146–147, pl. 20: figs. 16–22; 1942b:118.

Cylindrophyllia minima.—Wells, 1956:F426.—?Squires, 1958:58.—Eguchi, 1965:289, 2 figs.—Kikuchi, 1968:8, figs. 3a,b.—Zibrowius, 1980:112–113.

Kionotrochus (Cylindrophyllia) minima—Squires, 1960a:287–288, figs. 12–16.

Peponocyathus folliculus.—Cairns, 1979:113–115, pl. 22: figs. 1–4, pl. 20: fig. 11 [description and synonymy of Atlantic records].—Zibrowius, 1980:113–115, pl. 58: figs. A–L, pl. 59: figs. A–K [description and synonymy of Atlantic records].

Cylindrophyllia orientalis.—Mori and Minoura, 1983:185–191, figs. 1–6.

DESCRIPTION OF WESTERN PACIFIC SPECIMENS.—Corallum variable in shape: usually cylindrical with a flat or rounded base, but sometimes having constrictions or expansions of corallum diameter, producing an irregular shape (group B of Mori and Minoura, 1983). Mature coralla invariably greater in height than in calicular diameter, as much as 3.5 times. Largest corallum examined 4.0 mm in calicular diameter and 8.3 mm tall (ALB-5277), but most coralla 2.8–3.1 mm in calicular diameter. Costae equal in width (0.32–0.37 mm wide), uniformly covered by a very fine granulation, the granules about 0.06 mm tall. Intercostal furrows narrow (0.07–0.08 mm) and shallow (0.20–0.25 mm). C_1 extend to epicenter; C_2 bifurcate about 0.5 mm from epicenter, each forming two C_3. A new C_2 originates at point of bifurcation and sometimes fuses with one of the adjacent C_3. C_4, if present, originates as a bifurcation of a C_3 about 1.7 mm from the epicenter and always laterally on the corallum, well above the base.

Septa hexamerally arranged in three, and sometimes an incomplete fourth, cycles of septa, the number of septa having no apparent relationship to the calicular diameter (see group A-1 of Mori and Minoura, 1983). Maximum number of septa of the Philippine specimens is 36, with one pair of S_4 in each system. Septal formula: $S_1 > S_2 \leq S_3 > S_4$. S_1 moderately exsert, extend almost to the columella, and have straight inner edges. As in *P. australiensis*, the presence of paliform lobes is variable: small lobes are sometimes present on the lower, inner edges of the S_1 but are virtually indistinguishable from columellar elements. S_2 less exsert and extend about ²/₃ distance to columella, each bearing a robust, spiny palus on its inner margin. S_3 least exsert, their inner edges merging with a P_2. If pairs of S_4 are present, a P_3 occurs on the flanked S_3. Large granules about 0.10 mm tall cover septal faces but do not appear to be aligned.

Fossa absent, the pali and columella rising to the level of the upper septa and well above thecal edge. Columella papillose, composed of 4–8 basally united papillae.

DISCUSSION.—As noted in the generic discussion, the synonymy of *P. folliculus* has been complicated by its affiliation with *Cylindrophyllia*, a subgenus proposed by Yabe and Eguchi (1937) for the young stages of *P. folliculus*. To add to the confusion, *Cylindrophyllia* was subsequently synonymized with *Kionotrochus* (see Vaughan and Wells, 1943) or considered as a subgenus of *Kionotrochus* (see Squires, 1960a), but as Zibrowius (1980) pointed out, the young stages of many turbinoliid genera are very similar. More details concerning the synonymy of *P. folliculus*, especially its association with *Cylindrophyllia*, are found in the generic discussion.

As with *P. australiensis*, comparison of western Atlantic *P. folliculus* (Cairns, 1979; Zibrowius, 1980) with the western Pacific specimens revealed no specific differences. Adult *P. folliculus* are distinguished from *P. australiensis* by the corallum shape (which is variable, but usually cylindrical vs. usually hemispherical), costal granulation (fine granules vs. unilinear row of coarse teeth for *P. australiensis*), number of septa (rarely over 36 vs. 48), and insertion of C_4 (lateral vs. basally); however, small specimens of *Peponocyathus* are virtually indistinguishable.

MATERIAL EXAMINED.—ALB-5172 (1) USNM 81838; ALB-5217 (2) USNM 81839; ALB-5277 (1) USNM 81840; ALB-5311 (5) USNM 81841; ALB-5577 (1) USNM 81842; ALB-5584 (1) USNM 81837; specimens reported by Cairns (1979) and Zibrowius (1980); NZGS 9427 (1) USNM 67914 (*Cylindrophyllia minima* of Squires, 1958).

TYPES.—The holotype of *Stephanophyllia folliculus* is deposited at the MCZ. *Type Locality:* 24°12′40″N, 81°19′25″W (western Straits of Florida), 433 m.

Fourteen syntypes of *P. variabilis* Gravier, 1915, are deposited at the Museé Océanographique, Monaco. *Type Locality:* 39°26′10″N 31°21′30″W (north of the Azores), 650-914 m.

Five syntypes of *Peponocyathus orientalis* Yabe and Eguchi, 1932, are deposited at the TIUS (43423). *Type Locality:* Limestone plateau above Kamikatetsu, Kikai-jima, Japan (Pleistocene, Wan Formation).

Approximately 61 syntypes of *Discotrochus (Cylindrophyllia) minimus* from 16 localities are deposited at the TIUS. *Type Locality:* Neogene of Taiwan and Recent of Toyama Bay, Japan.

DISTRIBUTION.—*Oligocene:* New Zealand (Squires, 1958). *Neogene:* Taiwan (Yabe and Eguchi, 1937). *Miocene:* Japan (Eguchi, 1974). *Pleistocene:* Ryukyu Islands (Mori and Minoura, 1983). *Recent:* Off Honshū and Kyūshū, Japan (Kikuchi, 1968); off Hong Kong; Philippines (off Manila and Ragay Gulf, Luzon; Sulu Archipelago); off Sabah, Celebes Sea; Atlantic: Antilles (Cairns, 1979); Azores, Madeira to Portugal (Zibrowius, 1980); 50-582 m; 6.8°-17.2°C.

Tropidocyathus Milne Edwards and Haime, 1848

Flabellum.—Michelin, 1842:119 [in part].

Tropidocyathus Milne Edwards and Haime, 1848:326-327; 1850:xv; 1857:57.—Gardiner and Waugh, 1938:192-193.—Vaughan and Wells, 1943:213.—Wells, 1956:F426.—Chevalier, 1987:749, fig. 417,10.

Trochocyathus (Trochocyathus).—Alcock, 1902a:15 [in part: *T. pileus*].—Yabe and Eguchi, 1942b:123 [in part: *T. pileus*].

Trochocyathus (Tropidocyathus) Duncan, 1885:22.—Alcock, 1902a:17.—Yabe and Eguchi, 1942b:124.

Cyathotrochus Bourne, 1905:192.—Vaughan and Wells, 1943:213.

DIAGNOSIS.—Corallum cuneiform to campanulate with a rounded base and sometimes with alate lateral crests; transverse division lacking, but asexual fragmentation occurs in one species. Theca imperforate; costae serrate to granular and correspond to septa. Four cycles of highly exsert septa. Pali present in three crowns (P_{1-3}) before all but last septal cycle in adult stage. Columella papillose to lamellar.

DISCUSSION.—Although the type species of *Tropidocyathus* was originally described as a *Flabellum* by Michelin (1842), Milne Edwards and Haime (1848) were quick to establish a new genus for this species and correctly allied it to *Platytrochus*, a turbinoliid genus. Subsequently, however, *Tropidocyathus* was regarded as a subgenus of the caryophylliid genus *Trochocyathus* (see Duncan, 1885; Yabe and Eguchi, 1942b) until Vaughan and Wells (1943) resurrected it as a genus and transferred it to the subfamily Turbinoliinae, which was the original placement of Milne Edwards and Haime (1848). Wells (1956) suggested the synonymy of *Cyathotrochus* Bourne, 1905.

Of the three imperforate paliferous turbinoliid genera having pali before all but the last septal cycle (see Key 3) only *Tropidocyathus* maintains all three palar crowns in the adult stage. It is, perhaps, most similar to *Peponocyathus*, sharing with that genus the fusion of the higher-cycle septa and the ability to regenerate coralla from small fragments. *Tropidocyathus* is distinguished from *Peponocyathus* by its full expression of P_1 in the adult stage (P_1 are suppressed in *Peponocyathus*), cuneiform corallum shape (corallum variable in shape in *Peponocyathus*, but never cuneiform), and larger corallum size. Five species are assigned to *Tropidocyathus*: *T. lessoni* (Michelin, 1842); *T. nudus* Martin, 1880 (Miocene of Java); *T. affinis* Martin, 1880 (Miocene of Java); *T. pileus* (Alcock, 1902); and *T. nascornatus* Gardiner and Waugh, 1938. Characters of diagnostic value include: development of alate costae, costal granulation, and relative corallum fragility.

TYPE SPECIES.—*Flabellum lessonii* Michelin, 1842, by monotypy.

DISTRIBUTION.—*Miocene:* Java. *Pleistocene:* Japan. *Recent:* Indo-West Pacific; 68-522 m.

17. *Tropidocyathus lessoni* (Michelin, 1842)

PLATE 16*d-l*

Flabellum lessonii Michelin, 1842:119; 1843:1, pl. 6: 4 figs.

Tropidocyathus lessonii.—Milne Edwards and Haime, 1848:327.—Eguchi, 1965:289, 2 figs.

Tropidocyathus lessoni.—Milne Edwards and Haime, 1857:57.—Wells, 1956:F426, figs. 2a,b.—Gardiner and Waugh, 1938:194 [in part: 3 of 4 specimens].

Trochocyathus (Tropidocyathus) lessoni.—Alcock, 1902a:17, pl. 2: figs. 14, 14a.

Trochocyathus (Tropidocyathus) cf. *lessoni*.—Yabe and Eguchi, 1942b:124.

Trochocyathus (Tropidocyathus) wellsi Yabe and Eguchi, 1942b:153, pl. 10: figs. 22a,b.

Tropidocyathus wellsi.—Eguchi, 1965:290, 2 figs.

DESCRIPTION.—Corallum cuneiform, usually with a rounded base without evidence of original attachment. Thecal faces convex, diverging at a constant angle ranging between 48°-57°, except near calice, where thecal faces of larger coralla are vertical. Edge angle, exclusive of crests, 57°-66°. Largest specimen known, holotype of *T. wellsi*, 18×14 mm in calicular diameter and 17 mm tall. Calice variable in shape, ranging from diamond shaped to elliptical; GCD:LCD = 1.1-1.5. Edge crests robust but variable in size, ranging from 2.0-5.2 mm tall (the tallest that of Alcock's (1902a) figured specimen) and 0.6-1.4 mm thick. Costae broad and flat: C_{1-3}

about 0.5 mm wide, bearing 3 or 4 granules across their width, C_4 about 0.31–0.35 mm wide, bearing only 2 granules across its width. Intercostal furrows straight, except for the four furrows separating the two principal costae from their adjacent C_4. These furrows curve outward, following the edge of the crest, causing these four C_4 to be distinctly broad and irregular in shape, incorporating most of the crest coenosteum. Intercostal furrows narrow (about 0.15 mm) and relatively shallow (0.4 mm), degenerating about $^{2}/_{3}$ distance to corallum base. Costal granules triangular, about 0.15 mm tall, with a basal width of about 0.14 mm. Lower third of corallum and edge crests uniformly granulated, lacking costal furrows. Theca pale orange; septa white. Thecal thickness about 0.26 mm

Septa hexamerally arranged in 4 cycles. S_1 highly exsert (as much as 2.5 mm above upper theca), the farthest extend to the columella, and bear a small, independent palus about 0.3 mm broad. S_2 equally exsert but do not extend as far toward columella, usually bordered internally by a slightly larger palus about 0.5 mm broad; P_2 often missing. S_3 considerably less exsert than S_2 and extend only about half the distance to columella, each bearing a very large palus up to 1.6 mm broad, which often fuses with the pair of smaller P_2 in its system in a V-shaped structure. S_4 less exsert than S_3 but often extend slightly farther toward columella than the S_3. Inner edges of S_{1-2} vertical, straight, and flattened to slightly concave, the concavity forming a shallow groove along the inner edge of the septum. Inner edges of S_3 slightly sinuous, those of S_4 straight. Septal faces covered by pointed, mammiform granules up to 0.15 mm tall and about 0.27 mm in basal width (Plate 16*i*); palar granules up to 0.30 mm tall.

Fossa moderately shallow and filled with three cycles of pali and the columella. Columella elongate in alignment with the greater calicular diameter, composed of small basally fused papillae. In larger coralla the fused papillae produce a solid, almost lamellar, columella.

DISCUSSION.—Although the holotype of *F. lessonii* was not examined, the original description and subsequent illustrations (Michelin, 1843) leave little doubt about the identity of this distinctive species. Because Michelin's papers are relatively inaccessible, most identifications of *T. lessoni* have been based on Alcock's (1902a) excellent figures.

Again, although not examined, the description and illustrations of *T. wellsi* Yabe and Eguchi, 1942, are sufficient to synonymize it with *T. lessoni*. The alate end costae and orange corallum of *T. lessoni* distinguish it from all other species in the genus.

MATERIAL EXAMINED.—ALB-5133 (1) USNM 81843; ALB-5162 (1) USNM 81846; ALB-5178 (14) USNM 81845; ALB-5179 (1) USNM 81847; ALB-5311 (3) USNM 81844; MUSORSTOM 1-64 (1) MNHNP; MUSORSTOM 2-33 (1) MNHNP; MUSORSTOM 3-88 (1) MNHNP; MUSORSTOM 3-108 (1) MNHNP; MUSORSTOM 3-131 (1) MNHNP; JM 103 (3 of 4 specimens are *T. lessoni*, fourth is *Endopachys grayi*) BM 1950.1.9.1139-1141 (*T. lessoni* of Gardiner and Waugh, 1938). *Reference Material:* *Anton Bruun*-7-371 (1) USNM 77198; *Anton Bruun*-7-372 (4) USNM 77196, 77199; *Anton Bruun*-9-453 (3) USNM 77195; *Anton Bruun*-CH-5 (5) USNM 78582; *Siboga* 59 (1) ZMA 1411

TYPES.—The holotype of *F. lessonii* is deposited in the Michelin Collection at the MNHNP (Zibrowius, pers. comm.). No type locality was given.

The holotype of *Trochocyathus (Tropidocyathus) wellsi* Yabe and Eguchi, 1942, is deposited at the TIUS (43691). *Type Locality:* 31°52'N, 128°01'E (East China Sea, off Danjo Guntō, Japan), 155 m.

DISTRIBUTION.—*Pleistocene:* Ryukyu Islands (Yabe and Eguchi, 1942b). *Recent:* East China Sea, Kyūshū (Yabe and Eguchi, 1942b); South China Sea off Hong Kong; Philippines (off western Luzon, Mindanao, Sulu Archipelago); Indonesia (off Sabah, Celebes Sea; Flores Sea; Savu Sea; Ceram Sea; Timor Sea) (Alcock, 1902a); off Kenya (Gardiner and Waugh, 1938). Gardiner and Waugh's outlying record from the western Indian Ocean is substantiated by five additional records from the *Anton Bruun* that range from Natal, South Africa, to Somalia; 68–421 m; 11.7°–26.3°C.

18. *Tropidocyathus pileus* (Alcock, 1902), new combination

PLATE 17*a–h*

?*Tropidocyathus bougainvillei* Milne Edwards and Haime, 1857:57.

Trochocyathus (Trochocyathus) pileus Alcock, 1902a:15–16, pl. 2: figs. 11, 11a.—Faustino, 1927:81, pl. 7: figs. 7, 8.—Yabe and Eguchi, 1942b:123, pl. 10: figs. 19, 20.

?*Cyathotrochus herdmani* Bourne, 1905:193, pl. 1: figs. 2, 2a.

Trochocyathus (Tropidocyathus) intermedius Yabe and Eguchi, 1932b:443 [nomen nudum].

Not *Trochocyathus pileus*.—Gardiner and Waugh, 1938:187 [= *Premocyathus* sp.].

?*Tropidocyathus nascornatus* Gardiner and Waugh, 1938:193–194, pl. 5: fig. 10.

Trochocyathus pileus.—Eguchi, 1965:286, 2 figs.

DESCRIPTION.—Corallum variable in shape, ranging from trapezoidal (Plate 17*d*), to campanulate (Plate 17*a*), to triangular, the first two shapes having rounded bases, the latter having a slender, slightly curved base. Largest specimen examined (ALB-5506) 25.7×17.3 mm in calicular diameter and 18.8 mm tall. Calice elliptical, almost obscured by highly exsert septa; GCD:LCD = 1.5–1.65. No edge crests; however, in some trapezoidal and campanulate specimens the principal C_1 and two adjacent C_4 (or C_5) are quite prominent near the base (Plate 17*f,h*). Except for these costae, all others extend to the base of the corallum where they join their counterparts from the opposite face. Costae of equal width (0.36–0.39 mm), separated by deep intercostal furrows 0.18–0.25 mm wide. In larger coralla the intercostal space is much broader, up to 0.5 mm, and as much as 1 mm deep. This occurs because, as the corallum grows larger, its calicular circumference increases but the number of costae (48–56) and their width remain the same. Each costa bears a uniserial row of large, closely adjacent, blunt teeth, each about 0.22 mm in basal width, their appearance described as "milled" or serrate by Alcock (1902a). The lateral edges of each costa also bear smaller pointed granules up to 0.2 mm tall; the intercostal theca smooth. Corallum white.

Septa hexamerally arranged in four cycles, larger specimens having one or two pairs of S_5 in four half-systems adjacent to principal septa, for a total of 56–64 septa. S_1 highly exsert (up to 5 mm), with straight, vertical inner edges and a small, independent lamellar P_1 on its inner edge. In only one specimen, Alcock's (1902a) figured syntype, are the inner edges of the S_{1-2} grooved in the manner of *T. lessoni*. S_2 only slightly less exsert, also having a straight, vertical inner edge and a similar sized P_2, but one that extends slightly higher in the fossa. S_3 least exsert of all septa (about 1 mm), each bordered by a broad palus about twice as broad as the P_{1-2}. P_3 slightly recessed from columella and rise higher in fossa than other pali. As in *T. lessoni*, each pair of P_3 fuses with the enclosed P_2 in its septal system to form a V-shaped structure. S_4 moderately exsert (up to 3 mm), the theca between the S_4 and adjacent S_1 or S_2 raised about 2 mm, forming 12 rectangular projections around the circumference of the calice. S_4 extend slightly farther toward columella than S_3, their inner edges slightly overlapping and loosely fusing to the P_3. If pairs of S_5 are present, small P_4 are also present, each about the same size as a P_1 and recessed from the columella even more than the P_3. Septal and palar granules about 0.15 mm tall but quite scarce, resulting in relatively smooth septal faces. Septal granules vertically aligned short carinae in syntypes.

Fossa relatively shallow, filled with three cycles of pali and the columella. Columella variable in shape, ranging from a thin lamella to several basally fused, crispate papillae, to a spongy mass.

DISCUSSION.—The description of *T. bougainvillei* Milne Edwards and Haime, 1857, is very similar to that of *T. pileus*, but the type, stated to be deposited at the "Leiden Museum," is not present at the RMNH, and, unfortunately, Milne Edwards and Haime did not illustrate their specimen. If the type of *T. bougainvillei* is rediscovered and found to be conspecific with *T. pileus*, it would have nomenclatural priority.

Although not examined (type not at BM), *Cyathotrochus herdmani* Bourne, 1905, is tentatively placed in synonymy with *T. pileus* based on its original description and figures and the suggested synonymy of *Cyathotrochus* with *Tropidocyathus* by Wells (1956).

Tropidocyathus pileus is identical to *T. nascornatus* Gardiner and Waugh, 1938 (see Plate 17*i,j*), except that the coralla of populations of the latter always evidence asexual reproduction by fragmentation, which leads to oddly shaped asymmetrical coralla. Specimens from more populations need to be studied in order to determine if this is really a species-level difference.

Tropidocyathus pileus is easily distinguished from *T. lessoni* by its nonalate end costae; narrow costae that extend to the corallum base; coarse, uniserial, dentate costae; very deep and wide intercostal furrows; and white corallum.

MATERIAL EXAMINED.—ALB-5178 (8) USNM 81852; ALB-5277 (4) USNM 81851; ALB-5312 (1) USNM 81850; ALB-5317 (3) USNM 81849; ALB-5506 (1) USNM 81848; ALB-5508 (1) USNM 81854; ALB-5567 (15) USNM 81853; *Nimbus* 12 (1) USNM 78580; syntypes of *T. pileus*, ZMA. *Reference Material:* JM 207 (3) BM 1950.1.9.1262-1264 (syntypes of *T. nascornatus* Gardiner and Waugh, 1938); JM 106 (2) BM 1950.1.9.1062-1063 (*T. pileus* of Gardiner and Waugh, 1938); *Anton Bruun* 7-370 (2) USNM 77197, *T. nascornatus*.

TYPES.—The holotype of *T. bougainvillei* Milne Edwards and Haime, 1857, stated to be at the Leiden Museum in the original description, could not be found at the RMNH in 1988 (Borel-Best, pers. comm.). *Type Locality:* Not stated.

The four syntypes of *T. pileus* Alcock, 1902, all collected from *Siboga* 95, are deposited at the ZMA: the one figured by Alcock numbered 7352, the other three syntypes numbered 1326 (Van Soest, 1979)(Plate 17*d*). These four syntypes are labeled as "lectoholotype" and "lectoparatypen," respectively, but I know of no publication officially designating them as such and see no need to establish a lectotype since the syntype series is homogeneous. *Type Locality:* 5°43'N, 119°40'E (Sulu Archipelago), 522 m.

The deposition of the holotype of *Cyathotrochus herdmani* Bourne, 1905, is unknown. *Type Locality:* Periya Paar, Gulf of Manaar, depth unknown.

One hundred forty-four syntypes of *T. nascornatus* Gardiner and Waugh, 1938, from four JM stations are deposited at the BM, those from JM 207 are numbered BM 1950.1.9.1262-1264. *Type Locality:* Off Pemba Island, Tanzania, 207–438 m.

DISTRIBUTION.—*Pleistocene:* Ryukyu Islands (Yabe and Eguchi, 1942b). *Recent:* Off Japan (Yabe and Eguchi, 1942b); South China Sea off Hong Kong; Philippines (off Luzon, Sibuyan Sea, Bohol Sea, Sulu Archipelago); off Queensland, Australia; ?Gulf of Manaar, Indian Ocean (Bourne, 1905); ?off Pemba, Tanzania (Gardiner and Waugh, 1938); 123–522 m; 10.3°–15.5°C.

Idiotrochus Wells, 1935

Sphenotrochus.—Duncan, 1885:183–184.—Dennant, 1906:151.
Sphenotrochus (Idiotrochus) Wells, 1935:532–533.
Placotrochides.—Yabe and Eguchi, 1941a:104; 1942b:149.
Idiotrochus.—Vaughan and Wells, 1943:212.—Wells, 1956:F425.—Chevalier, 1987:746.

DIAGNOSIS.—Corallum cuneiform; anthocaulus often having a compressed but expansive base, which may bear two lateral projections; transverse division present. Theca imperforate; costae smooth; intercostal striae shallow. Septa alternate in position with costae. Three cycles of septa; septal faces carinate and granular. Pali present before first two septal cycles. Columella papillose to fascicular.

DISCUSSION.—Only two turbinoliid genera have costae that alternate in position with the septa: *Idiotrochus* and *Dunocyathus*. These genera are also similar in other characters, such as in having transverse division, P_{1-2} in one crown, and a papillose columella. The major point of difference is in corallum shape (Key 3): the anthocyathus of *Dunocyathus* is discoidal or patellate, the anthocyathus of *Idiotrochus* is cuneiform. Other differences are that the anthocaulus of *Dunocyathus* is always immersed in a bryozoan (the anthocaulus of *Idiotrochus* is as yet unknown), and the costae of *Dunocyathus* are granular, whereas those of *Idiotrochus* are smooth.

Four species are assigned to *Idiotrochus: I. emarciatus* (Duncan, 1865) (Miocene of South Australia), *I. australis* (Duncan, 1865) (Miocene of South Australia), *I. perexigua* (Dennant, 1906) (Recent, South Australia, 82-274 m), and *I. kikutii* (Yabe and Eguchi, 1941). Characters of diagnostic value include basal shape of anthocyathus and depth of intercostal striae.

TYPE SPECIES.—*Sphenotrochus emarciatus* Duncan, 1865, by original designation (Wells, 1935).

DISTRIBUTION.—Miocene: South Australia. *?Pliocene to Pleistocene:* Japan. *Recent:* Western Pacific from Japan to ?Australia; 82-645 m.

19. *Idiotrochus kikutii* (Yabe and Eguchi, 1941), new combination

PLATE 18*a,b,d-h*

Idiotrochus emarciatus.—Squires, 1961:18.—Chevalier, 1987:746.
Placotrochides kikutii Yabe and Eguchi, 1941a:104, 3 figs.; 1942b:149, pl. 9: figs. 16a–c.

DESCRIPTION.—Corallum (anthocyathus) variable in shape, but, in general, cuneiform, with a GCD:LCD ratio of 1.15-1.95. Basally the corallum is highly compressed, as though "pinched," the base often assuming a blade-like edge, which, sometimes, especially in large coralla, extends far beyond the thecal edges as a lateral crest (Plate 18*b*). In a minority of specimens the cylindrical corallum ends abruptly in a planar scar measuring about 2.0×1.5 mm in diameter. Thecal spines not present on anthocyathus. An anthocaulus, or a specimen in the process of transverse division, was not found in the study material. Largest specimen examined (MUSORSTOM 2-32) 4.6×3.6 mm in calicular diameter and 7.9 mm tall with a basal greater thecal diameter of 6.3 mm; but specimens are more typically 2.3×1.7 mm in calicular diameter and about 4.2 mm tall. Costae of small specimens wide (0.21 mm across) and smooth to slightly granular, separated by very narrow (0.03 mm) and shallow (0.02 mm) intercostal striae. Costae continuous from calice to base and alternate with septa. In larger coralla, costae are replaced by smooth, sometimes porcelaneous, dense theca; the costal definition only apparent at the calicular edge, if at all.

Septa hexamerally arranged in three cycles according to the formula: $S_1 > S_2 \geq S_3$. S_1 slightly exsert (e.g., 0.46 mm in a large specimen), extending almost 2/3 the distance to columella. S_2 less exsert (e.g., 0.30 mm), extending about 0.55 distance to columella. An elliptical crown of 10–12 P_{1-2} is present, the two principal P_1 often missing or greatly reduced in size. P_2 usually larger than P_1. Pali 0.3–0.4 mm wide and project to the level of calicular edge. S_3 equal to or slightly smaller than S_2. All septa and pali coarsely sinuous, the former bearing long obliquely oriented carinae along the summits of septal undulations, up to 0.10 mm tall and 0.7 mm long (Plate 18*f*) lower in the fossa. Septal faces also bear triangular granules about 0.10 mm tall on their upper, outer edges. Palar faces smooth, not granular.

Fossa shallow in small specimens, moderately deep in larger specimens, and contains the palar crown and columella. Columella composed of 3-7 twisted papillae in a linear or alternating arrangement, all basally interconnected among themselves and to the inner edges of the pali. Upper edges of columellar elements terminate below that of pali.

DISCUSSION.—The deeply incised intercostal furrows so characteristic of the turbinoliids are not present in *Idiotrochus kikutii*, although they are much better defined in the fossil congeners. Yabe and Eguchi's (1941a) provisional placement of this species in *Placotrochides*, a genus with transverse division, cuneiform corallum, and a porcelaneous, faintly costate theca, is easily understood; however, the presence of P_{1-2} clearly removes it from the Flabellidae. Yabe and Eguchi (1941a) also noted the resemblance of their species to *I. emarciatus*.

For the same reasons followed by Yabe and Eguchi (1941c), I did not originally consider this species to be a turbinoliid until I made direct comparisons to topotypic specimens of *I. emarciatus* and *I. australis* (see Plates 19*a* and 17*k*, respectively and "Material Examined" for specimen documentation). The calicular aspects of all three species are virtually identical, including the broad septal undulations with carinae, and the reduction or loss of the principal P_1. All three species also have the characteristic transverse division. The main difference between the fossil species and *I. kikutii* is that the former have shallow intercostal striae, continuous from calice to base, clearly revealing the turbinoliid nature of the genus, whereas *I. kikutii* usually has a porcelaneous theca. It is further distinguished from the fossil species in corallum shape: its base is blade-like with rounded edges, the fossil species have a characteristic "fish-tail" base, even *I. emarciatus*.

Although based on relatively few comparative specimens of *I. perexigua* (Dennant, 1906) (see Plate 18*c*), *I. kikutii* appears to differ from its Australian congener in having a larger corallum with a tapering, nonspinose anthocyathus base. The anthocyathus of *I. perexigua* is abruptly truncate and bears a pair of lateral thecal spines.

MATERIAL EXAMINED.—ALB-5162 (6) USNM 81907; ALB-5172 (2) USNM 81906; ALB-5178 (5) USNM 81908; ALB-5311 (5) USNM 81905; ALB-5584 (3) USNM 81909; ALB-5586 (1) USNM 81910; MUSORSTOM 2-32 (2)

MNHNP; MUSORSTOM 2-33 (18) USNM 81911, (391) MNHNP, (2) AM G15245. *Reference Material:* 31 topotypic specimens of *I. emarciatus* (USNM 67968, 68006, 77060, 77063, 77078 (Plate 19*a*)); 4 specimens of *I. australis* (USNM 68002, 68007, 77059 (Plate 17*k*)); 3 syntypes of *I. emarciatus* var. *perexigua* from off Neptune Island, 45 fms, South Australian Museum, Plate 18*c;* 4 specimens of *I. perexigua, Kimbla* 3-2639, AM G15236.

TYPES.—Six syntypes of *Placotrochides kikutii* Yabe and Eguchi, 1941, are deposited at the TIUS (63088). *Type Locality:* Toyama Bay, Japan, depth unknown.

DISTRIBUTION.—*Recent:* Toyama Bay, Honshū, Japan (Yabe and Eguchi, 1941a); South China Sea, off Hong Kong; Philippines (Verde Island Passage, Sibuyan Sea, Sulu Archipelago); off Sabah, Celebes Sea; 143-645 m; 6.7°-11.6°C.

Thrypticotrochus, new genus

Trochocyathus.—Dennant, 1906:153.

DIAGNOSIS.—Corallum small and conical; transverse division lacking, but regeneration from asexual fragmentation common. Theca imperforate; costae serrate, corresponding to septa. Four cycles of septa. One to three narrow paliform lobes on inner edges of every septum of first three cycles. Columella papillose.

DISCUSSION.—Among the 10 imperforate paliferous turbinoliid genera (see Key 3), *Thrypticotrochus* is distinguished as the only genus with multiple paliform lobes (not pali) on the S_{1-3}. Its tendency to regenerate from corallum fragments is shared with several other turbinoliids: e.g., *Tropidocyathus nascornatus* and *Peponocyathus australiensis.* Only one previously described species is known: *T. petterdi* (Dennant, 1906), new combination, known only from off Port Jackson, NSW, Australia.

ETYMOLOGY.—The generic name is from the Greek *thrypticotrochus* ("easily broken" plus "wheel"), and refers to the tendency of the corallum of this genus to easily fragment. Gender: masculine.

TYPE SPECIES.—*Thrypticotrochus multilobatus,* new species, here designated.

DISTRIBUTION.—*Recent:* Off Pratas Island, South China Sea; Philippines (Verde Island Passage, Ragay Gulf, Sulu Archipelago); off Lady Musgrave Island, Queensland; off Port Jackson, NSW; 130-507 m; 10.3°-17.2°C.

20. *Thrypticotrochus multilobatus,* new species

PLATE 19*b-g*

DESCRIPTION.—Corallum a narrow regular cone with a basal angle of 28°-30°. Five of the six specimens studied have an irregularly shaped base, as though the corallum had originated asexually from a smaller wedge-shaped fragment. Largest specimen (holotype) 3.8 mm in calicular diameter and 6.7 mm tall; calice circular. C_{1-2} about 0.17 mm wide; C_4, 0.09 mm wide, each costa separated by narrow (0.05-0.08 mm) furrows about 0.12 mm deep. Each costa bears a unilinear row of outward projecting blunt teeth about 0.10 mm tall and 0.07 mm in basal width, as well as less prominent lateral teeth about 0.06 mm tall and 0.04 mm in basal width (Plate 19*d*). Twelve C_{1-2} attain the epicenter. Each C_2 soon divides to form a pair of C_3; the C_3, in turn, dividing to form pairs of C_4; new C_1 and C_2 forming at points of bifurcation. The typical symmetry of turbinoliid costal arrangement is usually obscured by the irregularity of the corallum base, as mentioned previously.

Septa hexamerally arranged in four cycles according to the formula: $S_1>S_2\geq S_3>>S_4$. S_1 exsert (up to 0.6 mm) and extend about 0.9 distance to columella. Inner edges of S_1 moderately sinuous, the lower edges bearing 1-3 narrow paliform lobes, each up to 0.3 mm tall and 0.08 mm in width. S_2 slightly less exsert and extend about 0.7 distance to columella. Like the S_1, they also have moderately sinuous inner edges and 1-3 narrow paliform lobes on their lower, inner edges. S_3 less exsert than S_2 and extend toward columella an equal or slightly lesser distance than the S_2 (0.65-0.70 distance to columella). Inner edges of S_3 sinuous, bearing 0-3 narrow paliform lobes, the number depending on the space available in the fossa. All paliform lobes merge indistinguishably with the columella. S_4 least exsert of all septa, extending only 0.3 distance to columella; S_4 do not bear paliform lobes. Septal faces covered by prominent pointed granules up to 0.10 mm tall and with a basal width of about 0.55 mm. All septa independent, not joined to one another by their inner edges.

Fossa shallow, containing a central mass of paliform lobes and columellar papillae, indistinguishable in size and shape.

DISCUSSION.—*Thrypticotrochus multilobatus* is very similar to its only congener, *T. petterdi,* differing only in having much broader costae (much wider than intercostal furrows); the costae of *T. petterdi* are less wide than the intercostae. This comparison was made on limited materail; future comparisons may prove that the two species are conspecific.

ETYMOLOGY.—The species name, from the Latin *multilobatus* ("multiple" plus "lobes"), refers to the multiple paliform lobes on the S_{1-3}.

MATERIAL EXAMINED.—Types. *Reference Material:* 2 paratypes of *Trochocyathus petterdi* Dennant, 1906, AM G12050.

TYPES.—*Holotype:* ALB-5576, USNM 81901, Plate 19*b,c*. *Paratypes:* ALB-5217 (1) USNM 81902; ALB-5301 (3) USNM 81903; MUSORSTOM 2-33 (1) MNHNP; *Kimbla* 3-2634, AM G15259. *Type Locality:* 5°25′56″N, 120°03′39″E (off Tawi Tawi, Sulu Archipelago), 507 m.

DISTRIBUTION.—Same as for the genus.

Sphenotrochus Milne Edwards and Haime, 1848

Sphenotrochus Milne Edwards and Haime, 1848:240-241; 1850:xviii; 1857:65-66.—Duncan, 1885:16.—Wells, 1935:530 [in part: subgenus

Eusthenotrochus, but not *Idiotrochus*].—Vaughan and Wells, 1943:211-212.—Alloiteau, 1952:645.—Wells, 1956:F425.—Chevalier, 1961:302.—Zibrowius, 1980:108.—Chevalier, 1987:746.

DIAGNOSIS.—Corallum cuneiform with a rounded base; transverse division lacking. Theca imperforate; costae smooth, corresponding to septa. Costae sometimes degenerate into discontinuous fragments on basal or all of thecal face. Three or four cycles of septa. Pali absent; columella lamellar.

DISCUSSION.—Wells (1935) divided *Sphenotrochus* into three subgenera: nominate, *Eusthenotrochus*, and *Idiotrochus*. The latter was elevated to generic status by Vaughan and Wells (1943), but *Eusthenotrochus* is still considered a valid subgenus, characterized by discontinuous costae. The vast majority of species belong to the nominate subgenus.

There are eight recognized imperforate nonpaliferous turbinoliid genera (see Key 3 and discussion of subfamily). *Sphenotrochus* is distinguished from *Sphenotrochopsis* by its cuneiform corallum, the latter having a turbinate corallum. The only other genera that *Sphenotrochus* could be confused with are *Platytrochus* and *Koilotrochus*, both of which have cuneiform coralla but differ in having a papillose columella. *Platytrochus* and *Koilotrochus* were synonymized by Vaughan and Wells (1943) and separated again by Wells (1956), who distinguished them based on the presence of the thickened end costae in *Platytrochus*. The end costae of the type species of *Platytrochus*, *P. stokesi* Lea, 1833, are very distinctive, but species subsequently assigned to *Platytrochus* have much less developed end costae and therefore approximate *Koilotrochus*. The difference between these two genera is slight. Correspondingly, not all species currently assigned to *Sphenotrochus* have a distinct lamellar columella; some species, such as *S. gardineri* Squires, 1961; *S. ralphae* Squires, 1964; and *S. pulchellus* (Lea, 1833), have a uniserial row of papillae as a columella, similar to that of *Platytrochus* or *Koilotrochus*. Although not formally proposed here, it is suggested that this genus complex be revised, reserving *Sphenotrochus* for those imperforate nonpaliferous cuneiform turbinoliids with a lamellar columella, and *Platytrochus* for those cuneiform turbinoliids with a papillose columella, regardless of end costal morphology.

Approximately 33 valid species of *Sphenotrochus* are recognized, including 25 exclusively fossil species. Of the 25 fossil species, the majority (15) are restricted to the Eocene to Miocene of Europe; four are known from the Miocene of the western Pacific; and 6 are known from the Eocene to Miocene of the Caribbean and eastern United States. The eight Recent species are as follows: Pacific—*S. excavatus* Tenison-Woods, 1878; *S. hancocki* Durham and Barnard, 1952; *S. ralphae* Squires, 1964; South African—*S. aurantiacus* Marenzeller, 1904; *S. (E.) gilchristi* Gardiner, 1904; Subantarctic—*S. gardineri* Squires, 1961; Atlantic—*S. auritus* Pourtalès, 1874; and *S. andrewianus* Milne Edwards and Haime, 1848. Characters used to distinguish species include the shape of the corallum, nature of costal ornamentation, nature of columella, and number and relative exsertness of septa.

TYPE SPECIES.—*Turbinolia crispa* Lamarck, 1816, by subsequent designation (Milne Edwards and Haime, 1850).

DISTRIBUTION.—*Eocene to Recent:* Worldwide, including Antarctic; 9-403 m.

Subgenus *Sphenotrochus (Sphenotrochus)* Milne Edwards and Haime, 1848

DIAGNOSIS.—*Sphenotrochus* in which the costae are continuous from calice to base, or, at least, for upper part of thecal face.

21. *Sphenotrochus (S.) hancocki* Durham and Barnard, 1952

PLATE 20*a–h*

?*Turbinolia intermedia* Goldfuss, 1827:108, pl. 37: fig. 19.
Sphenotrochus hancocki Durham and Barnard, 1952:94–95, pl. 13: figs. 57a,b.—Wells, 1983:236.

DESCRIPTION.—Corallum smooth, cuneiform, and highly compressed; a typical large specimen only 2.2×1.5 mm in calicular diameter and 3.6 mm tall. Ratio of GCD:LCD 1.4-1.5. Base usually rounded, but sometimes irregular in shape caused by inclusion of a piece of the original substrate of attachment. Substrate inclusions for most specimens examined appear to be small pieces of bivalve shell. In one case the shell was too large to be fully incorporated into the coral base, resulting in a thin basal incrustation over a large part of the shell. All costae equal in width (0.16–0.18 mm), separated by broad (0.10 mm), shallow (0.08 mm) intercostal furrows. In the specimens examined by SEM, small pits 1.3–1.5 µm in diameter were very common in the intercostal furrows (Plate 20*e,f*), the function of which is unknown. Costae rounded, smooth, and porcelaneous, lacking granulation. On lower half to third of thecal faces the costae degenerate into discontinuous, elongate to round fragments of variable length but approximately the same width as a costa. Thecal thickness about 0.08 mm.

Septa hexamerally arranged in three cycles according to the formula: $S_1=S_2>>S_3$. S_{1-2} exsert (0.3 mm in large specimens) and extend 0.6 distance to columella. The six S_{1-2} that originate from the thecal lateral faces merge solidly with the columella about 0.5 mm below calicular edge. Inner septal edges of S_{1-2} moderately sinuous. S_3 less exsert (about 0.15 mm) and much reduced, composed of a low ridge about 0.05 mm tall made up of a discontinuous series of trabecular spines. Septal and columellar faces virtually smooth, bearing only sparse, blunt-tipped, cylindrical granules up to 0.05 mm tall with a basal width of 0.03 mm.

Columella highly exsert, attaining the level of the S_{1-2}. Columellar lamella a thin, straight plate with rounded edges and sharp upper crest, up to 1.1 mm long and 0.08–0.10 mm wide.

DISCUSSION.—As previously implied by Wells (1983), the

Philippine *Sphenotrochus* are very similar to *S. hancocki*. Direct comparison of the *Albatross* Philippine specimens to types of *S. hancocki* show them to be the same species, differing in that in the type specimens 10 S_{1-2} fuse with the columella, not 6, as in the Philippine specimens.

Miocene specimens of *S. intermedius* from Costa Rica alluded to by Wells (1983) are also indistinguishable from *S. hancocki*. The type locality of *S. intermedius* (Goldfuss, 1827) is the Miocene of Belgium, and most subsequently reported records of this species have come from the Miocene to Pliocene of Europe. Duncan's (1873) record of Recent specimens of *S. intermedius* from the eastern Atlantic are *S. andrewianus* (see Zibrowius, 1980), and Gardiner and Waugh's (1938) record of *S. intermedius* from the Gulf of Aden, although not examined, is probably not the fossil *S. intermedius*.

Only two other valid Recent western Pacific *Sphenotrochus* have been described: *S. excavatus* Tenison-Woods, 1878, and *S. ralphae* Squires, 1964. *Sphenotrochus hancocki* is distinguished from the Australian *S. excavatus* by its smooth costae, exsert columella, small corallum, and lack of edge crests. *Sphenotrochus ralphae*, known only from New Zealand, differs in having a papillose columella, continuous granular costae, and larger S_3. At least four valid fossil species have been described from the western Pacific: *S. javanus* Gerth, 1933 (Miocene of Java); *S. aschistus* Squires, 1958 (Miocene of New Zealand); *S. laculatus* Squires, 1962 (Tertiary of New Zealand); and *S.* n. sp. A Squires, 1962 (Tertiary of New Zealand). *Sphenotrochus hancocki* is distinguished from *S. javanus* by having discontinuous costae, and from the other three species by having considerably less septa (24 vs. ≥48). Many other *Sphenotrochus* species have been described from the Tertiary of Australia but most have been reassigned to other genera.

MATERIAL EXAMINED.—ALB-5145 (1) USNM 81896; ALB-5311 (3) USNM 81897; ALB-5312 (18) USNM 81898 (cited by Wells, 1983); ALB-5313 (15) USNM 81899; ALB-5315 (1) USNM 81900; USGS-8343 (10) USNM 64032, 68406 (cited by Wells, 1983); holotype and paratypes of *S. hancocki* (3) AHF.

TYPES.—The holotype (Plate 20*h*) and two paratypes of *S. hancocki* are deposited at the AHF (20). *Type Locality:* Stephen's Bay, Chatham Island, Galápagos, 59 m.

DISTRIBUTION.—*Miocene:* Costa Rica. *Recent:* Philippines (Sulu Archipelago, off Jolo Island); South China Sea off Hong Kong; Lower California; Galapágos (Durham and Barnard, 1952); 18–274 m; 12.4°–14.1°C.

Endocyathopora, new genus

DIAGNOSIS.—Corallum small and conical, with a rounded base; transverse division lacking. Theca imperforate; however, inside corallum there are longitudinal rows of circular depressions in each interseptal space. Costae correspond to septa. Three cycles of septa. Pali before second septal cycle; columella papillose.

DISCUSSION.—The turbinoliid genera can be divided into those that have a perforate theca or those that have an imperforate theca (Table 3). Those with a perforate theca have small, circular to elliptical pores arranged (1) in pairs, one on either side of a low pseudocostum (e.g., *Turbinolia*), (2) in an alternating arrangement in each intercostal space, or (3) unilinearly along each intercostal space. In all cases the pores penetrate the theca when the coral is alive and are easily visible externally on the corallum. Genera with imperforate theca have no such pores. *Endocyathopora* is intermediate between these two groups in having a unilinear row of large depressions inside the theca aligned in each intercostal space. In living specimens these depressions do not appear to penetrate the theca and thus are not visible externally. In worn coralla, however, they are visible externally, the depressions being sites of lesser thecal calcification that are apparently eroded faster. The depressions are very similar to the internal pits described in the guyniids, especially *Guynia*.

Among the four other perforate genera (*Turbinolia* Lamarck, 1816; *Conocyathus* d'Orbigny, 1849; *Trematotrochus* Tenison-Woods, 1879; and *Bothrophoria* Felix, 1910), *Endocyathopora* is most similar to *Conocyathus* in having large, distinctive P_2 and a solid columella, but can be distinguished by its internal thecal depressions and distinctively shaped granular costae. Among the imperforate genera, *Endocyathopora* is most similar to *Kionotrochus*, both having P_2 exclusively, but is distinguished by its internal thecal depressions, distinctive costae, and presence of P_3.

ETYMOLOGY.—The generic name is from the Greek *endocyathopora* ("within" plus "cup" plus "pore") and refers to the row of depressions found in each interseptal space inside the corallum. Gender: feminine.

TYPE SPECIES.—*Endocyathopora laticostata*, new species, here designated.

DISTRIBUTION.—*Recent:* Sulu Sea off Basilan Island and west of Mindanao; 46–70 m.

22. *Endocyathopora laticostata*, new species

PLATE 21*a–e*

DESCRIPTION.—Corallum a narrow, regular cone with a blunt rounded base; basal angle 19°. Holotype 3.3 mm in calicular diameter and 6.9 mm tall; calice circular. Costae equal in width and trapezoidal in cross section, the two parallel sides of the trapezoid being the interior (side adjacent to theca) and exterior (side open to view) costal sides and the two nonparallel sides are the lateral costal edges, which are equal in length and tilted outward such that the costa is wider (e.g., 0.28 mm wide) at the exterior surface than at the thecal surface (e.g., 0.15 mm wide). Correspondingly, the intercostal furrows, which are about 0.16 mm wide on the thecal face, decrease to about 0.04 mm wide at the level of the exterior edge of the costae. Viewed laterally, the costae thus appear to be broad, equal sized, and flat, separated by deep (0.16 mm) and narrow intercostal furrows, but viewed from above (calicular view), the trapezoidal cross section of each costa is revealed (Plate 21*e*). Costae covered by very low, equilateral triangular granules about 0.02 mm tall and 5-6 mm across the width of a costa near the calicular edge. Small granules also project laterally from upper, outer costal edges, producing a fine serration and obscuring the intercostal furrow. C_{1-2} originate at the base, the C_2 bifurcating to form the C_3 at a variable distance from base, a newly formed C_2 extending beyond the bifurcation. Aligned with each intercostal furrow, at intervals of every 0.3-0.4 mm on the interior of the corallum, are shallow, circular depressions 0.11-0.12 mm in diameter. The depressions are visible externally only as a variation in the translucency of the theca, barely visible through the narrow intercostal furrow.

Septa hexamerally arranged in three cycles according to the formula: $S_1 > S_2 = S_3$. S_1 slightly exsert (e.g., 0.45 mm), extend about 0.9 distance to columella, and have sinuous inner edges that are slightly undercut near the columella. S_{2-3} slightly less exsert (e.g., 0.40 mm), extend about 0.6 distance to columella, and also have sinuous inner edges. Each S_2 bordered by a palus about 0.32 mm long and 0.08 mm wide. Some S_3 have small irregularly shaped paliform lobes that extend above level of P_2. Septal and palar faces covered with large (0.04 mm tall) equilateral triangular, nonaligned granules.

Fossa moderately deep, containing a small columella composed of one papilla.

ETYMOLOGY.—The species name is from the Latin *laticostata* ("wide" plus "ribbed"), and refers to the broad costae of this species.

MATERIAL EXAMINED.—Types.

TYPES.—*Holotype:* ALB-5134, USNM 81894, Plate 21*a-e*. *Paratypes:* ALB-5133 (2) USNM 81895. *Type Locality:* 6°44′45″N, 121°48″E (Sulu Sea off Basilan Island), 46 m.

DISTRIBUTION.—As for the genus.

Superfamily FLABELLICAE Bourne, 1905

DIAGNOSIS.—Caryophylliina with an epithecal wall.

Family GUYNIIDAE Hickson, 1910

DIAGNOSIS.—Corallum small, solitary, fixed or free, ceratoid to scolecoid. Wall epithecal, penetrated by rows of mural pores in every or every other interseptal space, which are later replaced by stereome. Costae usually absent, epitheca smooth or folded in imbricate growth bands. Septa few in number, rarely more than 24, and nonexsert. Septa composed of a single fan system of numerous, closely spaced trabeculae, which produce a smooth septal edge. Pali present or absent; columella present or absent, if present: fascicular or papillose. Exclusively ahermatypic.

DISCUSSION.—*Guynia* Duncan, 1872, was originally described in the rugose coral family Cyathaxonidae, thought to have become extinct before the Mesozoic, although Duncan (1885:31) later admitted that the placement of a Recent genus in a Paleozoic family "gives much trouble to the classificatory zoologist." Hickson (1910) solved this problem by describing a new family for *Guynia*, which he allied to the scleractinian family Turbinoliidae (= Caryophylliidae). Gardiner and Waugh (1938) place *Guynia* and two other genera, *Schizocyathus* and *Stenocyathus*, in the Flabellidae; however, most subsequent revisers of the Scleractinia (e.g., Vaughan and Wells, 1943; Alloiteau, 1952), considering that the theca of the guyniids was septothecate, followed Hickson in placing the Guyniidae as one of four or five families in the superfamily Caryophylliicae. Alloiteau (1952) divided the family into two subfamilies: the nominate subfamily, which he defined as having mural pores, and Conosmilinae, defined as lacking mural pores. Finally, Wells (1956), recognizing the epithecal nature of the wall, transferred the family into the superfamily Flabellicae, and redefined the Guyniidae to include only those genera having thecal pores.

Guyniidae and Flabellidae are the only two families in the superfamily Flabellicae. The basic difference between the two families is that all guyniid genera have mural pores, flabellids do not. Other less consistent differences are that the guyniids often have pali, flabellids never have pali and only one genus has paliform lobes; the guyniids have tiny, ceratoid to cylindrical coralla, flabellids usually have larger, flabellate to turbinate coralla; and guyniids have relatively few (≤3 septal cycles) septa, flabellids usually have over three and as many as seven septal cycles.

Table 3 compares the eight known guyniid genera. Of these genera, six have fossil records, three of which are exclusively fossil. Sixteen species are recognized in the family, 15 of which have been described; 10 of the 16 species are exclusively fossil, and another two, *G. annulata* and *Pourtalocyathus hispidus*, are known from the Miocene to the Recent (Cairns and Wells, 1987).

DISTRIBUTION.—*Upper Jurassic to Recent:* Worldwide, but not the Antarctic; 28-1300 m.

Guynia Duncan, 1872

Guynia Duncan, 1872:32-33; 1885:32.—Vaughan and Wells, 1943:224.—Alloiteau, 1952:650.—Wells, 1956:F432-433; 1973:59-61.—Cairns, 1979:163.—Zibrowius, 1980:161.—Cairns and Wells, 1987:42.—Chevalier, 1987:751, fig. 416,8.
?Bistylia Tenison-Woods, 1878c:114.—Duncan, 1885:20.
Pyrophyllia Hickson, 1910:1-7.

DIAGNOSIS.—Corallum ceratoid to scolecoid, free or laterally attached. Theca covered by concentric, imbricate growth bands; rows of thecal pores equally spaced in every septal space. Twelve to 16 nonexsert septa arranged in two cycles: 6:6 or 8:8; secondary septa rudimentary. Pali absent;

TABLE 3.—Comparisons of the eight genera of the Guyniidae.

Characters	*Truncatoguynia*, new genus	*Onchotrochus* Duncan, 1870	*Schizocyathus* Pourtalès, 1874	*Cyathosmilia* Tenison-Woods, 1878	*Guynia* Duncan, 1872	*Stenocyathus* Pourtalès, 1871	*Microsmilia* Koby, 1888	*Pourtalosmilia* Cairns, 1979
Columella	absent	absent	absent	weak, rudimentary	1 twisted lath	1-2 twisted laths	several laths	papillose
Pali	absent	absent	P_2, P_3	P_1, P_2	absent	P_2	absent	P_2
Costae	absent	feeble striae	absent	broad, rounded	concentric epithecal growth bands	concentric epithecal growth bands	absent	hispid or smooth
Thecal pore arrangement	every interseptal space, flanking secondary septa	unknown	in half of interseptal spaces, flanking S_2	every interseptal space	equally spaced in every interseptal space	every interseptal space, flanking S_3	every interseptal space	every interseptal space, flanking S_3
Septal symmetry	16:16 or 7:7:14 (28-32 septa)	unknown	$S_1>S_3>>S_2$ (24 septa)	$S_{1-2}>S_3>S_4$ (24-48 septa)	6-8:6-8 (12-16 septa)	$S_1>S_2>S_3$ (24 septa)	unknown	$S_1>S_2>S_3$ (24 septa)
Corallum shape	compressed cylinder; truncate; free	scolecoid, nodular; free	ceratoid; free	ceratoid; fixed	ceratoid-scolecoid; laterally attached	ceratoid-cylindrical; free	ceratoid; fixed	ceratoid; free
Asexual budding	transverse division	absent	longitudinal parricidal budding	absent	extratentacular offshoots	absent	longitudinal parricidal budding	absent
Number of species (fossil + Recent)	0 + 2	2 + 0	0 + 1	2 + 0	?1 + 1	2 + 1	3 + 0	0 + 1
Distribution	Recent: W Pacific; 161-179 m	Upper Cretaceous: England	Recent: Atlantic; 88-1300 m	Eocene to Oligocene: Australia	Eocene to Recent: worldwide; 28-653 m	Paleocene: Alabama; Eocene: Tonga; Recent: Atlantic, IWP; 110-1229 m	Upper Jurassic: Switzerland	Miocene: Dominican Republic; Recent: W Atlantic; 349-1200 m

columella composed of one twisted lath.

DISCUSSION.—*Guynia* is easily distinguished from the other guyniid genera (Table 3) by having only one columellar lath, no pali, and a total septal complement of 12-16. Two species have been assigned to the genus: *G. annulata* and *G. adherens* (Tenison-Woods, 1878). The latter species is known only from syntypes collected from the Eocene to Oligocene of Aldinga, Australia, and differs from *G. annulata* in septal symmetry and number of columellar laths. I have not examined specimens of *G. adherens* and its generic attribution is considered doubtful.

TYPE SPECIES.—*Guynia annulata* Duncan, 1872, by monotypy.

DISTRIBUTION.—*?Eocene to Oligocene:* Australia (Tenison-Woods, 1878). *Miocene:* Dominican Republic. *Recent:* Atlantic, Persian Gulf, Red Sea (Zibrowius, pers. comm.), Hawaiian Islands, New Caledonia, South Australia (unpublished), Philippines; 28-653 m.

23. *Guynia annulata* Duncan, 1872

PLATES 21*f*, 22*a–e*

Guynia annulata Duncan, 1872:32, pl. 1: figs. 1-8.—Cairns, 1979:164-165, pl. 32: figs. 1-3 [complete synonymy].—Zibrowius, 1980:161-163, pl. 83: figs. A-Q [complete synonymy].—Cairns, 1984a:23, pl. 5, figs. A-B.—Cairns and Wells, 1987:42-43, pl. 11: figs. 8, 9, 12, 13.
Pyrophyllia inflata Hickson, 1910:1-7, figs. 1-4.
Guynia sp.—Goreau and Wells, 1967:449.

DESCRIPTION.—Corallum cylindrical and scolecoid, the longest specimen examined 10.4 mm long. Calice circular, 1.0-1.1 mm in diameter. Corallum basally or laterally attached to small sand grains, foraminifera, or bits of shell. Epitheca periodically ringed by slightly imbricate growth ridges, each ridge about 0.06 mm thick, occurring at intervals of about every 0.20 mm. Sixteen vertical ridges (costae) of about the same dimensions also usually present, one corresponding to each septum. Intersections of the vertical and circumferential ridges form a grid-like pattern of rectangles (almost squares). Within each rectangle is a round mural pore, each 0.08-0.11 mm in diameter. Viewed from the exterior, the pore is a chalky white thecal spot against a white corallum and is not visible in surface relief (e.g., by SEM); viewed from within the calice (Plate 22*b*,*c*,*e*) the pores are seen to be shallow pits, occasionally completely penetrating the theca.

Septa octamerally arranged in two size groups (8 primary and 8 secondary septa); however, the broken bases of four specimens reveal an originally hexameral symmetry of 12 septa. Primary septa have highly sinuous inner edges, are nonexsert, and are about 0.05 mm thick. The nonexsert nature of the S_1 is reinforced by having very narrow upper edges that only gradually widen deeper in the fossa. Secondary septa much smaller (about 1/4 as wide as primaries), less sinuous, and about 0.01 mm in diameter. The tiny secondary septa are recessed 0.6-1.0 mm from the calicular edge and, like the primaries, have a very narrow upper edge, such that they are visible only in a damaged corallum. They cannot be seen from a calicular view of an intact corallum.

Fossa shallow. Columella a single twisted or flanged ribbon about 0.22 mm in diameter.

DISCUSSION.— *Guynia annulata*, one of the smallest species of Scleractinia, is also one of the few species that is cosmopolitan in distribution. Previously known only from scattered Atlantic records in recent years it has been reported from various locations throughout the Indo-West Pacific and in the fossil record from the Miocene of the Dominican Republic. Careful examination of these specimens by means of SEM does not reveal any specific differences.

Atlantic specimens of *G. annulata* have either 12 or 16 septa, usually 16 (Cairns, 1979), which is also the case in the Pacific, where only one specimen has been reported with 12 septa (Cairns, 1984a).

Only one other species is attributed to *Guynia*, *Bistylia adherens* Tenison-Woods, 1878, an Oligocene fossil from Australia. Although not examined, based on the original description it is highly doubtful that *G. adherens* belongs in this genus.

MATERIAL EXAMINED.—MUSORSTOM 2-33 (8) MNHNP, Plates 21*f*, 22*a–e*; *Siboga* 153 (1) attached to syntype of *Bathyactis palifera:* syntypes of *G. annulata;* specimens reported by Cairns 1979, 1984a; Cairns and Wells, 1987; and Zibrowius, 1980.

TYPES.—Eighteen syntypes of *G. annulata* are deposited at the BM (1883.12.10.110-120). *Type Locality:* Adventure Bank, Mediterranean, 168 m.

The syntypes of *Pyrophyllia inflata* Hickson, 1910, are also deposited at the BM (1950.3.22.18). *Type Locality:* Gulf of Oman, 286 m.

DISTRIBUTION.—*Miocene:* Dominican Republic (Cairns and Wells, 1987). *Recent:* Philippines (Verde Island Passage); Moluccas, Indonesia; New Caledonia (Zibrowius, pers. comm.); Hawaiian Islands (Cairns, 1984a); Persian Gulf (Hickson, 1910); Atlantic (Cairns, 1979; Zibrowius, 1980); 28-653 m.

Truncatoguynia, new genus

DIAGNOSIS.—Corallum compressed-cylindrical, budding by transverse division; anthocaulus unknown. Epitheca smooth; rows of thecal pores occur in every interseptal space, appearing to flank the secondary septa. Twenty-eight to 32 nonexsert septa arranged in two or three size classes. Pali and columella absent.

DISCUSSION.—*Truncatoguynia* is easily distinguished from the other seven guyniid genera (Table 3) by having transverse division, which results in an anthocyathus with a truncate base. It is also the only genus within the family to have a laterally compressed corallum. In fact, *Truncatoguynia* is morphologically closer to various genera in its sister family, the Flabellidae, specifically *Placotrochides* and *Truncatoflabellum* than to genera in its own family. Both of these genera have truncate bases identical to *Truncatoguynia*, and *Placotrochides* is similar as well in corallum size and shape, and in lacking thecal edge crests and spines, which *Truncatoflabellum* usually have. *Placotrochides* and *Truncatoguynia* differ primarily in the highly weighted character of mural pores, which distinguishes the two respective families. The anthocaulus of *Placotrochides* is reinforced with stereome, a character that differentiates it from *Truncatoflabellum*. The anthocaulus of *Truncatoguynia* is as yet unknown, but it would be of interest to know if this is yet another similarity of the two genera.

One described and one undescribed species are known in the genus (see discussion of *T. irregularis*).

ETYMOLOGY.—The genus name is from the Latin *truncato* (truncate) plus the patronym for the preestablished genus *Guynia* (named for J. Gwyn Jeffreys), and refers to method of asexual reproduction by transverse division, resulting in an anthocyathus with a truncate base. Gender: feminine.

24. *Truncatoguynia irregularis*, new species

PLATES *22f,g, 23a–c,f*

DESCRIPTION.—Corallum a compressed cylinder: angle of rounded thecal edges only 5°–8°; inclination of lateral thecal faces, 7°–8°. Largest specimen (holotype) 5.3×2.8 mm in calicular diameter and 10.1 mm tall, with a basal scar of 5.0×2.6 mm; the upper millimeter of this specimen showing a slight retrenchment of growth from a previous calicular diameter of 6.3×3.5 mm. Three of 12 specimens show a constricted corallum caused by a temporary retrenchment in growth. Ratio of GCD:LCD = 1.5–2.2. Thecal spines absent. Basal scar elliptical: V-shaped when viewed from lateral thecal edge, and almost as large as the calice, testifying to the very low thecal edge and face angles and relatively short corallum (e.g., ratio of greater calicular diameter to greater scar diameter = 1.06–1.20). Anthocaulus unknown. Theca smooth, porcelaneous, and overall light brown, but usually white just above basal scar. Chevron-shaped growth striae present. Internal thecal pits, which occasionally penetrate the theca as pores, occur in lines, one line corresponding to each interseptal space. Lines of pits appear to be paired, flanking each secondary septum, as the distance between adjacent lines of pits on either side of a primary septum is about 0.25 mm, whereas the distance between adjacent lines of pits on either side of a secondary septum is about 0.08 mm. Thecal pits circular, about 0.20 mm in diameter, seen on outer theca as chalky white spots.

Septal symmetry and relative sizes of septa unclear due to damaged condition of all but one specimen. At level of columella 10 of the 12 specimens have 16 thick (0.18 mm), robust septa that join the columella. Between each of these primary septa is a much smaller (1/4 to 1/5 depth of primary), thinner (0.08 mm) secondary septum, making a total of 32 septa. Two specimens have 28 septa, including the undamaged corallum, which has septa of three size classes. Inner edges of larger septa of this specimen quite sinuous. Septal faces covered by large, blunt granules up to 0.13 mm tall.

Columella rudimentary, much as in the genus *Truncatoflabellum*.

DISCUSSION.—This species has not been previously reported in the literature, and the genus is monotypic; however, there is an undescribed congener in the collections of the NMNH (USNM 81893) from off Raoul Island, Kermadec Ridge, 179 m (see Plate 23*d,e*). It differs in having a much smaller calicular diameter (e.g., 3.8×2.5 mm), being quite elongate (up to 25 mm), and in having consistently hexameral symmetry (24 septa).

ETYMOLOGY.—The species name is from the Latin *irregularis* (not regular), and refers to the irregular, nonhexameral septal symmetry of this species.

MATERIAL EXAMINED.—Types.

TYPES.—*Holotype:* ALB-5311, USNM 81890, Plate 23*a,b*. *Paratypes:* ALB-5311 (10) USNM 81891, (1) AM G15252. *Type Locality:* 21°33'N, 116°15'E (South China Sea off Hong Kong), 161 m.

DISTRIBUTION.—Known only from the type locality.

Family FLABELLIDAE Bourne, 1905

DIAGNOSIS.—Corallum solitary, fixed or free. Wall epithecal (neotenic condition), sometimes secondarily thickened with stereome. Epitheca usually smooth, lacking costae. Septa imperforate, composed of a single fan system of numerous, closely spaced trabeculae, which produce a smooth septal edge. Pali, dissepiments, and synapticulae absent; paliform lobes present in one genus. Columella usually rudimentary or absent, but may be lamellar or papillose. Exclusively ahermatypic.

DISCUSSION.—Most of the genera now assigned to the Flabellidae have been organized, redefined, and synonymized many times (e.g., Milne Edwards and Haime, 1848; Duncan, 1885; Vaughan and Wells, 1943; Wells, 1956), however, the general tendency has been to include relatively few broadly defined genera in the family, some with very lengthy synonymies. Thus, as late as 1956, Wells considered only six genera in the family. Zibrowius (1974) began the process of fragmentation by resurrecting *Javania* and *Placotrochides*, suggesting that *Flabellum* could be divided into at least three "groups," and discussing many other species and groups of species that did not fit into the conventionally defined flabellid genera. Cairns (in press a) applied the "key innovation" concept to flabellid taxonomy, i.e., any character, such as transverse division, that potentially allows the exploitation of a new habitat and/or is central to an adaptive radiation, is considered to be a key innovation and of generic importance. This led him to consider *Truncatoflabellum* and *Blastotrochus* as separate genera. *Polymyces* was described by Cairns in 1979, and, in this paper, *Rhizotrochus* is resurrected, *Flabellum* is divided into two subgenera, and two more unnamed species complexes are recognized. But even with this fragmentation of the family into 14 taxa, the genus *Flabellum* still contains approximately 195 species.

Table 4 is an elaboration of Zibrowius's (1974) comparative table in which four character complexes are effectively used to distinguish all flabellid genera and subgenera. Three pairs of taxa emerge as identical except for the character of transverse division: *Flabellum (Flabellum)*—*Truncatoflabellum*, *"Placotrochus" deltoides* spp. complex—*Placotrochus*, and *Javania*—*Placotrochides*.

To summarize the table, 12 described genera and two species complexes are listed in the Flabellidae, two of which are exclusively fossil: *Conosmilia* and *Adkinsella*. *Tortoflabellum* Squires, 1958, is considered to be a euphylliid, similar, if not identical to *Catalaphyllia* Wells, 1971. Approximately 263 species pertain to these twelve genera, 166 of which are exclusively fossil and 97 of which are valid Recent species. *Flabellum* contains approximately 191 species (144 fossil, 47 Recent), and three taxa are monotypic: *Adkinsella*, *Placotrochus*, and *"Placotrochus" fuscus*.

DISTRIBUTION.—*Lower Cretaceous to Recent:* Worldwide, including Antarctic, 0–3200 m.

Flabellum Lesson, 1831

Flabellum Lesson, 1831:2.—Milne Edwards and Haime, 1848:256–260 [in part: *flabella pedicillata* and *flabella fixa*]; 1850:xviii; 1857:79–80 [in part: *flabella subpedicellata* and *flabella fixa*].—Duncan, 1885:13–14 [in part: not sections 3, 5].—Vaughan, 1907:48.—Yabe and Eguchi, 1942a:87–89 [in part: not truncate species].—Vaughan and Wells, 1943:226–227 [in part: not *Placotrochides*, *Vasillum*, *Microtrochus*, or *Blastotrochus*].—Alloiteau, 1952:653 [in part: not *Blastotrochus*].—Wells, 1956:F432 [in part: not *Placotrochides*, *Placotrochus*, or *Vasillum*).—Squires, 1958:62–63.—Chevalier, 1961:378–379 [in part: not *Blastotrochus*, *Placotrochides*, or *Vasillum*).—Zibrowius, 1974: 18–20, 26 [in part: groups 1, 3].—Chevalier, 1987:752 [in part: not *Blastotrochus*, *Vasillum*].

Phyllodes Philippi, 1841:665.

Ulocyathus M. Sars, 1851:141.

Lithomyces Philippi, 1887:235.

Flabellum (Cycloflabellum) Chevalier, 1961:398.

DIAGNOSIS.—Corallum cuneiform, campanulate, or compressed turbinate. Base not reinforced and therefore corallum tending to become free in adult stage. Transverse division lacking. Lateral thecal spines absent but thecal edges often crested. Septa numerous: 4–7 septal cycles. Calicular edge smooth or jagged. Fossa deep; columella rudimentary: a simple fusion of lower, inner edges of major septa.

DISCUSSION.—Milne Edwards and Haime (1848, 1857), in the first great synthesis of scleractinian taxonomy, divided the 43–47 known species of *Flabellum* into three informal sections: *flabella subpedicellata (= Flabellum (Flabellum))*, *flabella truncata (= Truncatoflabellum)*, and *flabella fixa* (two species now attributed to *Flabellum (Flabellum)* and *Monomyces*). Milne Edwards and Haime (1850) correctly synonymized *Phyllodes* Philippi, 1841, but incorrectly (Milne Edwards and Haime, 1857) included *Monomyces* as a junior synonym of *Flabellum*. In the next comprehensive revision of the Scleractinia, Duncan (1885) correctly recognized the synonymy of both *Phyllodes* and *Ulocyathus* Sars, 1851, but also included *Vasillum* Tenison-Woods, 1879, as a junior synonym of *Flabellum*, which subsequent revisers have tacitly accepted. The figures of *Vasillum tuberculatum* Tenison-Woods, 1879, however, clearly show a ring of incipient rootlets, which would place it as a junior synonym of *Rhizotrochus*. Interestingly, Gardiner (1902a) considered *Rhizotrochus* to be a junior synonym of *Flabellum*, a view not adopted by anyone else; most authors consider *Rhizotrochus* to be a junior synonym of *Monomyces* Ehrenberg, 1834.

The modern revision of Vaughan and Wells (1943) and later Wells (1956) reiterated the synonymies detected by Milne Edwards and Haime and Duncan, and added *Microtrochus*, *Lithomyces*, and *Placotrochides* as junior synonyms of *Flabellum*. Of *Lithomyces* there can be no doubt that it is synonymous with *Flabellum*, but *Microtrochus* was later synonymized with *Placotrochus*, and *Placotrochides* was resurrected by Zibrowius (1974) as a valid genus.

Following its original description, *Blastotrochus* Milne Edwards and Haime, 1848, was periodically considered as a separate genus, a subgenus of *Flabellum*, or simply a synonym of *Flabellum*. Its history and synonymy are more fully discussed in the generic account of *Blastotrochus*.

The latest revision of the family was that of Zibrowius (1974), who redefined the flabellid genera based on their method of fixation, calicular edge shape, transverse division, and columellar type. He resurrected *Placotrochides* based on its stereome-reinforced base, and informally suggested that the species of *Flabellum* be divided into three "groups." His three groups equate to the following classification of this paper: group 1 = *Flabellum (Flabellum)*, group 2 = *Truncatoflabellum* and *Blastotrochus*, and group 3 = *Flabellum (Ulocyathus)*. Although implied by Squires (1963:10), Zibrowius (1974) was the first to suggest a separate genus for the truncate flabellids, with the provisional name of *Blastotrochus*. I essentially agree with the classification of Zibrowius and have found his table of comparisons of great value, except that I consider his groups 1 and 3 as subgenera of *Flabellum*, not as distinct genera, and I separate *Blastotrochus* from his group 2, the remainder of which requires a new name, i.e., *Truncatoflabellum*.

Within the family Flabellidae, *Flabellum* is morphologically the simplest of the genera. It is characterized by having a simple fused columella, if any; an unmodified pedicel; and lacking transverse division (Table 4). It is distinguished from both *Truncatoflabellum* and *Blastotrochus* by its lack of transverse division.

Flabellum is divided into two subgenera: nominate and *F. (Ulocyathus)*, based on the character of the shape of the calicular edge. Inasmuch as species have a definite reality, and genera can be supposed to represent adaptive radiation based on a key adaptation, my concept of a subgenus is one of convenience, in order to divide an otherwise speciose genus.

TABLE 4.—Comparisons of the genera of the Flabellidae

Taxa	Fixation			Thecal edge spines	Columella			Transverse division		Calicular edge		Number of species (fossil + Recent)
	Simple	Simple plus rootlets	Stereome-reinforced		Rudimentary: simple fusion	Lamellar	Papillose	Present	Absent	Smooth	Jagged	
Flabellum (Flabellum)	X				X				X	X		~72 + 28
Flabellum (Ulocyathus)	X				X				X		X	~72 + 19
Truncatoflabellum	X			X	X			X		X		7 + 21
Blastotrochus	X			X	X			X[1]		X		1 + 1
"*Placotrochus*" *deltoideus* species complex[2]	X					X			X	X		6 + 1
Placotrochus	X			X		X		X		X		0 + 1
"*Placotrochus*" *fuscus*			X			X			X	X		0 + 1
Javania			X		X				X		X	3 + 5
Placotrochides			X		X[3]			X		X		0 + 2
Monomyces		X[4]			X				X	X		0 + 2
Rhizotrochus		X[5]			X				X	X		0 + 5
Polymyces		X[6]			X				X		X	0 + 2
Gardineria		X[7]					X[8]		X	X		0 + 7
Conosmilia	X						X[9]		X		X	6 + 0
Adkinsella	?				X[10]				X	X		1 + 0

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[1] Anthoblast method of reproduction.

[2] See "Discussion" of *Placotrochus* for species assigned to this complex.

[3] Columella crispate.

[4] Accessory fixation by one large rootlet inseparably fused to pedicel.

[5] Accessory fixation by cycles of slender, hollow rootlets; discrete from pedicel.

[6] Accessory fixation by six pairs of symmetrically arranged rootlets that are inseparably fused to pedicel.

[7] Accessory fixation sometimes by one large rootlet inseparably fused to pedicel, as in *Monomyces*.

[8] Paliform lobes also present.

[9] Columella fascicular.

[10] Columella absent.

Although the character of calicular edge shape is easily applied to Recent species, this subgeneric attribution to fossil species will regrettably be difficult to apply because their calicular edges are often too damaged.

Flabellum, the nominate genus of the family, is the most speciose of the azooxanthellate genera, containing 47 valid Recent species and approximately 144 nominal fossil species (Felix, 1929, updated through 1987).

TYPE SPECIES.—*Flabellum pavoninum* Lesson, 1831, by monotypy.

DISTRIBUTION.—*Upper Cretaceous to Recent:* Worldwide, including Antarctic; 22–3200 m.

Subgenus *Flabellum (Flabellum)* Lesson, 1831

Flabellum Lesson, 1831:2.—Milne Edwards and Haime, 1848:257 [in part: *flabella pedicellata* and *flabella fixa*]; 1857:79–80 [in part: *flabella subpedicellata* and *flabella fixa*].—Duncan, 1885:13 [in part].—Yabe and Eguchi, 1942a:87–89 [in part].—Vaughan and Wells, 1943:226–227 [in part].—Alloiteau, 1952:653 [in part].—Wells, 1956:F432 [in part].—Squires, 1958:62–63 [in part].—Zibrowius, 1974:18–19 [in part: group 1].—Chevalier, 1987:752 [in part].

Lithomyces Philippi, 1887:235.

Flabellum (Cycloflabellum) Chevalier, 1961:398.

DIAGNOSIS.—*Flabellum* with a smooth calicular edge.

DISCUSSION.—Except for Philippi (1841) and Sars (1851), the nominate subgenus and *F. (Ulocyathus)* were not considered as separate taxa at any level until Zibrowius (1974) suggested the division into groups based on calicular edge morphology, which explains why the synonymy of both subgenera so often include "in part."

Twenty-eight Recent species are attributed to *Flabellum (Flabellum): F. pavoninum* Lesson, 1831 (= *F. distinctum* Milne Edwards and Haime, 1848); *F. thouarsii* Milne Edwards and Haime, 1848; *F. campanulatum* Holdsworth, 1862; *F. patens* Moseley, 1881; *F. australe* Moseley, 1881; *F. transversale* Moseley, 1881; *F. curvatum* Moseley, 1881; *F. coalitum* Marenzeller, 1889; *F. lamellulosum* Alcock, 1902; *F. dens* Alcock, 1902; *F. pavoninum* of Gardiner, 1902a; *F. chunii* Marenzeller, 1904; *F. magnificum* Marenzeller, 1904 (= *F. suluense* Alcock, 1902); *F. sibogae* of Gardiner 1904; *F. pavoninum* typical of Vaughan, 1907; *F. angiostomum* Folkeson, 1919; *F. transversale conicum* Yabe and Eguchi, 1942a; *F. knoxi* Ralph and Squires, 1962; *F. gracile* of Squires and Ralph, 1962; *F. impensum* Squires, 1962; *F. ongulense* Eguchi, 1965; *F. fragile* Cairns, 1977; *F. atlanticum* Cairns, 1979; *F. areum* Cairns, 1982; *F. gardineri* Cairns, 1982; *F. flexuosum* Cairns, 1982; *F. vaughani* Cairns, 1984; and *F. politum*, new species.

Many more fossil species belong to this subgenus, six of which from the Indo-West Pacific are *F. gambierensis* Duncan, 1864; *F. circulare* Tenison-Woods, 1880; *F. radians* Tenison-Woods, 1880; *F. mariae* Tenison-Woods, 1880; *F. laticostatum* Tenison-Woods, 1880; and *F. angustum* Yabe and Eguchi, 1942a.

Characters of diagnostic value at the species level are listed in Table 5, and characters arrived at by discriminant analysis are discussed by Cairns (in press b).

TYPE SPECIES.—Same as for the genus.

DISTRIBUTION.—*Upper Cretaceous to Recent:* Worldwide, including Antarctic; 22–2300 m.

25. *Flabellum (Flabellum) pavoninum* Lesson, 1831

PLATES 23*g–l*, 24*a–d*

Flabellum pavoninum Lesson, 1831:2 [in part: largest specimen, pl. 14: figs. A–C].—Lamarck, 1836:365.—Gray, 1849:75–76 [in part].—Milne Edwards and Haime, 1850:xviii [designation as type species for genus].—Marenzeller, 1889:41–42.—Faustino, 1927:45–46 [in part: only ALB-5312, other 20 lots are *F. lamellulosum, F. politum, F. magnificum, F. patens, F. paripavoninum*, and *F. messum*, see synonymy of these species for details].—Zibrowius, 1980:18.—Cairns, in press b.

Not *Euphyllia pavonina*.—Dana, 1846:159–160, pl. 6: figs. 5, 6.

Not *Flabellum pavoninum*.—Milne Edwards and Haime, 1848:260–261 [= *F. patens*]; 1957:80.—Gardiner, 1902a:123–125, pl. 4: figs. 18–21; 1904:98.—Vaughan, 1907:49–51, 52–55, pl. 1: figs. 2, 3 [= undescribed species close to *F. magnificum*].— Gardiner, 1929:302–305.—Hoffmeister, 1933:2–5 [= *F. australe*].—Gardiner and Waugh, 1938:174.—Yabe and Eguchi, 1942a:90–91, pl. 5: fig. 2 [= *F. magnificum*]; 1942b:129, pl. 11: fig. 7 [= *F. magnificum*].—Rossi, 1960:10 [= *F. chunii*].—Squires, 1964a:15 [= *F. magnificum* and *F. lamellulosum*].—Wells, 1964:114, pl. 1: figs. 13–14 [= ?*F. australe*].—Zibrowius, Southward, and Day, 1975:98–99, pl. 2: figs. D,E [= *F. patens* and an undescribed species].—Boshoff, 1981:35 [undescribed South African species].—Shepard and Veron, 1982:177, fig. 4-54i [= ?*F. australe*].—Cairns, 1984a:20 [undescribed species close to *F. magnificum*].—Zibrowius and Grygier, 1985:122 [undescribed South African species].

Flabellum distinctum Milne Edwards and Haime, 1848:262; 1857:80–81.—?Duncan, 1870:299, pl. 20: fig. 2.—Marenzeller, 1889:42.—Zibrowius, 1974:18.

Not *Flabellum distinctum*.—Duncan, 1873:322, pl. 39: figs. 1–13 [= *F. chunii*].—Alcock, 1902a:30 [= in part *F. lamellulosum*].—Yabe and Eguchi, 1932a:387; 1932b:443; 1942a:93–95, pl. 5: figs. 3–6, pl. 6: figs. 3, 4, 9, 10, pl. 7: fig. 7 [= *F. coalitum*]; 1942b:130–131, pl. 11: figs. 10–12.—Eguchi, 1965:291, bottom two figures.—?Eguchi, 1968:C44.—Mori and Minoura, 1980:321–326, figs. 3–5 [= *F. coalitum*].

Not *Flabellum pavoninum* var. *lamellulosum*.—Vaughan, 1907:51–52, pl. 1: fig. 1 [= *F. lamellulosum*].

Not *Flabellum pavoninum* var. *latum*.—Vaughan, 1907:55–56, pl. 2: fig. 2 [undescribed species 3 of Cairns, in press b].

Flabellum pavoninum var. *distinctum*.—Vaughan, 1907:56–59, pl. 2: fig. 5.

Not *Flabellum pavoninum* var. *paripavoninum*.—Vaughan, 1907:59–62, pl. 3: figs. 1–4 [= *F. vaughani*].—Umbgrove, 1938:264 [= *F.* sp.]; 1950:639, pl. 81: figs. 1, 2 [= *F.* sp.].

Not *Flabellum pavoninum* var. *distinctum*.—Gravier, 1920:67, pl. 7: figs. 116, 117 [= *F. chunii*].—Gerth, 1921:401 [= *F. politum*].—Hoffmeister, 1933:5–7 [= ?*F. australe*).—Umbgrove, 1950:639, pl. 81: figs. 1, 2 [= ?*F. patens*].

Not *Flabellum pavoninum magnificum*.—Yabe and Eguchi, 1942a:89–90, pl. 5: fig. 1 [= *F. magnificum*]; 1942b:129, pl. 11: fig. 8 [= *F. magnificum*].

Not *Flabellum pavoninum paripavoninum*.—Yabe and Eguchi, 1942a:91–92, pl. 5: figs. 7, 8 [= *F. patens* and *F. politum*]; 1942b:129–130, pl. 11: fig. 9 [= *F. politum*].

Not *Flabellum pavoninum pavoninum*.—Squires, 1958:63–64, pl. 13: figs. 17, 18 [= *F. mariae*].

Not *Flabellum pavoninum circulare* Squires, 1958:64, pl. 12: figs. 10–18 [= *F. circulare*].

TABLE 5.—Range, mean, and standard deviation of characteristics of selected species of *Flabellum (Flabellum)*. (Measurements of first eight species used in discriminant analysis of Cairns (in press b). Abbreviations: FAN = face angle, EAN = edge angle, GCD = greater calicular diameter, LCD = lesser calicular diameter, LEL = lateral edge length, CRE = height of edge crest, SSI = septal sinuosity index, SCI = septal concavity index.)

Character	*F. politum* (N=38)	*F. magnificum* (N=8)	*F. pavoninum* typ. sensu Vaughan, 1907 (N=10)	*F. patens* (N=3)	*F. vaughani* (N=38)	*F. pavoninum* sensu Gardiner, 1902a (N=10)	*F. pavoninum* (= *F. distinctum*) (N=5)	*F. lamellulosum* (N=33)	*F. dens* (N=9, syntypes)	*F. suluense* (N=1, holotype)	*F. coalitum* (N=1, holotype)
FAN (in degrees)	30–*37.2*–45 ±3.9	44–*49.8*–58 ±5.1	25–*41.9*–53 ±9.3	20–*22*–24 ±2.0	39–*47.1*–53 ±3.2	28–*34.5*–41 ±3.6	32–*35.6*–42 ±2.9	32–*42.7*–51 ±4.6	14–18	28	27
EAN (in degrees)	90–*107.4*–136 ±11.0	140–*156.9*–172 ±11.0	152–*169.7*–180 ±8.6	117–*122*–125 ±4.4	85–*109.6*–137 ±11.3	104–*123.8*–137 ±11.9	107–*125.4*–139 ±7.5	130–*165.5*–206 ±18.4	21–25/58–79	117	74
GCD (mm)	23.6–*31.7*–40.5 ±3.5	66.4–*78.5*–88.0 ±8.3	38.2–*50.3*–71.8 ±12.7	43.1–*44.3*–45.9 ±1.4	34.8–*40.3*–54.8 ±3.2	29.4–*37.9*–46.1 ±5.6	41.1–*50.5*–60.6 ±7.4	38.9–*49.3*–61.3 ±5.3	13.8	23.2	32.3
LCD (mm)	13.3–*18.3*–23.2 ±2.5	38.1–*44.3*–47.8 ±3.3	19.9–*24.5*–32.9 ±4.5	18.3–*19.8*–21.1 ±1.4	27.2–*30.9*–42.1 ±2.9	12.4–*17.5*–22.6 ±3.4	17.8–*21.9*–25.1 ±2.9	30.0–*34.7*–44.0 ±4.0	6.7	10.4	14.3
Height (mm)	22.0–*29.0*–35.4 ±3.0	46.9–*53.2*–60.0 ±5.5	28.3–*33.5*–42.6 ±5.7	42.0–*42.5*–43.4 ±0.74	29.7–*36.5*–46.7 ±3.0	24.2–*29.0*–33.2 ±3.4	32.7–*37.5*–42.9 ±3.8	38.7–*47.3*–61.2 ±6.4	22.5	15.1	30.0
Pedicel diameter (mm)	1.00–*1.23*–1.40 ±0.10	1.50–*1.84*–2.30 ±0.31	0.60–*1.11*–1.50 ±0.27	1.50–*1.70*–2.00 ±0.27	0.71–*1.01*–1.59 ±0.19	1.21–*1.34*–1.40 ±0.07	1.1–*1.32*–1.5 ±0.14	1.50–*1.69*–2.10 ±0.16	1.3–1.4	?	1.4
LEL (in mm)	13.7–*17.6*–23.4 ±2.4	29.5–*36.9*–45.6 ±4.9	16.0–*23.0*–33.9 ±6.6	20.7–*22.1*–24.0 ±1.7	18.8–*21.6*–27.9 ±1.8	14.8–*18.9*–22.4 ±2.5	22.3–*26.6*–31.5 ±3.5	17.2–*22.5*–30.1 ±2.9	-	-	24.7
CRE (in mm)	0.30–*0.85*–2.00 ±0.37	0.60–*2.40*–3.90 ±1.02	0.00–*0.22*–0.80 ±0.31	4.8–*5.5*–6.1 ±0.67	0.00–*0.16*–1.00 ±0.32	1.4–*2.4*–4.1 ±0.82	2.5–*3.5*–3.8 ±0.26	2.5–*4.5*–8.2 ±1.27	0	1.5–2.0	1.7
Number of septa	104–*152.9*–198 ±20.2	196–*301*–376 ±54.6	188–*225.6*–340 ±47.4	178–*192*–200 ±12.2	134–*180.4*–202 ±14.6	158–*185.2*–204 ±14.0	184–*189.2*–192 ±3.0	188–*243*–340 ±50.7	56–58	>104	130
SSI	1.6–*5.0*–9.9 ±1.8	2.3–*4.8*–6.6 ±1.6	2.0–*4.1*–6.0 ±1.2	2.0–*2.4*–2.7 ±0.35	1.0–*1.5*–3.0 ±0.53	2.5–*3.9*–5.8 ±1.15	2.0–*3.1*–4.4 ±0.94	1.0–*1.13*–2.6 ±0.35	high	7	3.5
GCD : LCD	1.49–*1.74*–2.15 ±0.15	1.65–*1.77*–1.96 ±0.12	1.43–*2.47*–2.99 ±0.50	2.04–*2.25*–2.51 ±0.24	1.14–*1.31*–1.55 ±010	2.00–*2.19*–2.55 ±0.17	1.98–*2.30*–2.41 ±0.15	1.20–*1.43*–1.77 ±0.16	1.7–2.3	2.3	2.25
GCD : H	0.98–*1.10*–1.30 ±0.07	1.29–*1.48*–1.71 ±0.15	1.30–*1.48*–1.7 ±0.15	1.03–*1.04*–1.06 ±0.02	0.96–*1.11*–1.35 ±0.09	1.19–*1.31*–1.46 ±0.10	1.16–*1.34*–1.47 ±0.13	0.79–*1.05*–1.29 ±0.13	0.68–0.82	-	1.08
LEL : H	0.46–*0.61*–0.78 ±0.06	0.60–*0.70*–0.78 ±0.08	0.54–*0.67*–0.80 ±0.09	0.49–*0.52*–0.55 ±0.03	0.50–*0.59*–0.66 ±0.04	0.58–*0.65*–0.71 ±0.05	0.63–*0.71*–0.74 ±0.05	0.32–*0.48*–0.61 ±0.07	0.92–0.93	-	0.82
SCI	1.0–*2.4*–4.0 ±0.9	10.0–*14.7*–19.0 ±3.1	3.0–*5.4*–7.0 ±1.8	5.0–*8.0*–10.0 ±2.6	5.0–*8.7*–12.0 ±1.9	3.0–*5.3*–9.0 ±3.2	2.0–*2.5*–3.0 ±0.007	5.0–*9.4*–16 ±3.3	low	-	?
Septal arrangement	$S_{1-3}>S_4>S_5>S_6$	$S_{1-4}>>S_5>S_6>S_7$	$S_{1-4}>>S_5>S_6>S_7$	$S_{1-4}>S_5>S_6$	$S_{1-3}>S_4>S_5>S_6$	$S_{1-3}>S_4>S_5>S_6$	$S_{1-3}>S_4>S_5>S_6$	$S_{1-2}>S_3>S_4$ or 20:20:16–18	$S_{1-3}>S_4>>S_5>S_6$	$S_{1-3}>S_4>S_5>S_6$	
Other characters	corallum small; columella rudimentary; theca shiny	columella well developed; largest corallum		corallum dense, columella rudimentary	pedicel usually worn; S_4 almost as large as S_{1-3}	fossa narrow	fossa wide; columella dense; theca striped	fossa open; red-brown theca	smallest corallum; edge angle changes		

?*Flabellum pavoninum distinctum*.—Squires, 1958:65 [in part: pl. 13: figs. 5, 6, 10, 12].

DESCRIPTION.—Angle of thecal edges 107°-139°; inclination of lateral faces 32°-42°. Largest specimen examined (lectotype of *F. distinctum*, Plate 24*a*) 60.6×25.1 mm in calicular diameter and 42.8 mm tall, with 194 septa. Lectotype of *F. pavoninum* (Plate 23*g-i*) 54.7×22.9 mm in calicular diameter and 38.8 mm tall, with 192 septa. Thecal edge crests 2.5-3.8 mm tall. Lateral thecal edges quite long in relation to height of corallum, producing a LEL:H of 0.63-*0.71*-0.74, the highest average of any species of *Flabellum* analyzed. Corallum robust and dense. Thecal faces flat and pigmented with fine brownish black stripes corresponding to each septum. Upper calicular edges of S_{1-3} also pigmented a dark brown. Pedicel 1.1-1.5 mm in diameter. Ratio of GCD:LCD = 1.98-2.41; GCD:H = 1.16-1.47 (Table 5).

Septa hexamerally arranged in six cycles, the largest specimen examined having a pair of small S_7, or 194 septa. Septal formula: $S_{1-3}>S_4\geq S_5>S_6$. Upper calicular edges of S_{1-3} slightly notched but lower in the fossa expand into an exsert lobe that extends well into fossa. Lower inner edges of S_{1-3} thickened and sinuous (SSI = 2.0-4.4), all joining with the columella. S_4 variable in size, some almost as large as the S_{1-3}, others considerably smaller. In the lectotype of *F. pavoninum*, 8 S_4 are accelerated in growth to the same size as the S_{1-3}, giving the impression of octameral symmetry: 32 : 32 : 64 : 64 (192 septa). S_4 thinner than S_{1-3} and usually not exsert. S_4 have straight inner edges that often merge with the columella. S_5 about half the size of S_4; S_6 about 1/3 size of S_5.

Fossa deep, containing a rudimentary, elongate, spongy columella.

DISCUSSION.—The two specimens figured by Dana (1846) could not be located for examination, but, based on their illustrations, they can be excluded from identification as *F. pavoninum*. The discriminant analysis (Cairns, in press b) placed the specimen figured (Dana, 1846, pl. 6: fig. 6) as "species 3," or *F. pavoninum* typical sensu Vaughan, 1907, known only from Hawaii. Dana did not cite a locality for his specimens, but the U.S. Exploring Expedition did visit Hawaii and it is therefore conceivable that this specimen was collected from the Hawaiian Islands. The other figured specimen (Dana, 1846, pl. 6: fig. 5) is not figured well enough to allow identification.

Gray (1849) was the first to attribute a large number of nominal species to *F. pavoninum*. Although he was correct in considering *F. distinctum* as a junior synonym, he incorrectly synonymized 15 species of truncate *Flabellum*, *Placotrochus laevis*, and *Acanthocyathus grayi* with *F. pavoninum* and implied that *Rhizotrochus typus* and *Blastotrochus nutrix* were also junior synonyms, all species described the previous year by Milne Edwards and Haime (1848).

Gardiner (1902a, 1904) attributed nine specimens collected off South Africa to *F. pavoninum* and synonymized *F. patens* Moseley, 1881, *F. australe* Moseley, 1881, and *F. paripavoninum* Alcock, 1898, as *F. pavoninum*. Some western Indian Ocean specimens were included in the discriminant analysis (Cairns, in press b) as "species 6" (see Plate 24*g,h*), and the classification of this group is very close to that of *F. pavoninum*, but characters such as fossa width, columellar aspect, and subtle aspects of corallum shape (characters not used in the discriminant analysis) lead me to believe that the western Indian Ocean specimens are different from *F. pavoninum*, a belief that is substantiated by the ability of the discriminant analysis to distinguish species 6 from *F. pavoninum* using multivariate characters. Contrary to Gardiner (1902a), *F. patens*, *F. australe*, and *F. paripavoninum* are all considered to be distinct species.

Vaughan (1907), in his revision of the Hawaiian Scleractinia, followed Gardiner's synonymy of *F. pavoninum* and added still another three species to it: *F. lamellulosum* Alcock, 1902, *F. latum* Studer, 1978, and *F. chunii* Marenzeller, 1904, but differentiated five of the synonymized names as varieties of the species. It is interesting to note that in Vaughan's key to the varieties Vaughan used edge angle, GCD:H, and crest height as important characters, which are also heavily weighted in the discriminant analysis. My reidentifications of his varieties are listed in the synonymy but it is also interesting to note that the three specimens identified as *F. pavoninum* var. *distinctum* do, in fact, appear to be *F. distinctum (= F. pavoninum)*, which substantiates the Hawaiian Island origin of the type series of *F. pavoninum*.

Faustino (1927) followed Vaughan's synonymy, identifying seven species of *Flabellum* from 21 lots as *F. pavoninum* (see synonymy), including one lot of true *F. pavoninum*.

Gardiner (1929) reaffirmed his earlier synonymy of 1902a, suggesting that the "varieties" of Vaughan (1907) were no more than environmental growth forms determined by variation in sedimentation, food availability, water movement, depth, and temperature, in that order, although he allowed that they might represent different species, but differing only by polyp characteristcs.

The next attack on *F. pavoninum* was that of Yabe and Eguchi (1942a), who lumped most of the nominal species into two species, *F. pavoninum* and *F. distinctum*, but recognized subspecies status for several of the previously described species. They also added another species, *F. coalitum* Marenzeller, 1889, to the synonymy of *F. distinctum*. Their key to the species and subspecies stressed edge angle, adult corallum size, GCD:H, and crest size, in that order. Although the type locality of *F. distinctum* is off Japan, it would appear that most of the specimens identified by Yabe and Eguchi (1942a,b) as *F. distinctum* are *F. coalitum*, a species also having its type locality off Japan. I have compared three lots of Yabe and Eguchi's (1942a) *F. distinctum* to the holotype of *F. coalitum* (see "Material Examined: *Reference Material*").

Squires (1958), in his revision of the Tertiary and Cretaceous corals of New Zealand, followed the subspecies approach concerning *F. pavoninum*, but, unlike Yabe and Eguchi (1942a), he made *F. distinctum* a subspecies of *F. pavoninum.* His key to the species emphasized edge angle, crest height, and costae, in that order. Because he was working with Tertiary specimens from New Zealand, his subspecies were Eocene to Miocene in age; however, most of his subspecies had a very low GCD:H ratio and are therefore more similar to *F. lamellulosum* than *F. pavoninum.* His *F. pavoninum distinctum* included the type of *F. laticostatum* Tenison-Woods, 1880 (Oligocene, New Zealand), which cannot be distinguished from *F. pavoninum* based on the specimens illustrated.

After a long tradition of lumping dating back to Gray (1849), Squires (1964a:15) was the first to imply that many of Vaughan's varieties were valid species and that there were at least three morphologically similar undescribed species in the Indo-West Pacific. Squires had access to the *Albatross* Philippine coral collection and might have been referring to *F. politum*, new species, *F. lamellulosum* (as resurrected), *F. vaughani*, and/or *F. patens*, as redefined.

Zibrowius, Southward, and Day (1975) also questioned the widespread polymorphic nature of *F. pavoninum* but did not fully discuss their reasons. Cairns (1984a) also advocated splitting off many of the species previously assigned to *F. pavoninum* but still confused several species as *F. pavoninum.* He advocated a worldwide revision of the species complex.

The recommended revision was partially accomplished by Cairns (in in press b) and in this paper, using discriminant analysis to characterize and discriminate eight Indo-West Pacific species of *Flabellum* chosen a priori. Following the discriminant analysis, types of some of the controversial nominal species were added to the analysis for classification purposes. The results of this analysis pertinent to this discussion are that both syntype series of *F. pavoninum* and *F. distinctum* represented mixed lots, but that the subsequently chosen lectotypes (this paper) are identical. *Flabellum vaughani, F. lamellulosum*, and *F. magnificum* were easily diagnosed using multivariate characters and were interpreted as separate species. The syntype series of *F. patens* also proved to be a mixed lot, but a choice of lectotype (this paper) defines the species, which is distinct from all others. One new species is herein described, *F. politum*, which had previously been identified as *F. patens* (in part) and *F. pavoninum* (in part) by Faustino (1927) and "species 3" by Cairns (in press b). The taxon described as *F. pavoninum* typical by Vaughan (1907) from Hawaii was considered to be an undescribed species with close affinities to *F. magnificum* (see discussion of *F. magnificum*). Finally, the specimens reported by Gardiner (1902a) and others from the western Indian Ocean are very similar to *F. pavoninum* but different in subtle ways (Cairns, in press b), which leads me to believe that they are a different species.

It is little wonder that so many species were misidentified as *F. pavoninum* over the years. Not only was the syntype series of both *F. pavoninum* and *F. distinctum* mixed lots, but Table 5 shows that it is nondistinctive in any one character; however, regarding indices, it has the highest average GCD:LCD and LEL:H, and lowest average septal concavity index of the Indo-West Pacific species analyzed. The discriminant analysis readily characterizes *F. pavoninum* using multivariate characters, but on a less abstract level, *F. pavoninum* can be distinguished from other species by its relatively low edge angle, and relatively high crest height, along with the extremes in indices mentioned above. Most previous keys to the *F. pavoninum* species complex have used edge angle as the first key character, which, a perusal of Table 5 shows, can be very misleading. For instance, *F. lamellulosum* has been keyed (Vaughan, 1907; Squires, 1958) as having an edge angle in excess of 180°, based on one specimen (the holotype) with an edge angle of 285° (actually 240°). In reality, the range of edge angle for this species is 130°-*165*°-240°. Edge angle is an important character, but must be used in concert with others in a multivariate fashion to properly distinguish the species.

Because the Australian species of *Flabellum* were not included in the discriminant analysis, it should be noted that *F. australe* Moseley, 1881, is very similar to *F. pavoninum.* It appears to be differentiated by its lower face angle and much higher septal concavity index, the septa being nonexsert.

MATERIAL EXAMINED.—ALB-3999 (1) USNM 20712; ALB-4101 (2) USNM 20714 (both *F. pavoninum* var. *distinctum* of Vaughan, 1907); ALB-5312 (3) USNM 40752; syntypes of *F. pavoninum*, MNHNP; syntypes of *F. distinctum*, BM, Plates *23j,l, 24a,b,e,f; F. pavoninum* of Marenzeller, 1899 (3) NMW 8201, Plate *24d; F. distinctum* of Marenzeller, 1899 (1) NMW 8197, Plate *24c. Reference Material: F. pavoninum* of Gardiner, 1902a (3) BM 1950.11.30, Plate *24g,h; F. pavoninum* of Vaughan (1907) USNM; *F. pavoninum* of Hoffmeister (1933) specimens 3, 11, and 30 at USNM; *F. pavoninum* of Yabe and Eguchi (1942a,b) *Sôyô-maru* 437 (1) TIUS 43448; *F. pavoninum* of Squires (1964a) USNM; *F. pavoninum* of Wells (1964) USNM 68375; *F. pavoninum* of Zibrowius, Southward, and Day (1975); *F. pavoninum* of Cairns (1984a) USNM; *F. distinctum* of Alcock, 1902a, *Siboga* 12, 51, 166 (ZMA 1410, 1211, 1210, respectively); *F. distinctum* of Yabe and Eguchi, 1942a, *Sôyô-maru* 429 (1) TIUS 39732, Sagamai Bay (1) TIUS 43409 (Plate *24i,l*): near Seto (2) TIUS 39236 (all *F. coalitum*); holotype of *F. coalitum*, NMW 8196, Plate *24j,k; F. p. magnificum* of Yabe and Eguchi, 1942a, *Sôyô-maru* 416, TIUS 50094; *F. p. paripavoninum* of Yabe and Eguchi, 1942a, *Sôyô-maru* 343 (1) TIUS 43445, *Sôyô-maru* 419 (2) TIUS 43441; *F. p. paripavoninum* of Umbgrove, 1938, RGM 35452; *F. p. distinctum* of Umbgrove (1950) RGM 77842 and Gerth (1921) RGM 3788; *F. p. pavoninum* of Squires, 1958, USNM 67946; *F. p. distinctum* of Squires, 1958, USNM 649158, 67943.

TYPES.—Five syntypes of *F. pavoninum* are deposited at the MNHNP (372), the largest of which is quite similar but not identical to Lesson's figured specimen. Three of the other four specimens are probably smaller specimens of *F. lamellulosum*

(Plate 27*c,f,i*), the fifth remains unidentified. Because of the mixed status of the syntype series, a lectotype is chosen: the largest specimen (Plate 23*g–i*), the other four specimens considered as paralectotypes Plate 27*c,f,i*). *Type Locality:* "Sandwich Islands" (?Hawaiian Islands), depth unknown.

Three syntypes of *F. distinctum* are deposited at the BM (1840.4.6.81-83), and one syntype is deposited at the MNHNP (1022). Two of the BM specimens and the MNHNP specimen are conspecific, but BM 1840.4.6.83 (Plate 24*e,f*) is very different, having a face angle of only 78°, a pedicel diameter of 2.1 mm, and nonexsert primary septa. It resembles and may be *F. coalitum* Marenzeller, 1889. Because this specimen is considered to be a different species, a lectotype was chosen (BM 1840.4.6.82), the specimen that agrees with the measurements given by Milne Edwards and Haime (1848) in the original description (Plates 24*a*, 23*j–l*). *Type Locality:* Although Milne Edwards and Haime (1848) originally designated the Red Sea as the type locality for this species, subsequent authors, including themselves (Gray, 1849; Milne Edwards and Haime, 1857; Yabe and Eguchi, 1942a; Zibrowius, Southward, and Day, 1975) corrected this locality to off Japan, depth unknown.

DISTRIBUTION.—*Recent:* Although the synonymy is long, *F. pavoninum* is known from relatively few records: represented by only 14 specimens (Lesson, 1831; Milne Edwards and Haime, 1848; Marenzeller, 1889; Vaughan, 1907; and ALB-5312, reported herein). *Flabellum pavoninum* is known only from off Japan, the South China Sea off Hong Kong, and off Hawaii, 223-271 m, 14.2°-15.5°C. It is not known from the Philippines but was included to elucidate the complex synonymies of related species.

26. *Flabellum (Flabellum) magnificum* Marenzeller, 1904

PLATE 25*a–j*

?*Flabellum suluense* Alcock, 1902a:31-32, pl. 4: figs. 29a,b.—Faustino, 1927:58, pl. 4: figs. 3-5.

Flabellum magnificum Marenzeller, 1904:276–277, pl. 17: fig. 13.—Utinomi, 1965:255.—Zibrowius, 1974:18.

Not *Flabellum magnificum*.—Harrison, 1911:1020-1021, pl. 57: figs. 1–3 [= *Rhizotrochus typus*].

Flabellum pavoninum.—Faustino, 1927:46 [in part: ALB-5118, 5412, 5586].—Yabe and Eguchi, 1942a:90–91, pl. 5: figs. 2a–c [in part: sta 437]; 1942b:129, pl. 11: figs. 7a–c.—Squires, 1964a:15–21 [in part: ALB-5118, 5280, 5281, 5412, 5523, 5590].

Flabellum pavoninum magnificum.—Yabe and Eguchi, 1942a:89–90, pl. 5: figs. 1a–c; 1942b:129, pl. 11: figs. 8a–c.

DESCRIPTION.—Angle of thecal edges, exclusive of crests, 140°–172°; inclination of thecal faces, 44°–58°. Largest specimen examined (ALB-5590) 88.0×45.0 mm in calicular diameter and 60.0 mm tall. Thecal faces flat to very slightly concave, meeting in acute thecal edges (rarely rounded), usually with a poorly developed, discontinuous crest up to 3.9 mm tall. Length of a thecal edge from calice to upper pedicel (LEL) up to 45.6 mm in larger specimens. Ratio of LEL:H = 0.60–0.78. C_{1-4} slightly ridged; transverse chevron-shaped growth lines common. In well-preserved coralla, theca bears reddish brown stripes, those associated with C_{1-4} about 0.5 mm wide, those following the C_{5-6}, about 0.2 mm wide. Most coralla, however, are uniformly white to gray and rarely encrusted. Pedicel 2-3 mm tall and 1.5-2.3 mm in diameter. Ratio of GCD:LCD = 1.65–1.96, this ratio tending to increase with increasing greater calicular diameter. Ratio of GCD:H = 1.29-1.71.

Septa hexamerally arranged in seven cycles, the last cycle never complete. One of the largest specimens (ALB-5280) has 376 septa: a full sixth cycle and all but four pair of S_7. The first-formed S_7 pairs usually begin to form in systems along the middle of the thecal faces. S_{1-4} equal in size and not exsert, being the same relatively narrow width as higher-cycle septa in the vicinity of calicular edge, which results in a very high septal concavity index of 10–19. Ten to 12 mm lower in fossa, the S_{1-4} gradually widen into broad lobes. Toward the lateral thecal edges, the transition from the narrow upper septal width to wide septum is much shorter, occurring 4–5 mm below the calicular edge. Upper edges of S_{1-4} slightly sinuous and finely serrate, bearing small teeth about 0.1 mm tall spaced 0.2 mm apart (Plate 25*d,g*); lower, inner edges quite sinuous. S_{1-4} easily distinguished from higher-cycle septa by their much greater width, very sinuous lower edges (SSI = 2.3-6.6), and by being the only ones to fuse with the columella. S_5 half size of S_{1-4}, having straight inner edges. S_6 about 1/3 width of S_5, extend about halfway down the thecal face, and also have straight inner edges. S_7, when present, about 2/3 width of S_6, extending only 2–10 mm down inner thecal face. Septal granules pointed but sparse, 0.08–0.14 mm tall.

Fossa deep, long, and narrow but easily affording a view of the rudimentary columella formed by the lower, inner edges of the S_{1-4}.

DISCUSSION.—*Flabellum magnificum* is a species of extremes, not only in absolute corallum size, second only to the Antarctic *F. impensum* Squires, 1962, in greater calicular diameter, but in other characters as well. Of the 10 Indo-West Pacific species of *Flabellum (Flabellum)* (Table 5), it has the highest average face angle, greater calicular diameter, lesser calicular diameter, height, pedicel diameter, LEL, number of septa, GCD : H, LEL : H, and septal concavity index. According to the discriminant analysis (Cairns, in press b), it is morphologically most similar to *F. lamellulosum*, particularly regarding corallum size, face angle, pedicel diameter, and number of septa. Because of the similarity of corallum shape of *F. magnificum* and *F. lamellulosum* they have been confusing in the past. For instance, Squires (1964a) used equal numbers of both species in his morphometric analysis of *F. pavoninum*, and, of Faustino's (1927) 21 records of *F. pavoninum*, seven lots were *F. lamellulosum* and three lots were *F. magnificum*. *Flabellum magnificum* differs dramatically, however, in the GCD : H and LEL : H ratios, reflecting that the corallum of *F. magnificum* is considerably broader than high, whereas that of *F. lamellulosum* is about as wide as high. *F. magnificum* also has smaller crests, a more clear-cut septal symmetry, and distinctively shaped larger septa: low near the calicular margin but quite broad slightly lower in the fossa.

Flabellum magnificum is also very similar to *F. pavoninum* typical of Vaughan (1907) from the Hawaiian Islands. These species are similar in SSI, number of septa, corallum size and shape, face angle, GCD:H, and LEL:H. The Hawaiian specimens differ in having a smaller pedicel diameter, virtually no crest, and having a lower septal concavity index. Because the Hawaiian specimens are different from *F. magnificum* and *F. pavoninum*, this species will require a new name.

Alcock's (1902a) *F. suluense* is tentatively synonymized with *F. magnificum* based on its very sinuous inner septal edges, crest height, and relative sizes of the septal cycles; however, its edge and face angles are both less than typical *F. magnificum*. Unfortunately, the holotype of *F. suluense* is quite small and worn (greater calicular diameter = 23.2 mm); no specimens of *F. magnificum* of comparable size are available for comparison. If *F. suluense* proves to be conspecific with *F. magnificum*, it would have nomenclatural priority by two years.

Yabe and Eguchi's (1942a) *Flabellum pavoninum magnificum* (TIUS 50094), which was examined after the discriminant analysis, is a typical *F. magnificum*, except that its thickened inner septal edges are straight, having a SSI of 1.0. Likewise, Yabe and Eguchi's (1942a) *F. pavoninum* typical from *Sôyô-maru* station 437 proves to be a relatively small (greater calicular diameter = 47.3 mm) *F. magnificum*.

MATERIAL EXAMINED.—ALB-5116 (1) USNM 81948; ALB-5118 (1) USNM 40740; ALB-5280 (1) USNM 81949; ALB-5281 (2) USNM 81950; ALB-5412 (1) USNM 40746; ALB-5523 (1) USNM 81951; ALB-5586 (1) USNM 40748; ALB-5590 (1) USNM 81952; holotype of *F. suluense*, ZMA, Plate 25*i,j*; "holotype" of *F. magnificum*, ZMB; *Sôyô-maru* 416 (1) TIUS 50094 (*F. p. magnificum* of Yabe and Eguchi, 1942a) Plate 25*e,f* *Sôyô-maru* 437 (1) TIUS 43448 (*F. pavoninum* of Yabe and Eguchi, 1942a) Plate 25*h*.

TYPES.—The holotype of *F. magnificum* was requested from the ZMB, but the specimen sent (5088, Plate 33*j*) as the type was a large specimen of *Truncatoflabellum stokesi*, having very different dimensions from the type. The holotype is therefore assumed to be lost or temporarily misplaced. *Type Locality:* 0°15.5'N, 98°04'E (off western Sumatra), 470 m.

The holotype of *F. suluense*, collected at *Siboga* 100 (Plate 25*i,j*), is deposited at the ZMA (1231). *Type Locality:* 6°11'N, 120°37'E (Sulu Archipelago), 450 m.

DISTRIBUTION.—*Recent:* Japan (off southwestern Kyūshū; ?Sagami Bay) (Yabe and Eguchi, 1942a); Philippines (off Luzon near Manila; off Cebu; Sulu Archipelago); off Sabah, Indonesia; off western Sumatra (Marenzeller, 1904); 291-700 m; 6.7°-13.9°C.

27. *Flabellum (Flabellum) patens* Moseley, 1881

PLATE 26*a-i*

?*Flabellum pavoninum*.—Milne Edwards and Haime, 1848:260-261.—Faustino, 1927:46 [in part: ALB-5173, 5289].—Zibrowius, Southward, and Day, 1975:89-99 [in part: pl. 2: fig. D].

Flabellum patens Moseley, 1881:172, [in part: pl. 6: fig. 5].

Flabellum paripavoninum.—Faustino, 1927:47 [in part: ALB-5301, part of ALB-5373].

Flabellum pavoninum paripavoninum.—Yabe and Eguchi, 1942a:91-93 [in part: pl. 5: figs. 7a-c: *Sôyô-maru* 343 and part of 419); 1942b:129 [in part: *Sôyô-maru* 343, part of 419, not pl. 11: fig. 9].—Eguchi, 1965:291, 3rd figure from bottom.

?*Flabellum pavoninum* var. *distinctum*.—Umbgrove, 1950: 639, pl. 81: figs. 1-2.

DESCRIPTION.—Angle of thecal edges, exclusive of lateral crests, 117°-125°; inclination of thecal faces, 20°-24°. Largest intact specimen examined 45.3×17.9 mm in calicular diameter and 43.3 mm tall (ALB-5289). Thecal faces meet in acute thecal edges, which bear a continuous crest 4-6 mm high beginning 6-8 mm from the pedicel and usually terminating slightly below calicular edge. Thecal edges about half length of corallum height: LEL:H = 0.49-0.55. Corallum robust and dense. Thecal faces flat, without evidence of costae or pigmentation; however, all specimens examined had indications of symbiosis with a polychaete (*Lumbrineris*, see Zibrowius, Southward, and Day, 1975), evidenced by a crescent-shaped, parchment-like tube 3 mm in width that parallels the calicular edge. The polychaete produces a white band on an otherwise corroded gray theca, and occurs on both faces of the corallum. Pedicel circular, 1.5-2.0 mm in diameter. Ratio of GCD:LCD high, 2.04-2.51. Ratio of GCD:H = 1.03-1.06, the height and width almost the same size.

Septa hexamerally arranged in six cycles. Larger specimens with several pairs of S_7, but coralla with more than 200 septa were not found. S_{1-4} equal in size and nonexsert, equal in width to higher-cycle septa at calicular edge, gradually widening to a maximum width and then descending vertically into the fossa. Upper septal edges finely sinuous (SSI = 2.0-2.7); lower inner edges greatly thickened. S_{1-4} very symmetrically arranged, especially near principal septa, each major septum having a counterpart directly across the fossa. S_5 about $^3/_4$ size of S_{1-4} and also finely sinuous, but do not reach the columella. S_6 small and straight, about $^1/_3$ width of S_5 and extending about $^1/_3$ distance down thecal face.

Fossa extremely narrow and deep, the lower, inner edges of the S_{1-4} almost meeting along the midline. Columella absent or rudimentary, formed by the lower inner edges of the S_{1-4}.

DISCUSSION.—Five of the six syntypes of *F. patens* were included in the discriminant analysis of *Flabellum (Flabellum)* (Cairns, in press b), the measurements of one specimen (Moseley, 1881, pl. 6: fig. 4) taken from Moseley's illustration, the sixth specimen presumed missing. The discriminant analysis classified each of the five specimens as different species. The classification of two of the specimens was considered suspect because either the specimen was badly damaged or the measurements were taken from a drawing, which was potentially misleading. Another specimen classified with 99% probability as *F. pavoninum* typical of Vaughan (1907), but its corallum was also damaged and its attribution suspect. A fourth specimen classified with 82% probability as

F. politum; the fifth specimen classified with 47% probability as "species 6" and 33% probability as "species 4" (= *F. patens*). I chose the fifth specimen as lectotype for *F. patens* (Moseley's 1881, pl. 6: fig. 5) despite its split classification, because it was well illustrated by Moseley and represented one of the eight species included in the analysis: species 4. Species 4 was chosen instead of species 6 because the characters weighting the classification toward species 6 were primarily size dependent, whereas its shape indices (face angle, SSI) and number of septa were clearly closer to species 4.

Flabellum patens, as restricted by the lectotype and characterized by those specimens classified as species 4, is characterized by a very compressed corallum (low face angle), which produces a relatively high GCD:LCD, and a very high crest height. It also has the lowest average GCD:H (1.04) of the species analyzed, being almost exactly as tall as wide.

Although not examined, the specimens reported by Milne Edwards and Haime (1848) as *F. pavoninum* (one illustrated by Zibrowius, Southward, and Day, 1975) appear to be *F. patens,* having the characteristic polychaete association and corallum shape.

At least three specimens reported by Yabe and Eguchi (1942a) as *F. p. paripavoninum* are also *F. patens.* Examined after the discriminant analysis, they extend the range of face angle and edge angle to 32° and 143°, respectively.

MATERIAL EXAMINED.—ALB-5173 (3) USNM 40720, 40742; ALB-5289 (2) USNM 40745; ALB-5301 (1) USNM 40722; ALB-5577 (1) USNM 81984; 4 of 6 syntypes of *F. patens,* BM; *Sôyô-maru* 343 (1) TIUS 43445 (*F. p. paripavoninum* of Yabe and Eguchi, 1942a); *Sôyô-maru* 419 (2) TIUS 43441 (*F. p. paripavoninum* of Yabe and Eguchi, 1942a) Plate 26*g; F. pavoninum* var. *distinctum* of Umbgrove (1950) RGM 77842, Plate 26*h*.

TYPES.—Four of the six syntypes of *F. patens* were examined (BM 1880.11.25.79), one of which is herein designated as lectotype (Moseley's 1881, pl. 6: fig. 5 (figured herein as Plate 26*a–c,i*)), the remaining specimens designated as paralectotypes. *Type Locality:* 5°49'N, 132°14'E (Kei Island, Banda Sea), 256 m.

DISTRIBUTION.—*?Pleistocene:* Java (Umbgrove, 1950). *Recent:* Off Japan (southern Shikoku, southwest of Kyūshū) (Yabe and Eguchi, 1942a); Pratas Island, South China Sea; Philippines (off Luzon near Manila, Sulu Archipelago); off Kei Island, Banda Sea (Moseley, 1881); 256–439 m; 9.1°–12.4°C.

28. *Flabellum (Flabellum) lamellulosum* Alcock, 1902

PLATE 27*a–l*

Flabellum pavoninum Lesson, 1831:2 pp. [in part: 3 of 5 syntypes].

Flabellum lamellulosum Alcock, 1902a:30, pl. 4: figs. 28, 28a,b.—Zibrowius, 1974:18.

Flabellum distinctum.—Alcock, 1902a:30 [in part: *Siboga* 12].

Flabellum pavoninum.—Faustino, 1927:45–46 [in part: 7 of 21 stations: ALB-5116, 5117, 5212, 5273, 5392, 5393, and Calapan Mindoro].—Squires, 1964a:15–21 [in part: ALB-5116, 5117, 5273, 5392, 5393, 5505, pl. 1: figs. 1–3, pl. 2: figs. 1–2].

Flabellum pavoninum var. *lamellulosum.*—Vaughan, 1907:51–42, pl. 1: figs. 1a,b.—Squires, 1958:63.—?Yabe and Eguchi, 1942b:131.

DESCRIPTION.—Angle of thecal edges, exclusive of crests, quite variable, ranging from 130°–240°, with 165.5° as the average. Inclination of lateral faces 32°–51°. One of the largest specimens (ALB-5212) 55.5×41.6 mm in calicular diameter and 56.4 mm tall. Thecal faces flat to slightly concave, meeting in acute thecal edges that are crested. Edge crests up to 8.2 mm tall and irregular in shape, formed by successive eversions (spurs) of the calice associated with the two principal costae (Plate 27*h,k*) and subsequent retrenchment of the calice edge, together forming a relatively straight thecal edge but with an irregular margin. Up to 5 or 6 of these spurs are formed along a thecal edge, the eversions hollow. Length of thecal edge up to 30.0 mm; LEL:H = 0.32–0.61. Thecal faces lack costal ridges but are often encrusted with barnacles, anemones, serpulid tubes, and foraminifera (see Squires, 1964a). Well-preserved theca and septa uniformly reddish brown. Pedicel small and circular, 1.5–2.1 mm in diameter. Ratio of GCD:LCD variable, ranging from 1.20–1.77, but averaging 1.43. Ratio of GCD:H = 0.79–1.29, averaging 1.05.

Septa hexamerally arranged in seven cycles, the last cycle never complete. Largest number of septa observed, 340 (ALB-5273), having 74 pairs of S_7. Hexameral symmetry often difficult to determine in large specimens because some S_5 extend to columella, approximating S_4 in size, and the S_7 insertions are very irregular. In fact, in some large coralla there appear to be 50, instead of 48, major septa (S_{1-4}). S_{1-4} equal in size in large coralla; in smaller coralla S_4 are slightly less exsert than S_{1-3} and less thickened near the columella. S_{1-4} not exsert, the same width as higher-cycle septa near calicular edge, gradually broadening into moderately wide septa with straight inner edges (SSI average = 1.13); thickened near the columella. S_5 about 3/4 size of S_{1-4} and usually do not attain the columella. S_6 about 3/4 size of S_5; S_7 rudimentary, pairs beginning to form at a greater calicular diameter of 47–50 mm.

Fossa elongate and relatively open. Columella well developed: crescent-shaped and elongate, formed from the thickened inner edges of the S_{1-4}.

DISCUSSION.—Alcock (1902a) originally described *F. lamellulosum* based on one specimen with an unusually high edge angle of 240° (not 285° as Alcock reported). No additional specimens were subsequently reported as that species, but both Vaughan (1907) and Squires (1958) differentiated this taxon, which they relegated to a subspecies of *F. pavoninum,* from other taxa by having an edge angle in excess of 180°. Examination of a large suite of additional specimens reported herein show that the edge angle is quite variable, ranging from 130°–240°, with an average of only 166° (exclusive of crests). Edge angle, therefore, should not be used as a key character for this species.

Multivariate characters derived from discriminant analysis

(Cairns, in press b) easily distinguish *F. lamellulosum* from all other species analyzed (Table 4) and indicated a morphological similarity to *F. patens* and *F. magnificum. Flabellum lamellulosum* is similar to *F. patens* in general corallum shape (GCD:H, LEL:H), septal shape (SSI, septal concavity index), crest height, and pedicel diameter, but differs significantly in face angle, edge angle, and GCD:LCD (Table 4). *Flabellum lamellulosum* resembles *F. magnificum* in edge angle, general size, and pedicel diameter, but differs in having a much higher, discontinuous crest; virtually straight inner septal edges (average SSI = 1.13); and much lower GCD:H and LEL:H ratios, indicating its squarish shape vs. the rectangular shape of *F. magnificum.*

It should also be noted that three species described from the Eocene to Miocene of New Zealand—*F. circulare, F. radians,* and *F. mariae* (all Tenison-Woods, 1880, and all subsequently illustrated by Squires, 1958)—are indistinguishable from *F. lamellulosum* based on the characters used in their description: greater and lesser calicular diameters, height, and edge angle. All of these species belong to a species complex characterized by having a corallum about as tall as wide (GCD:H~1.0) and a high edge angle, often over 180°.

MATERIAL EXAMINED.—ALB-5116 (3) USNM 40738; ALB-5117 (1) USNM 40739; ALB-5212 (8) USNM 40744; ALB-5273 (38) USNM 40747, 45483, and 45484, (2) AM G15243; ALB-5391 (4) USNM 81982; ALB-5392 (15) USNM 40753, 45485; ALB-5393 (6) USNM 40754; ALB-5505 (2) USNM 81983; Calapan, Musoro (1) USNM 40758; paralectotypes of *F. pavoninum* (3) MNHNP 372 (Plate 27*c,f,i*); holotype of *F. lamellulosum,* ZMA; *Siboga* 12 (2) ZMA 1410 (*F. distinctum* of Alcock, 1902a); all specimens reported as *F. pavoninum* by Faustino (1927) and Squires (1964a), USNM.

TYPES.—The holotype of *F. lamellulosum,* collected at *Siboga* 251, is deposited at the ZMA (1215) (Van Soest, 1979) Plate 27*a,d,g,j. Type Locality:* 5°28.4′S, 132°02′E (off Kei Island, Banda Sea), 204 m.

DISTRIBUTION.—*Recent:* ?Kyūshū, Japan (Yabe and Eguchi, 1942b); Philippines (off Luzon; Mindoro; Samar Sea; Bohol Sea); Indonesia (Banda Sea, Java Sea) (Alcock, 1902a); 198–402 m; 10.1°–15.5°C.

29. *Flabellum (Flabellum) politum,* new species

PLATE 28*a–f*

Flabellum patens Moseley, 1881:172 [in part: 1 of 7 syntypes].

Flabellum pavoninum var. *distinctum.*—Gerth, 1921:401.

Flabellum pavoninum.—Faustino, 1927:46 [in part: ALB-5178, 5217, 5311, 5212].

Flabellum paripavoninum.—Faustino, 1927:47 [in part: ALB-5212, 5311, 5527, 5312, 5392].

Flabellum pavoninum paripavoninum.—Yabe and Eguchi, 1942a:91–93 [in part: pl. 5: fig. 8a–c, *Sôyô-maru* 419, in part: specimen 1]; 1942b:129–130 [in part: pl. 11: fig. 9].

DESCRIPTION.—Angle of thecal edges 90°–136°, averaging 107°; inclination of lateral faces, 30°–45°. Coralla dense and relatively small, the largest specimen examined (ALB-5392) 36.1×22.0 mm in calicular diameter and 31.8 mm tall. Thecal faces meet in very acute thecal edges, which bear very low crests. Ratio of LEL:H = 0.46–0.78, the higher ratio corresponding to specimens with a low thecal edge angle. Thecal faces planar, sometimes with costal ribbing, but usually flat and smooth, almost porcelaneous. In large specimens with a fully intact calicular edge, the upper thecal faces are highly arched centrally, flanked by a shallow notch a short distance toward the thecal edge, followed by another small lobe nearer the calicular edge (Plate 28*a,b*). Thecal faces of some specimens, especially smaller specimens, sometimes have reddish brown stripes corresponding to the septa, but more often the coralla are uniformly white. Pedicel circular in cross section (1.0–1.4 mm in diameter), elongate (up to 5 mm), and invariably broken above the basal plate, clearly revealing the six protosepta. Ratio of GCD:LCD = 1.49–2.15, the higher ratios corresponding to specimens with long, intact pedicels and a low thecal edge angle. Ratio of GCD:H = 0.98–1.30, roughly equally wide as tall.

Septa hexamerally arranged in six cycles (192 septa) according to the formula: $S_{1-3}>S_4>S_5>S_6$. At a greater calicular diameter of 23 mm there are only five cycles; between 24–31 mm in greater calicular diameter progressively more pairs of S_6 are added; and by a calicular diameter of over 31 mm most specimens have a full sixth cycle. Largest specimen examined has one pair of S_7 (194 septa) in the space adjacent to a principal septum. S_{1-3} easily distinguished by their greater size and broad, sinuous inner septal edges (average SSI = 5.0), which fuse together to form the columella. Upper edges of S_{1-3} extend almost as high as calicular edge. S_4 0.8–0.9 width of S_{1-3}, slightly less sinuous, and do not attain the columella. S_5 and S_6 progressively less sinuous: S_5 $^1/_3$ to $^1/_2$ size of S_4; S_6 rudimentary. Septal granules low and massive, about 0.07 mm tall.

Fossa elongate, deep, and narrow. Columella rudimentary.

DISCUSSION.—*Flabellum politum* was previously reported as at least four different species, but, according to the discriminant analysis (Cairns, in press b), it is one of the most distinctive species of those analyzed. With the exception of *F. dens,* it has the smallest adult corallum, lowest edge angle, lowest average number of septa, and highest SSI of all species (Table 5). It is further distinguished by its smooth, lustrous theca, from which the species name derives.

ETYMOLOGY.—The species name is from the Latin *politum* (polished), and refers to the smooth, almost porcelaneous, thecal faces of this species.

MATERIAL EXAMINED.—Types; syntypes of *F. patens,* BM 1880.11.25.79 (only 1 of which is *F. politum,* Plate 28*d*); *F. pavoninum* var. *distinctum* of Gerth (1921) RGM 3788 (1).

TYPES.—*Holotype:* ALB-5391, USNM 81945, Plate 28*a,b. Paratypes:* ALB-5133 (4) USNM 81942; ALB-5136 (1) USNM 81943; ALB-5178 (10) USNM 40743; ALB-5212 (7) USNM 40725, 40756; ALB-5217 (2) USNM 40749;

ALB-5311 (5) USNM 40723, 40755; ALB-5212 (4) USNM 40731; ALB-5313 (1) USNM 81944; ALB-5391 (32) USNM 40724, (2) AM G15257; ALB-5392 (1050) USNM 40733; ALB-5393 (12) USNM 81946; ALB-5527 (1) USNM 40726; off Calapan (1) USNM 81947. *Type Locality:* 12°13'15"N, 124°05'03"E (Samar Sea, east of Masbate), 216 m.

DISTRIBUTION.—*Miocene:* Java (Gerth, 1921). *Recent:* Off southwestern Kyūshū, Japan; South China Sea off Hong Kong; Philippines (Sibuyan Sea, Samar Sea, Bohol Sea, Sulu Archipelago); Kei Island, Banda Sea; 40–402 m; 9.6°–15.5°C.

30. *Flabellum (Flabellum) dens* Alcock, 1902

PLATE 28*g–k*

Flabellum dens Alcock, 1902a:32, pl. 4: figs. 30, 30a.—Faustino, 1927:59, pl. 4: figs. 6, 7.—Zibrowius, 1974:20.

DESCRIPTION.—Corallum small and highly compressed; inclination of lateral faces 14°–18°. Angle of rounded thecal edges changes abruptly at a height of 5–6 mm, changing from 58°–79° to 21°–35°. Alcock's (1902a) figured syntype 12.5×5.6 mm in calicular diameter and 15.7 mm tall, although another syntype (Plate 28*j,k*) is larger: 13.8×6.7 mm in calicular diameter and 22.5 mm tall, but is badly worn and damaged. Because of the relatively elongate corallum and low thecal edge angle, the LEL:H is consistently 0.92–0.93. Theca smooth and worn in syntype series. Pedicel usually broken, but, when present, 1.3–1.4 mm in diameter; transverse division not present. Ratio of GCD:LCD = 1.7–2.3; GCD:H = 0.68–0.82.

Septa hexamerally arranged in four cycles (48 septa) in smaller coralla. In larger coralla there are 20 primary septa, 20 secondary septa, and 8 or 9 pairs of tertiary septa, totaling 56–58 septa. S_{1-2} (or primary septa) equal in size; S_3 (secondary septa) about half size of S_{1-2}; S_4 (tertiaries) are rudimentary. Inner edges of larger septa vertical and very sinuous, enclosing a deep and narrow fossa. Columella rudimentary.

DISCUSSION.—Although Zibrowius (1974) placed *F. dens* in the truncate *Flabellum* group (*Truncatoflabellum*), it clearly belongs in the subgenus *Flabellum (Flabellum)*. This error probably originated because Alcock (1902a) figured only one specimen that had an accidentally broken base; other syntypes reveal a typical pedicel diameter of 1.3–1.4 mm. Although not included in the discriminant analysis, *F. dens* is one of the most distinctive and easily identified species in the subgenus (Table 5). It has the smallest adult corallum, the lowest face angle, and the least number of septa. Particularly distinctive is the change of edge angle with height, giving the corallum a unique shape.

MATERIAL EXAMINED.—Syntypes.

TYPES.—Nine syntypes, all collected at *Siboga* 95, are deposited at the ZMA: the originally figured syntype (1209, Plate 28*g–i*) and 8 other syntypes (1449, Plate 28*g–i*). *Type Locality:* 5°43.5'N, 119°40'E (Pangutaran Group, Sulu Archipelago), 522 m.

DISTRIBUTION.—Known only from the type locality.

Subgenus *Flabellum (Ulocyathus)* Sars, 1851

Phyllodes Philippi, 1841:665 [preoccupied by *Phyllodes* Boisdural, 1832, Lepidoptera].

Ulocyathus M. Sars, 1851:141.

Flabellum.—Duncan, 1885:13–14 [in part].—Yabe and Eguchi, 1942a:87–89 [in part].—Vaughan and Wells, 1943:226–227 [in part].—Alloiteau, 1952:653 [in part].—Wells, 1956:432 [in part].—Squires, 1958:62–63 [in part].—Zibrowius, 1974:20–21 [in part: group 3].—Chevalier, 1987:752 [in part].

DIAGNOSIS.—*Flabellum* with a jagged calicular edge.

DISCUSSION.—To facilitate comparison among the 22 species of *Flabellum (Ulocyathus)* known from the Recent and fossil Indo-West Pacific, the subgenus can be further subdivided into three groups based on corallum morphology: laterally compressed, bowl-shaped, and constricted. Species with laterally compressed coralla generally have flat to only slightly convex thecal faces, which meet in acute thecal edges, often having thecal crests. The thecal edge angle and inclination of lateral faces are usually a constant, and, viewed from the side, the lower half of the corallum is triangular. Nine Recent and Indo-West Pacific fossil species are included in this category: *F. japonicum*, Moseley, 1881; *F. deludens* Marenzeller, 1904; *F. apertum apertum* of Squires, 1958; *F. apertum deludens* of Squires, 1958; *F. japonicum* of Hoffmeister, 1933; *F. daphnensis* Durham and Barnard, 1952; *F. planus* Squires, 1962; *F. aotearoa* Squires, 1964; and *F. marenzelleri*, new species. *Flabellum laciniatum* (Philippi, 1841) (Plio-Pleistocene, Italy) also belongs to this group.

Species with bowl-shaped coralla have convex thecal faces and thecal edges that are rounded, rarely crested. The thecal edge angle is often very large basally but decreases closer to the calice. The inclination of the lateral faces usually also decreases with height, both effects producing a campanulate corallum, many of which were compared by Cairns (1982). Six Recent species are included in this group: *F. angulare* Moseley, 1876; *F. conuis* Moseley, 1881; *F. apertum* Moseley, 1976; *F. tuthilli* Hoffmeister, 1933; *F. japonicum* of Alcock, 1898, and Gardiner, 1929; and *F. raukawaensis* Squires and Keyes, 1967.

Species with constricted coralla have convex lateral faces, high thecal edge angles, and often have thecal crests. Four species are attributed to this group: *F. alabastrum* Moseley, 1876; *F. messum* Alcock, 1902; *F. lowekeyesei* Squires and Ralph, 1965; and *F. marcus* Keller, 1974. Three additional species have unique corallum morphologies: *F. moseleyi* Pourtalès, 1880 (curved cornute corallum); *F. macandrewi* Gray, 1849 (= ?*F. laciniatum* (Philippi, 1841)) (fissiparous corallum), and *F. sexcostatum*, new species, which is intermediate between the laterally compressed and bowl-shaped groups.

TYPE SPECIES.—*Ulocyathus arcticus* Sars, 1851 (= *Flabellum macandrewi* Gray, 1849), by monotypy.

DISTRIBUTION.—*Miocene to Pliocene:* Italy, New Zealand, Australia. *Recent:* Cosmopolitan (Atlantic, Pacific, Indian Oceans, Subantarctic); 180-3200 m, but predominantly deeper than 500 m.

31. *Flabellum (Ulocyathus) deludens* Marenzeller, 1904

PLATE 29*a-f*

Flabellum japonicum.—Marenzeller, 1889:45-46.

Flabellum laciniatum.—Wood-Mason and Alcock, 1891b:450-451; Alcock, 1898:21-23, pl. 2: figs. 4, 4a; 1902b:150, fig. 19.

Flabellum deludens Marenzeller, 1904:269-272, pl. 17: figs. 10, 10a.—Faustino, 1927:48-50, pl. 2: figs. 7-8 [in part: 16 of 24 stations, see text].—Gardiner, 1929:305.—Yabe and Eguchi, 1942a:101-103, pl. 5: figs. 9-11; 1942b:135-136, pl. 12: fig. 1.—Utinomi, 1965:256.—Eguchi, 1965:292, fig.; 1968:C44, pl. C22: fig. 45, pl. C25: figs. 3, 4.—Zibrowius, 1974:21.—Zibrowius and Grygier, 1985:122, figs. 16-17.

Not *Flabellum deludens.*—Vaughan, 1907:63-64, pl. 3: figs. 5a,b [= *F. marcus* Keller, 1974]; 1919, pl. 12: figs. 3, 3a [= *F. marcus*].—Gravier, 1920:69-71, figs. 118, 119 [= *F. angulare* Moseley, 1876].—Pax, 1934:57 [= *F. macandrewi*].—Ralph and Squires, 1962:12, pl. 4: figs. 7, 8 [= *F. raukawaensis* Squires and Keyes, 1967].

Not *Flabellum apertum deludens.*—Squires, 1958:68, pl. 13: fig. 13.

Not *Flabellum* cf. *deludens.*—Wells, 1984:215, pl. 4: figs. 8-10 [in part: figured specimen is *F. aotearoa* Squires, 1964b].

DESCRIPTION.—Angle of thecal edges 115°-150°, most about 135°; inclination of thecal faces, 64°-80°. Largest specimen examined 53.0 × 39.0 mm in calicular diameter and 29.4 mm tall (ALB-5110); however, entire populations are composed of specimens smaller than 30 mm in greater calicular diameter (e.g., ALB-5453, 5273). Thecal faces virtually flat, with very little convexity, meeting at an acute angle at thecal edges. Each thecal edge bears a continuous low (rarely over 2 mm tall), thin (0.1 mm) crest. Theca and septa fragile; upper septal edges invariably broken. C_{1-2}, including thecal crests, and upper, outer edges of S_{1-2} reddish brown, producing a distinctive pattern of radiating stripes on a white background. C_3 also reddish brown, but less conspicuous than pigmentation of C_{1-2}. Theca of some specimens uniformly reddish brown. C_{1-2} slightly ridged in larger coralla, ridges composed of finely granulated chevron-shaped growth lines. Pedicel usually elliptical in cross section and basally grooved, reflecting a probable original attachment to a small-diameter cylindrical substrate, although none of the over 1000 specimens examined showed signs of attachment. Instead, only sand grains were normally found to be incorporated into the pedicel scar. Pedicel scar up to 2.3 mm long and about 1.0 mm wide, the greater axis aligned with the thecal edges.

Septa hexamerally arranged in five incomplete cycles according to the formula: $S_{1-2}>S_3>S_4>>S_5$. S_{1-2} extremely exsert, having straight to slightly sinuous vertical inner edges. S_3 about $^3/_4$ size of S_{1-2}, not exsert, and have sinuous inner edges. S_4 $^1/_2$ to $^3/_4$ size of S_3 but considerably taller than the S_3, each S_4, together with its adjacent S_1 or S_2, projecting upward as a rectangular thecal extension 1.6-2.0 mm wide and up to 6.5 mm beyond the adjacent calice. At a greater calicular diameter of 28-42 mm, rudimentary S_5 begin to form, but only in spaces between S_3 and S_4, not in those spaces between the S_4 and the S_1 or S_2 on the thecal extensions, which often results in a corallum of 72 septa. Only in the largest coralla (e.g., greater calicular diameter over 50 mm) are additional S_5 present in end half-systems. S_5 present in thecal extensions are greatly enlarged—almost to the size of an S_4—and merge with adjacent S_4 at their inner edges. These accelerated S_5 often have rudimentary pairs of S_6 flanking them, adding another 24 septa to the calice, resulting in 96 septa, but with curiously incomplete fifth and sixth cycles. The upper, outer edges of S_{1-2} form acute apices on the thecal extensions, and their adjacent S_4 also form smaller apices; upper, outer edges of S_3 also terminate in apices. Septal apices and thecal extensions contribute to a very lacerate calicular margin. Septal faces corrugated, the ridges oriented perpendicular to septal edges. Each ridge covered by a diffuse, unilinear row of fine granules (0.15-0.16 mm in diameter), sometimes becoming multiple rows on those ridges near the theca (Plate 29*f*).

Fossa elongate. Rudimentary columella formed by fusion of thickened lower, inner edges of S_{1-2}. S_3 also fused to columella.

DISCUSSION.—*Flabellum deludens* has had a long history of misidentifications. First reported as the Italian Pliocene *F. laciniatum* Philippi, 1841, by Wood-Mason and Alcock (1891b), it was subsequently described as a new species by Marenzeller (1904) based on specimens collected by the *Valdivia* from west of Sumatra. *Flabellum deludens* is one of the few species for which Faustino (1927) reported new records, listing it from 24 *Albatross* stations from the Philippines and off Japan. Only 16 of these records are confirmed herein (see "Material Examined"); two are *F. marenzelleri*, new species; three are *F. japonicum*; two are too damaged to identify (ALB-5144, 5301); and one appears to be lost (ALB-5257). Additional *Albatross* records are reported herein.

Squires's (1958) specimen of *F. apertum deludens* from the Lower Miocene of New Zealand is very similar to *F. deludens* in its thecal extensions, hexameral symmetry, and flattened thecal faces but can be distinguished by having a considerably smaller inclination of the lateral faces (40°) and a lesser thecal edge angle (95°). The specimen figured and identified by Wells (1984) as *F.* cf. *deludens* from the Pleistocene of Vanuatu (= New Hebrides) is, without a doubt, *F. aotearoa* Squires, 1964. The other four fragments reported by Wells are unidentifiable. Other misidentifications are listed in the synonymy.

Distinctive characters of *F. deludens* are its very high thecal extensions and associated thecal striping; its tendency for unequal development of S_5 in larger coralla; and its virtually flat thecal faces. Among the eight other laterally compressed *Flabellum (Ulocyathus)* listed in the subgeneric discussion, it is most similar to *F. marenzelleri* and *F. japonicum*, both of which are compared to *F. deludens* in their respective species discussions.

Three specimens from ALB-5256 have octameral symmetry; each with 16 major septa and a corresponding number of higher-cycle septa. These specimens also have relatively high thecal edge angles and very pronounced edge crests (up to 3.5 mm). All other characters are the same as typical *F. deludens*. It was undoubtedly this lot that led Faustino (1927:49) to describe *F. deludens* as having 5, sometimes 7, broad low costae per septal face; the five costae pertaining to the typical hexameral specimens, and the 7 corresponding to the octameral form.

MATERIAL EXAMINED.—ALB-4915 (45) USNM 40052; ALB-5094 (3) USNM 40761; ALB-5110 (1000+) USNM 81926, (4) AM G15250; ALB-5117 (1) USNM 40765; ALB-5118 (1) USNM 40691; ALB-5136 (3) USNM 81913; ALB-5197 (11) USNM 40766; ALB-5202 (1) USNM 40714; ALB-5256 (3) USNM 40762; ALB-5273 (500+) USNM 40685; ALB-5278 (6) USNM 40764; ALB-5297 (29) USNM 40763; ALB-5298 (2) USNM 81914; ALB-5369 (1) USNM 81915; ALB-5392 (45) USNM 81916; ALB-5374 (46) USNM 81927; ALB-5387 (5) USNM 81917; ALB-5388 (1) USNM 81918; ALB-5403 (4) USNM 81919; ALB-5408 (2) USNM 40770; ALB-5411 (8) USNM 81920; ALB-5412 (2) USNM 40769; ALB-5417 (1) USNM 81921; ALB-5418 (9) USNM 40716; ALB-5419 (27) USNM 40767; ALB-5453 (400+) USNM 40768; ALB-5454 (3) USNM 40717; ALB-5506 (4) 40696; ALB-5508 (2) USNM 81922; ALB-5536 (6) USNM 81923; ALB-5567 (3) USNM 81924; MUSORSTOM 2-66 (5) USNM 81925; Marenzeller's (1889) *F. japonicum*, NMW 15508; syntypes of F. *deludens*, ZMB; *Marion Dufresne* 27-4-CP06 (4) USNM 82013 (Zibrowius and Grygier, 1985). *Reference Material: Flabellum deludens* of Vaughan (1907); *F. apertum deludens* of Squires (1958) USNM 649155; *F. deludens* of Wells (1984) USNM 71859, 73970.

TYPES.—Two syntypes of *F. deludens* are deposited at the ZMB: *Valdivia* 185 (ZMB 7086, Plate 29*a,b*) and *Valdivia* 203 (ZMB 5086). *Type Locality:* West of Sumatra, eastern Indian Ocean, 614–660 m.

DISTRIBUTION.—*Recent:* Off Japan (Yabe and Eguchi, 1942a); throughout Philippines; eastern Indian Ocean (off Sumatra, Bay of Bengal, Andaman Sea, off Ceylon); western Indian Ocean (Laccadive Sea, Saya de Malha) (Gardiner, 1929); 106–1035 m, although most Philippine records are 180–350 m, the deeper records are from the Indian Ocean; 4.3°–18.4°C.

32. *Flabellum (Ulocyathus) japonicum* Moseley, 1881

PLATE 29*g–i*

Flabellum japonicum Moseley, 1881:168–169, pl. 7: figs. 4, 4a, pl. 16: fig. 12.—Alcock, 1902a:32–33.—Faustino, 1927:47–48, pl. 2: figs. 5, 6.—Yabe and Eguchi, 1932a:389; 1942a:101, pl. 7: figs. 11a–c; 1942b:136, pl. 12: fig. 2.—Eguchi, 1968:C45, pl. C28: figs. 2, 3.—Zibrowius, 1974:21.

Not *Flabellum japonicum*.—Marenzeller, 1889:45–46 [= *F. deludens*].—Wood-Mason and Alcock, 1891b:449.—Alcock, 1898:23.—Gardiner, 1929:306–308, pl. 13: figs. 1–6.—Hoffmeister, 1933:7, pl. 1: figs. 1, 2.

DESCRIPTION.—Angle of thecal edges 96°–108°; inclination of convex thecal faces 76°–88°. Largest specimen examined (ALB-5221) 52.5 × 38.7 mm in calicular diameter and 29.3 mm tall. Each thecal edge bears a low (rarely over 1.0 mm tall) crest, beginning near the pedicel but often disappearing at a corallum height of 12–14 mm. Above this height thecal edges are evenly rounded without evidence of crests or ridges. Corallum very delicate, like *F. deludens:* upper septal edges often broken. Theca white to light reddish brown, but with no stripes; inner septal edges adjacent to theca usually more darkly pigmented. C_{1-2} slightly ridged on lower half of large coralla, the theca becoming flat in upper corallum. Pedicel elliptical in cross section, 2.5 × 1.5–1.8 mm in diameter. Ratio of GCD : LCD = 1.3–1.4.

Septa hexamerally arranged in five complete cycles. S_5 begin to appear in end half-systems adjacent to S_3 at a greater calicular diameter of about 28 mm; a full fifth cycle is present only in specimens over 50 mm in greater calicular diameter. S_{1-2} moderately exsert with sinuous, vertical inner edges that define a very deep and narrow fossa. S_3 about $^3/_4$ size of S_{1-2} and also have sinuous inner edges. S_4 about half the width of S_3 but slightly more exsert than S_3, joining with its adjacent S_1 or S_2 to form a small triangular thecal extension extending up to 3.5 mm beyond the adjacent calice. Upper edges of S_3 also terminate in small apices, creating a moderately lacerate calicular perimeter. S_5 rudimentary. Septal granules up to 0.3 mm tall.

Fossa deep and elongate. Columella composed of a fusion of nonthickened lower, inner edges of S_{1-2}. Lower edges of S_3 also attain the columella.

DISCUSSION.—Shortly after *F. japonicum* was described by Moseley from off Japan, Wood-Mason and Alcock (1891b), Alcock (1898), and finally Gardiner (1929) reported it from the Indian Ocean, specifically from off Bombay, Luccadive Sea, and in the vicinity of Ceylon in the Bay of Bengal (102–1713 m). Specimens were examined from the Bay of Bengal (1240 m) that were donated to the USNM by the Indian Museum, Calcutta (USNM 18156), and from off Ceylon (*Marion Dufresne* 27-4-CP07: USNM 77203). Based on these specimens and Gardiner's (1929) figures, it is clear that the northern Indian Ocean *Flabellum* is not the same as *F. japonicum*, which is known only from the western Pacific. It differs in having a more distinctly bowl-shaped corallum (and therefore grouped with the campanulate *Flabellum* (*Ulocyathus*)); having much higher thecal extensions; having a white corallum; and in lacking thecal edge crests. Most of these differences were noted by Gardiner but were not considered by him to be of specific importance. Gardiner (1929) also synonymized *F. angulare* Moseley, 1876; *F. apertum* Moseley, 1876; and *F. conuis* Moseley, 1881, with *F. japonicum*, even though both *F.*

angulare and *F. apertum* had priority over *F. japonicum*, stating that the Indian Ocean specimens were most similar to the North Atlantic *F. angulare*. Indeed, the Indian Ocean specimens are most similar to this Atlantic species, not to *F. japonicum*, and I maintain that all of the nominal species synonymized by Gardiner are distinct, valid species, including the Indian Ocean species, which requires a description and a new name.

Hoffmeister (1933) reported four specimens of *F. japonicum* from southeastern Australia and Tasmania (110-366 m), one of which is deposited at the NMNH (*Endeavour* 5557, USNM 82012, Plate 29*j,k*). Although similar to *F. japonicum* in corallum shape and color, the corallum of the Australian specimen is much denser and the septal arrangement is different, the figured specimen having a full six cycles of septa ($S_{1-3}>S_4>S_5>S_6$), and the NMNH specimen having 16 primary septa, 16 secondary septa, 32 tertiary septa, and about 40 quaternary septa. In addition, the septa of the Australian specimens are more closely spaced and the inclination of the lateral faces less than that of *F. japonicum* (59° for *Endeavour* 5557 vs. 76°-88° for *F. japonicum*). This southeastern Australian species thus requires a new name.

Finally, in a synonymy like that of Gardiner, Keller (1974) synonymized *F. japonicum*, *F. deludens*, *F. deludens* of Gravier, 1920, and *F. raukawaensis* as *F. apertum* Moseley, 1876. Comparisons to *F. deludens* are made later in this discussion; however, the other three species differ from *F. japonicum* in (1) having campanulate coralla with lateral edge angles considerably higher than the maximum known for *F. japonicum* (i.e., 88°), (2) being white, not reddish brown, and (3) having well-developed C_1 and no lateral edge crests. Furthermore, one of these three species, *F. deludens* of Gravier, 1920, has been synonymized by Zibrowius (1980) with *F. angulare* Moseley, 1876, a species only known from the North Atlantic from 1600-3200 m. In short, all of Keller's synonymized species are considered to be valid species with distinct geographic ranges, except for *F. japonicum* and *F. deludens*, which overlap in the western Pacific.

Among the eight other laterally compressed *Flabellum (Ulocyathus)*, *F. japonicum* most closely resembles *F. deludens*. *Flabellum japonicum* is distinguished by its much less exsert triangular thecal extensions; less prominent edge crests, which usually disappear near the calicular edge; slightly convex thecal faces; less-pronounced thecal stripes; and lower thecal edge angle (96°-108° vs. 115°-150° for *F. deludens*).

Another species from this region that could be confused with *F. japonicum* is *F. apertum* of Yabe and Eguchi (1942a,b) and Cheng (1977) from the East China Sea at 307-600 m. Three additional lots of this form are present at the NMNH from off Japan (ALB-4960, USNM 40703; ALB-5054, USNM 40706; and ALB-5086, USNM 40710). They are most easily distinguished from *F. japonicum* by having white coralla and S_3 that fall short of the columella. The Japanese *F. apertum* were compared to typical *F. apertum*, previously known only from the circum-Subantarctic at 220-1500 m (Cairns, 1982), and some minor differences were found; however, the information obtained from the small size and poor condition of the few Japanese specimens that are available is not sufficient to confidently distinguish this form.

MATERIAL EXAMINED.—ALB-3698 (1) USNM 22058; ALB-5083 (1) USNM 40709; ALB-5091 (3) USNM 40712; ALB-5092 (2) USNM 40713; ALB-5124 (3) USNM 40692; ALB-5198 (3) USNM 40694; ALB-5221 (1) USNM 40690; ALB-5222 (1) USNM 40689; ALB-5373 (7) USNM 81929; ALB-5505 (4) USNM 81930; ALB-5527 (3) USNM 81931; ALB-5535 (2) USNM 40697; ALB-5536 (4) USNM 81932; ALB-5537 (2) USNM 40698; ALB-5538 (1) USNM 40699; ALB-5564 (1) USNM 81933; 1 syntype, BM. *Reference Material: Endeavour* 5557 (1) USNM 82012 (*F. japonicum* of Hoffmeister, 1933); Bay of Bengal (2) USNM 18156; *Marion Dufresne* 27-4-CP07 (1) USNM 77203; *F. japonicum* of Cheng (1977) three *Albatross* stations (see "Discussion").

TYPES.—Eight syntypes of *F. japonicum* are deposited at the BM (Plate 29*g,h*). *Type Locality:* 35°11'N, 139°28'E (Sagami Bay, Honshū, Japan), 631 m.

DISTRIBUTION.—Recent: off southeastern Honshū, Japan (Yabe and Eguchi, 1942a; Moseley, 1881); throughout Philippines; ?Indonesia (Java Sea, Flores Sea) (Alcock, 1902a); 128-1141 m, although most Philippine records are 365-550 m; 8.0°-12.2°C.

33. *Flabellum (Ulocyathus) marenzelleri*, new species

PLATE 30*a–e*

Flabellum deludens.—Faustino, 1927:49 [in part: ALB-5289, 5265].

DESCRIPTION.—Angle of thecal edges 92°-97°; inclination of thecal faces, 39°-47°. Largest specimen examined (holotype) 41.8 × 23.6 mm in calicular diameter and 30.5 mm tall. Thecal faces slightly convex, meeting in an acute angle at thecal edges. Each thecal edge bears a continuous low (rarely over 2 mm tall) crest. Corallum more robust than that of *F. deludens*; upper septal edges often intact. Theca uniformly light brown with slightly darker pigmentation in stripes corresponding to primary costae. Some specimens with one or more transverse, crescent-shaped white bands on thecal faces. Primary costae, corresponding to theca covering primary and adjacent tertiary septa, slightly raised and about 1.8 mm wide. Secondary costae also slightly elevated and about 0.8 mm wide. All costae covered by a fine granulation, which obscures the chevron-shaped growth lines.

Septa octamerally arranged in four size classes, the largest specimen (holotype) having 104 septa arranged according to the formula: 16 : 16 : 32 : 40 (having an incomplete fourth size class instead of an optimal 64). The 16 large exsert primary septa have sinuous, vertical inner edges. The 16 secondary septa are about $^{2}/_{3}$ size of primaries and also have sinuous inner edges. The 32 tertiary septa (equivalent to S_4 of *F. deludens*) are about $^{2}/_{3}$ width of a secondary septum but considerably more exsert. Each primary septum, along with its pair of flanking S_3, produce a tall rectangular thecal extension projecting up to 4 mm above the adjacent calice. An incomplete cycle of rudimentary quaternary septa present in larger specimens, relegated to half-systems adjacent to the lateral thecal faces. As in *F. deludens*, pairs of quaternaries (S_5 of *F. deludens*) usually flank only secondary septa (S_3 of *F. deludens*), but when all four quaternaries are present in a half-system those adjacent to the primaries are the same size as those adjacent to the secondaries. Upper, outer edges of secondary septa form small apices, which, together with the thecal extensions of the primary and tertiary septa, form a highly lacerate thecal margin. Septal faces slightly corrugated, covered by unilinear rows of coarse blunt granules, each about 0.3 mm tall.

Fossa elongate and deep. Rudimentary columella formed by fusion of greatly thickened lower, inner edges of primary septa. Secondary septa also fuse with columella.

DISCUSSION.—*Flabellum marenzelleri* has been reported only once before by Faustino (1927) as *F. deludens*, based on some of the specimens used in the preceding description. Among the eight other species of laterally compressed *Flabellum (Ulocyathus)* (see discussion of subgenus), *F. marenzelleri* is most similar to *F. deludens* but can be distinguished by corallum shape: having a significantly lower thecal edge angle, lower angle of inclination of lateral faces, and a correspondingly higher GCD : LCD. Another major difference is its octameral septal symmetry, although some specimens of *F. deludens* are also known to have octameral symmetry (e.g., ALB-5256). Other differences include a different thecal pigmentation, an equal development of highest-cycle septa, and a lesser degree of thecal extension exsertness.

In shape and coloration *F. marenzelleri* is similar to *F. aotearoa* Squires, 1964, known only from off New Zealand, but *F. aotearoa* is distinguished by its septal symmetry (five complete hexamerally symmetrical septal cycles), much lower thecal extensions, and peculiar granular costal texture.

One aberrant specimen (Plate 30*d,e*) from ALB-5268 differs in shape and septal symmetry, presumably caused by an injury early in ontogeny. It is 31.5 × 23.7 mm in calicular diameter (GCD : LCD = 1.32) and 33.5 mm tall, with a thecal edge angle of 61°, inclination of lateral faces of 42°, and 13 primary septa.

ETYMOLOGY.—This species is named in honor of Emil von Marenzeller, author of the report on deep-water Scleractinia of the *Valdivia* expedition (Marenzeller, 1904), among other coral publications between 1887 and 1907.

MATERIAL EXAMINED.—Types. *Reference Material: Ikatare* B-26 (1) USNM 68261 (paratype of *F. aotearoa*); *F. aotearoa* from 31°47′S, 167°51′E, 319 m (1) USNM 49233; USGS 24918 (1) USNM 71859 (*F.* cf. *deludens* of Wells, 1984, = *F. aotearoa*).

TYPES.—*Holotype:* ALB-5289, USNM 40686, Plate 30*a–c*. *Paratypes:* ALB-5289 (1) USNM 81889; ALB-5265 (3) USNM 40687; ALB-5268 (1) USNM 81887; ALB-5298 (2) USNM 81888. *Type Locality:* 13°41′50″N, 120°58′30″E (Matocot Point, Verde Island Passage, Luzon, Philippines), 315 m.

DISTRIBUTION.—Known only from Verde Island Passage, Luzon, Philippines; 247–315 m.

34. *Flabellum (Ulocyathus) messum* Alcock, 1902, new rank

PLATE 30*f–i,k*

Flabellum laciniatum var. *messum* Alcock, 1902a:31.—Van Soest, 1979:113, pl. 2: fig. 5.

Flabellum pavoninum.—Faustino, 1927:46 [in part: ALB-5647].

DESCRIPTION.—Angle of straight thecal edges 131°–152°; inclination of concave lateral faces at point of greatest calicular constriction 36°–44°. Largest specimen examined ("off Luzon," USNM 81937) 49.3 × 24.6 mm in calicular diameter and 38.8 mm tall. Corallum delicate and uniformly reddish brown except for thecal crests and crescent-shaped region near pedicel, which are white. Each thecal edge bears a prominent continuous crest that increases in height toward the calice. At calice, crest up to 4.5 mm tall and continuous with principal septa. C_{1-3} very slightly raised and covered with chevron-shaped growth lines. Lateral faces and crests granular, producing a tactually rough texture. Pedicel circular and large, 2.4–2.8 mm in diameter. Ratio of GCD : LCD (taken at point of corallum constriction) = 1.7–2.0.

Septa hexamerally arranged in five cycles according to the formula: $S_{1-3}>S_4>S_5$, with very few pairs of S_6 present. S_{1-3} slightly exsert, with straight, vertical inner edges. Apices of S_{1-3} and adjacent S_5 form thecal extensions up to 5 mm tall; however, the two principal S_1 and their adjacent pairs of S_5 form a distinctively taller extension up to 8.0 mm, accentuated by deep notches between the S_4 and S_5 adjacent to the principal septa. S_4 about half size of S_{1-3}, forming smaller apices about 1.5 mm tall. S_5 1/3 width of S_4 but slightly more exsert than S_4, joining with its adjacent S_{1-3} to form the thecal extensions. Septal granules small, about 0.08 mm tall, and sparse.

Fossa deep and narrow. Trabecular columella elongate and crescent shaped, composed of a fusion of lower, inner edges of the S_{1-3}.

DISCUSSION.—Of the three other species of constricted *Flabellum (Ulocyathus)* (see discussion of subgenus), *F. messum* is most similar to *F. lowekeyesei* Squires and Ralph, 1965, known only from off New Zealand at 378–732 m (see Squires and Keyes, 1967). They have similarly shaped coralla, equivalent-sized S_{1-3}, and the same exaggerated principal septa thecal extensions. *Flabellum lowekeyesei* differs in having an even greater thecal edge angle (≥180°); a larger white corallum; a smaller pedicel; and a tendency for the lower, inner edges of the S_4 to fuse with adjacent S_{1-3}.

MATERIAL EXAMINED.—ALB-5281 (3) USNM 81938; ALB-5585 (1) USNM 81939; ALB-5589 (2) USNM 81940;

ALB-5591 (2) USNM 81941; ALB-5647 (1) USNM 40751; unknown ALB station off Luzon, Philippines (4) USNM 81937; syntype of *F. laciniatum* var. *messum* (1) ZMA 1214.

TYPES.—Five syntypes of *F. laciniatum* var. *messum*, collected at three *Siboga* stations (45, 284, and 314), are deposited at the ZMA (1214 (Plate 30*g,h,k*), 1401, 1867) (Van Soest, 1979). *Type Locality:* Indonesia, 694-828 m.

DISTRIBUTION.—*Recent:* Philippines (off Luzon; Celebes Sea; south of Basilan); Indonesia (off Sabah, Flores Sea, Banda Sea) (Alcock, 1902a); 368–949 m; 5.1°-10.2°C.

35. *Flabellum (Ulocyathus) sexcostatum*, new species

PLATES 30*j*, 31*a,b*

DESCRIPTION.—Corallum laterally compressed basally but campanulate distally, the change occurring at a height of 12-15 mm. Basal thecal edge angle 55°–75°, upper thecal edge angle 115°–130°. Inclination of basal lateral faces 61°–73°, upper thecal faces only 29°–36°. Largest paratype 49.3 × 30.4 mm in calicular diameter and 40.4 mm tall. Theca fragile, white to pale reddish brown. C_1 ridged (up to 2 mm high) for about 15 mm beginning at a height of 12-15 mm and corresponding to the region at which the thecal edges and faces are inflected upward. In the holotype, C_2 are also slightly ridged, but much less than the C_1. Pedicel elliptical in cross section, about 2.0 × 1.5 mm in diameter, the greater diameter aligned with the principal costae. Ratio of GCD : LCD = 1.5–1.6.

Septa hexamerally arranged in five cycles, the fifth cycle complete at a greater calicular diameter of about 45 mm. S_{1-2} large and exsert, with straight, vertical inner edges. S_3 about $^3/_4$ size of S_{1-2}, each forming a small triangular apex about 1.5 mm tall. S_4 about $^1/_2$ width of S_3 but slightly more exsert than S_3, each S_4 together with its adjacent S_1 or S_2 projecting upward in a triangular extension 4-5 mm tall. S_5 small, extending only about $^1/_3$ distance down theca. Septal granules small and sparse, about 0.11 tall.

Fossa extremely deep and narrow. Columella rudimentary, formed by a loose fusion of the lower, inner edges of the S_{1-2}; inner edges of S_3 attain the columella but do not significantly enlarge it.

DISCUSSION.—*Flabellum sexcostatum* cannot be attributed to any of the three species groups of *Flabellum (Ulocyathus)* previously described (see discussion of subgenus) but rather forms a transition between those species having laterally compressed coralla and those that are bowl-shaped. Its lower half is laterally compressed and has thecal edge crests, but the edges of the upper corallum are reflected upward forming a bowl-shaped calice. Among the laterally compressed *F. (Ulocyathus)*, *F. sexcostatum* is most similar to *F. japonicum* and *F. japonicum* of Hoffmeister, 1933, all three species having rounded upper thecal edges, but is distinguished by its prominent C_1, higher GCD : LCD (resulting from its decrease in thecal edge angle in the upper corallum), and lesser number of septa (regarding *F. japonicum* of Hoffmeister). Among the campanulate *F. (Ulocyathus)*, *F. sexcostatum* is most similar to *F. apertum* Moseley, 1876, particularly in its prominent expression of C_1. It is distinguished by having a much more laterally compressed corallum, S_3 that reach the columella, and a greater number of S_5 at a corresponding calicular diameter.

ETYMOLOGY.—The species name is from the Latin *sexcostatum* ("six" plus "ribbed"), and refers to the six-ridged C_1.

MATERIAL EXAMINED.—Types.

TYPES.—*Holotype:* ALB-5284, USNM 81934. *Paratypes:* ALB-5284 (6) USNM 81935, (1) AM G15258. *Type Locality:* 13°42′05″N, 120°30′45″E (South China Sea off Luzon), 772 m, 5.7°C.

DISTRIBUTION.—Known only from the type locality.

36. *?Flabellum (Ulocyathus) conuis* Moseley, 1881

PLATE 31*c–g*

Flabellum conuis Moseley, 1881:165–166, pl. 7, figs. 6a,b.

DESCRIPTION.—Corallum campanulate, the lateral edges sometimes diverging almost horizontally, with basal edge angles ranging from 115°–170°. At a height of 6-8 mm the thecal edges are sharply inflected upwards, forming a smaller edge angle of 45°–65°. Inclination of lateral faces also broad, 120°–160° at basal part of corallum, 35°–50° above point of inflection. All seven Philippine specimens examined were dead when collected and therefore not well preserved, making observations of calicular diameter and septal exsertness approximate. Largest specimen 32.4 × 28.9 mm in calicular diameter (Plate 31*f*) and 28.2 mm tall. C_1 slightly ridged for basal part of corallum and prominent at point of corallum inflection, but above this height all costae are smooth and equal in width, marked by chevron-shaped growth lines. Theca and septa very delicate, both uniformly light reddish brown. Pedicel well developed: about 1.5 mm tall and 2.0–2.2 mm in diameter. Base of pedicel circular, showing evidence of original 12 septa on basal disc. Ratio of GCD : LCD = 1.10–1.15.

Septa hexamerally arranged in five cycles, the fifth cycle beginning to appear at a greater calicular diameter of 28–30 mm. S_{1-2} slightly exsert, with straight, vertical inner edges. S_{1-2} terminate in low apices about 2.0 mm higher than adjacent calice. S_3 about $^2/_3$ width of S_{1-2} and also terminate in very low apices about 0.5 mm tall. S_4 about $^1/_2$ width of S_3 but, because the S_{1-2} apices are so low, the adjacent S_4 do not extend above the S_3 as in other species of *F. (Ulocyathus)*. S_5 rudimentary, but full cycle present in largest corallum of 32 mm calicular diameter. Upper margins of larger septa corrugated, with low granules (0.10–0.15 mm tall) aligned on summits of corrugations.

Fossa deep and narrow. Columella rudimentary, composed of the lower, inner edges of S_{1-2}. Inner edges of S_3 recessed 1.0–1.5 mm from inner edges of S_{1-2} but nonetheless appear to contribute to the columella.

DISCUSSION.—The holotype of *F. conuis* differs from the Philippine *Albatross* specimens by having (1) much larger C_1, extending almost to the calicular edge, (2) small C_2, (3) a thecal edge angle of only 82°-83°, and (4) only four cycles of septa. But it must be remembered that *F. conuis* is known from only one specimen, the holotype, and only seven additional specimens are reported herein, the latter of which display great variation in thecal edge angle. Furthermore, the holotype of 29.5 mm greater calicular diameter would not necessarily have developed S_5 at that size, and differences in costal expression may represent variation. Because of the small sample size and the slight differences between the holotype and the Philippine specimens, I have only tentatively identified the latter as *F. conuis*.

MATERIAL EXAMINED.—ALB-5428 (7) USNM 81936. *Reference Material:* Holotype of *F. conuis*, BM.

TYPES.—The holotype of *F. conuis*, collected at *Challenger* station 218, is deposited at the BM (1880.11.25.71), Plate 31*d,e*. *Type Locality:* 2°33'S, 144°04'E (Admiralty Islands), 1994 m.

DISTRIBUTION.—Admiralty Islands (Moseley, 1881); ?Philippines (Sulu Sea off Palawan); 1994-2021 m; 9.7°C.

Truncatoflabellum, new genus

Flabellum.—Milne Edwards and Haime, 1848:257, 259 [in part: *"flabella truncata"*]; 1857:80 [in part: *"flabella truncata"*].—Duncan, 1885:13-14 [in part: sections 3 and 5].—Yabe and Eguchi, 1942a:87-89 [in part].—Vaughan and Wells, 1943:226-227 [in part].—Alloiteau, 1952:653 [in part].—Wells, 1956:F432 [in part].—Zibrowius, 1974:19 [in part: group 2, but not *B. nutrix*].

DIAGNOSIS.—Like *Flabellum*, but reproducing asexually by transverse division: producing distal anthocyathi from anthocauli. Upper calicular margin smooth to slightly scalloped. Most species with one or more pairs of thecal edge spines on anthocyathus and one pair on anthocaulus.

DISCUSSION.—As the name and diagnosis imply, *Truncatoflabellum* is distinguished from *Flabellum* by the characteristic basal scar resulting from transverse fission of the corallum in asexual reproduction. The scar is not the result of accidental breakage, as implied by Gardiner (1902a), but a natural result of asexual reproduction: the size and shape of the scar is usually a species-specific character (Table 6). Because the basal scar is so easily recognized, these "truncate *Flabellum*" were usually segregated in one way or another from the nontruncate species of *Flabellum*, which together formed the most speciose genus of ahermatypic coral. Milne Edwards and Haime (1848) keyed and diagnosed these species as "flabellines tronquees," or *"flabella truncata,"* and designated them as a "section" of the genus *Flabellum*. Squires (1963:10, 25) suggested that the truncate *Flabellum* constituted a distinct species group and that once more was learned about the process of transverse division they should be separated as a distinct genus. Zibrowius (1974) relegated these species to his "second group" of *Flabellum*, implying that they might constitute a separate genus; he informally suggested the name *Blastotrochus* Milne Edwards and Haime, 1848, for this species complex. Finally, Cairns (in press a) asserted that transverse division constituted a "key innovation" in scleractinian evolution—a separate mode of asexual reproduction that allowed an adaptive radiation of species—and strongly urged the establishment of new genera for all groups of Scleractinia that had developed transverse division. The name *Blastotrochus* is not available for the truncate *Flabellum*, being reserved for *B. nutrix*, which has a slightly different mode of reproduction (see Cairns, in press a). Therefore, a new generic name is herein proposed for the truncate *Flabellum: i.e., Truncatoflabellum*.

Milne Edwards and Haime (1848) described 15 species of truncate *Flabellum*, most based on single specimens, some not illustrated, and most without specific locality data. These species have been an endless source of confusion to many authors over the last century. Only one year after their description, Gray (1849) synonymized all but one (*F. affine*) of the 15 species as well as *F. distinctum*, *Placotrochus*, and *Acanthocyathus grayi* as the nontruncate *Flabellum pavoninum*. Not quite so extreme, Semper (1872) synonymized six of the species described by Milne Edwards and Haime as one of his two newly described species of truncate *Flabellum*, *F. variabile*, despite the obvious violation of priority. Gardiner (1902a,b), in a morphometric analysis of 535 South African specimens of *Flabellum*, synonymized as *F. rubrum* most of the species described by Milne Edwards and Haime, plus *F. spheniscus* (Dana, 1846), and one of Semper's species. *Flabellum rubrum* was later shown to be a nontruncate *Flabellum* endemic to New Zealand (Squires, 1963). Bourne (1905), and apparently Brueggemann (fide Gardiner, 1929:309), contrary to previous opinion, suggested that the species originally described by Milne Edwards and Haime were valid, and Bourne suggested that Gardiner's morphometric analysis was not valid (see Cairns, in press a). Gardiner (1929:309) rebutted Bourne much later, writing: "I have searched for and cannot find differences in the characters Bourne suggests and I have to confess my inability to differentiate between the two forms." Most subsequent authors followed Gardiner's reasoning and synonymized most of the truncate *Flabellum*. Faustino (1927), for instance, identified two species from the Philippines, *F. rubrum* and *F. stokesii* (including eight junior synonyms). In reality, his *F. rubrum*, which he reported from 17 stations, includes at least five species. Umbgrove (1938, 1950) followed Faustino in acknowledging two species, and Yabe and Eguchi (1942a,b) and Eguchi (1968) followed suit, but classified *F. rubrum* and *F. stokesii* as subspecies of *F. rubrum*. They distinguished the two subspecies based exclusively on the thecal edge angle and were the first to include the Miocene *F. victoriae* Duncan, 1864, as a junior synonym of *F. rubrum*. Squires (1963) reviewed much of the history of this species complex as it relates to the misattribution of the name *F. rubrum* to non-New Zealand specimens. Finally, Zibrowius (1974) assumed that all truncate *Flabellum* were ultimately referable to two or three species.

The confusion surrounding the species complex of truncate *Flabellum* was approached by examining as many type specimens as possible, using a large collection as a basis, and examining and comparing as many characters as possible. For instance, of the 15 species described by Milne Edwards and Haime (1848), nine were examined; of the remaining six that are presumed to be lost, two neotypes were designated. Furthermore, types and figured specimens were examined of Dana (1846), Semper (1872), Studer (1878), Marenzeller (1904), Gerth (1921), Umbgrove (1938, 1950), and Wells (1984), and topotypic reference specimens were studied from the Australian and New Zealand Miocene. Approximately 75 new specimens representing 14 species were studied from the *Albatross* and MUSORSTOM collections. As a result, I have recognized many, but not all, of the species originally described by Milne Edwards and Haime and described four new species. Milne Edwards and Haime described some species twice, once based on the anthocaulus and a second time based on the anthocyathus, and they also described different growth stages of the same species as different species in at least one instance.

As currently defined, there are 28 valid species and about eight junior synonyms assigned to *Truncatoflabellum*. Nineteen are listed in Table 6. The remaining nine species are *T. compressum* (Lamarck, 1816); *T. victoriae* (Duncan, 1865); *Flabellum candeanum* sensu (Duncan, 1870); *T. martensii* (Studer, 1878); *T. corbicula* (Tenison-Woods, 1880); *T. gippslandicus* (Dennant, 1889); *T. inconstans* (Marenzeller, 1904); *T. stabile* (Marenzeller, 1904); and *F. crassum* sensu Bourne, 1905. *Truncatoflabellum elongatum* (Milne Edwards and Haime, 1848), collected by Cuming from the Philippine Islands, has not been examined but clearly also belongs to this genus. It is probably a junior synonym of one of the other Philippine species but is not considered further in this revision. Discriminating characters used to identify species in this genus include septal number and symmetry, thecal edge angle, basal scar dimensions, septal shape, thecal spines, and thecal texture and color, in descending order of value (Table 6).

ETYMOLOGY.—The genus name is from the Latin *truncatoflabellum* ("truncate" plus "fan"), and alludes to its similarity to the genus *Flabellum*, but differing primarily in its ability to reproduce asexually by transverse division, resulting in an anthocyathus with a truncate base. Gender: neuter.

TYPE SPECIES.—*Euphyllia spheniscus* Dana, 1846, here designated.

DISTRIBUTION.—*Oligocene to Recent:* Indo-Pacific, including New Zealand; ?Cape Verde Islands; 0–1163 m.

37. *Truncatoflabellum aculeatum* (Milne Edwards and Haime, 1848), new combination

PLATES 31*h,l*, 32*a–c*

Flabellum aculeatum Milne Edwards and Haime, 1848:272, pl. 8: figs. 3,3a; 1857:87–88.

?*Flabellum spinosum* Milne Edwards and Haime, 1848:271, pl. 8, fig. 4; 1857:88.—Tenison-Woods, 1878b:310.—Marenzeller, 1889:36–37.—Brueggemann in Gardiner, 1929:309.

Flabellum variabile Semper, 1872:245–251, pl. 17, pl. 18: figs. 1–10.

Flabellum rubrum.—Faustino, 1927:53 [in part: ALB-5156, 5161, 5164].—Umbgrove, 1938:264 [in part: 1 of 8 specimens].

Flabellum stokesii.—Faustino, 1927:54 [in part: pl. 3: figs. 10–16, 18,19].

Flabellum candeanum.—Brueggemann in Gardiner, 1929:309.

?*Flabellum stokesi*.—Veron, 1986:602, fig. 1.

DESCRIPTION.—Angle of rounded thecal edges 31°–82°; inclination of evenly convex thecal faces 17°–27°. Largest anthocyathus examined (RGM 35461) 35.4 mm tall and 37.4 × 15.1 mm in calicular diameter; however, a more typical specimen is 20 mm tall with a greater calicular diameter of 23 mm. Thecal faces sometimes slightly flared near calicular edge. A pair of downward-projecting thecal spines up to 6 mm long occurs on lower thecal edges of anthocyathus. Occasionally a second pair of spines is present 9–10 mm above the basal scar, but rarely a third pair above that. Thecal spines often intact; spines, scar, and theca usually free of encrustation. Basal scar large and wedge-shaped, 10.7–15.2 × 4.4–6.4 mm in size; 24–30 complete septa originate from the scar. Anthocaulus 9.5–12.0 mm high at point of division, with a pedicel diameter of 1.7 mm and a calicular diameter equal to that of anthocyathus's basal scar. Maximum height of anthocauli about 17 mm, but coralla of this height have incipient transverse fracture lines, which, after fracture, result in an anthocaulus about 10 mm tall and an anthocyathus about 5 mm tall. One pair of large thecal spines up to 7 mm long occurs midway on anthocaulus's thecal edges. Anthocaulus septa hexamerally arranged in four cycles, occasionally with several pairs of S_5, according to the formula: $S_{1-3}>S_4>S_5$. Theca milky white and relatively smooth, bearing very faint longitudinal striae, one corresponding to each septum. Ratio of GCD : LCD = 1.8–3.7, the higher ratios belonging to those coralla with elongate calices that are often constricted in the center (e.g., syntypes of *F. variabile*).

Septa of anthocyathus hexamerally arranged up to a greater calicular diameter of about 24 mm according to the formula: $S_{1-3}>S_4>S_5$ (96 septa). S_{1-3} moderately exsert, their upper, outer edges forming a distinct notch about 0.3 mm from theca. S_4 considerably smaller (about $^1/_4$ width of S_{1-3}) and nonexsert. S_5 rudimentary, only about $^1/_4$ size of S_4. Above a greater calicular diameter of about 24 mm, hexameral symmetry is lost. Above this size coralla have 25–36 primary septa equivalent in size and shape to S_{1-3}, and a corresponding number of secondary (S_4 size) and tertiary (S_5 size) septa, up to 144 septa in a large coralla (see "Remarks"). Lower, inner edges of S_{1-3} quite sinuous: those on opposite sides of the fossa symmetrical, almost meeting in center of fossa (separated by about 0.4 mm), and rising vertically in parallel fashion for 4–5 mm above columella. Inner edges of S_4 also slightly sinuous. Septal granules blunt, about 0.12 mm tall.

Fossa narrow, elongate, and deep. Columella rudimentary, a loose fusion of lower, inner edges of the S_{1-3}.

TABLE 6.—Characteristics of the Pacific *Truncatoflabellum*, exclusive of Australia and New Zealand.

Species	EAN; FAN (in degrees)	Thecal edge spination	Basal scar (mm)	Thecal color and texture	GCD : LCD	Septal symmetry (maximum number of septa)	Shape of inner edges of larger septa	Columella	Other morphological characters	Distribution
T. aculeatum (Milne Edwards and Haime, 1848)	31-82; 17-27	1-3 (usually 1) pair(s)	10.7-15.2 × 4.4-6.4	white, smooth	1.8-3.7	25-36:25-36:50-72 1°>2°>3° (144)	notched, sinuous	rudimentary	inner edges of opposing 1° septa vertical and closely adjacent	Pleistocene to Recent: western Pacific; 11-33 m
T. crassum (Milne Edwards and Haime, 1848)	48; 16	1 basal pair	6.5 × 4.2	white, smooth	1.8	$S_{1-2}>S_3>>S_4>S_5>S_6$ (114)	notched, straight	rudimentary		Philippines; depth unknown
T. spheniscus (Dana, 1846)	82-86; 20-25	1-2 pair(s)	10.0-11.2 × 3.9-4.8	white, usually encrusted	2.8-3.4	40-44:40-44:80-88: 4-14; 1°>2°>3°>4° (190)	notched, slightly sinuous	well developed	anthocaulus lacks thecal spines; upper thecal faces highly arched	Japan to northern Australia; western Australia; 2-106 m
F. variabile[1] of Gerth, 1921	65-118; 16-18	1-2 pair(s); short edges	14-18 × 5-6	red brown, granular	3.1-4.1	42-44:42-44:84-88 1°>2°>3° (176)	unknown, straight to slightly sinuous	well developed	basal scar and upper thecal faces strongly arched; anthocaulus with 1 pair of spines	Miocene of Java; Recent: Arafura Sea; 52-90 m
T. stokesi (Milne Edwards and Haime, 1848)	53-67; 24-29	1-3 pair(s)	10.7-13.7 × 5.5-7.1	white, shallow longitudinal striae	1.9-2.4	$S_{1-2}>S_4>S_5>S_6$ (110)	slightly exsert; moderately sinuous	well developed		Miocene of Java; Recent: Indo-West Pacific; 12-256 m
T. bairdi (Milne Edwards and Haime, 1848)	57; 20	1 basal pair	10.7 × 4.8	black brown, rough longitudinal striae	2.9	$S_{1-3}>S_4>S_5>S_6$ (118)	slightly exsert; slightly sinuous	well developed	anthocaulus lacks thecal spines	?Sumatra; depth unknown
T. profundum (Milne Edwards and Haime, 1848)	60-71; 24-29	1 pair; edges sharp	13.5 × 7.3	light brown, coarse longitudinal costae	2.4-2.7	20:20:40:80:6 1°>=2°>>3°>4°>5° (166)	unknown, slightly sinuous	well developed	upper calicular margin slightly scalloped; species with largest corallum	off China and Japan; depth unknown
T. irregulare (Semper, 1872)	36-43; 19-21	1 basal pair	3.9-4.0 × 2.9-3.0	white, heavily encrusted	1.6-2.0	16-18:16-18:32-36 1°=>2°>>3° (72-80)	notched and dentate, straight	moderately developed		Philippines, Indonesia; 11-42 m
T. incrustatum, new species	23-32; 15-19	1 basal pair	5.0-6.0 × 3.5-4.0	black brown, heavily encrusted	1.6-2.1	$S_{1-2}>S_3>S_4>S_5$ (96)	slightly exsert, slightly sinuous	well developed, spongy		Philippines; 37-315 m
T. cumingi (Milne Edwards and Haime, 1848)	31-44; 18-23	2 pairs, well separated	7.6-9.0 × 4.2-4.9	white, smooth	1.8-2.0	16-18:16-18:32-36 1°=>2°>>3° (72)	slightly exsert; slightly sinuous	well developed		Philippines, Molucca Passage; 46-55 m

TABLE 6.—Continued.

Species	EAN; FAN (in degrees)	Thecal edge spination	Basal scar (mm)	Thecal color and texture	GCD : LCD	Septal symmetry (maximum number of septa)	Shape of inner edges of larger septa	Columella	Other morphological characters	Distribution
T. formosum new species	37–43; 18–21	1-2 pair(s)	4.5–5.5 × 2.8–3.1	red brown, usually encrusted	1.4–1.8	20:20:40 $1^\circ>2^\circ>>3^\circ$ (80)	attenuate, moderately sinuous	rudimentary		western Pacific; 37–933 m
T. vanuatu[1] Wells, 1984	20–27; 17	4–5 pairs, rounded edges	4.1–4.9 × 3.0–3.3	white, encrusted	1.6–1.8	16–20:16–20:32–40 $1^\circ>2^\circ>3^\circ$ (80)	slightly exsert, straight	rudimentary	tall anthocyathus (low GCD : H, e.g., 0.55–0.65)	Pleistocene of Vanuatu
T. candeanum (Milne Edwards and Haime, 1848)	50–80; 30–41	3 pairs, quite elongate	4.2–5.7 × 3.0–3.6	red brown stripes	1.6–1.7	18–24:18–24:36–48 $1^\circ>2^\circ>3^\circ$ (96)	slightly exsert, very sinuous	well developed	upper calicular margin slightly scalloped	western Pacific; 70–249 m
T. pusillum, new species	14–18; 18	2–3 pairs	2.4–3.2 × 1.7–1.8	red brown stripes, porcelaneous	1.4–1.7	$S_{1-2}>S_3>S_4$ (32)	unknown, very sinuous	rudimentary	species with smallest corallum	Philippines; 143–146 m
F. irregulare[1] of Gerth, 1921	19; 13	1 basal pair	5.9 × 3.8	white	1.4	$S_{1-2}>S_3>S_4$ (52)	unknown, straight	moderately developed	specimens poorly preserved	Miocene of Java
F. paripavoninum[1,2] of Wells, 1984	64; 21	3–4 pairs, sharp edges	8.3 × 4.6	purple brown	2.3	32:32:64:2 $1^\circ>2^\circ>3^\circ>4^\circ$ (130)	slightly exsert; very sinuous	moderately developed		Pleistocene of Vanuatu
T. paripavoninum (Alcock, 1894)	65–135; 32–62	nonspinose sharp edges	6.8–14.5 × 4.1–6.8	light brown, often encrusted	1.4–2.0	$S_{1-3}=>S_4>S_5>S_6$ ($\geq$192)	attenuate; slightly sinuous	well developed	corallum delicate; upper thecal faces strongly arched	Indo-West Pacific; 476–1163 m
T. carinatum, new species	35–50; 18–32	4 pairs; sharp, carinate edges	4.5–5.2 × 1.7–2.0	light reddish brown	1.6–1.9	$S_{1-3}>S_4>S_5$ (96)	unknown, very sinuous	well developed		Miocene of Java; Pliocene of Japan; Recent: South China Sea; 223–274 m
T. trapezoideum[1] (Keller, 1981)	45–70; 22–28	nonspinose rounded edges	9–14 × 5-9	white, broad C_{1-3}	1.4–2.2	$S_{1-3}>S_4>S_5$ (96)	unknown; slightly sinuous	very well developed		Marcus-Necker Ridge, Falkland Plateau; 595–1896 m

[1] Species not described in text.

[2] Observations based on larger figured specimen from USGS 25715. Smaller specimen from USGS 25718 is an anthocaulus stage.

REMARKS.—Each septum of *T. aculeatum* is separated from its neighbor by about 0.5 mm, regardless of the septal cycle being considered or the greater calicular diameter. Therefore, as the corallum increases in size (over a greater calicular diameter of 20 mm) and thereby increases its calicular perimeter, new septa are added to maintain the 0.5 mm separation. Many coral species add an additional cycle of very small septa, which immediately doubles the number of septa while maintaining hexameral symmetry, but others, such as *F. aculeatum*, use a different method. On the average, for every additional millimeter of greater calicular diameter an S_4 is accelerated in growth to the size of an S_{1-3} (now considered as primary septa), the former pair of S_5 that flanked each accelerated S_4 is also accelerated to the size of S_4 (now considered secondary septa), and two additional pairs of S_5 (tertiary septa) are newly formed to flank each of the accelerated S_4. This retains the three size classes of septa and results in an increase of four septa in the corallum, which, if separated by 0.5 mm, would fill the additional 1 mm greater calicular diameter (roughly 3.1 mm calicular perimeter). At a greater calicular diameter of 24 mm there are usually 24 primary septa (96 total septa), but at a greater calicular diameter of 30 mm there would be 30 primary septa (120 total septa), and at a greater calicular diameter of 36 mm there are about 36 primary septa (144 total septa). These ideal numbers of total septa are rarely achieved, however, because pairs of tertiary septa are often missing.

DISCUSSION.—*Flabellum spinosum* is tentatively considered as a junior synonym of *T. aculeatum* based on the original description and figures of Milne Edwards and Haime (1848). Unfortunately the type is not present at the MNHNP or BM.

Semper's (1872) *F. variabile* is synonymous with *T. aculeatum*, and through Semper's detailed description and 160 syntypes much information is provided about the variation of the species.

One of eight specimens of *F. rubrum* reported by Umbgrove (1938) from the Holocene of Talaud, Celebes, is *T. aculeatum*. The other seven specimens represent unidentified species of *Truncatoflabellum* and three specimens of a truncate *Trochocyathus*.

Among the western Pacific *Truncatoflabellum*, *T. aculeatum* is most similar to those species having large basal scars, the greater axis exceeding 10 mm, i.e., *T. spheniscus*, *T. stokesi*, *T. profundum*, and *T. bairdi* (see Table 6). Comparisons to *T. stokesi* are made in the account of that species. *Truncatoflabellum aculeatum* is distinguished from the three other species by its very sinuous and closely adjacent inner septal edges, notched S_{1-3}, and relatively lower thecal face and edge angles (Table 6).

MATERIAL EXAMINED.—ALB-5156 (15) USNM 40781; ALB-5161 (5) USNM 40782; ALB-5164 (28) USNM 40783, (1) AM G15242; holotype of *F. aculeatum*, MNHNP; 10 syntypes of *F. variabile*, NMW; *F. rubrum* of Faustino (1927); RGM 35461 (1) *F. rubrum* of Umbgrove (1938), Plate 32*c*; NMW 1709, 1710, 8206 (3) *F. spinosum* of Marenzeller (1899); *F. spinosum* of Brueggemann in Gardiner (1929), BM 1842.11.28.23, 25-27.

TYPES.—*Flabellum aculeatum* is based on a holotype consisting of a complete anthocaulus and an attached anthocyathus (Plate 31*h,i*). The corallum is 12.9 × 5.9 mm in calicular diameter and 16.5 mm tall, with a pedicel diameter of 1.7 mm; the anthocaulus portion is 11.8 mm tall, with an incipient fracture diameter of 11.0 × 5.0 mm. Septa are hexamerally arranged in the anthocyathus, including nine pairs of S_5, or 66 total septa. Inner edges of S_{1-3} are very sinuous, and the columella is relatively well developed and 0.9 mm wide. It is deposited at the MNHNP (1016). *Type Locality:* Philippines, depth unknown.

The type of *F. spinosum* is not present at the BM or MNHNP and is therefore presumed to be lost. *Type Locality:* Off China.

Flabellum variabile Semper, 1872, was based on 150-160 syntypes now deposited at the NMW. Ten are numbered 8205 (Plate 31*j-l*). *Type Locality:* Lapinig Canal off Bohol, Philippines, 6-10 fms (11-18 m).

DISTRIBUTION.—*Pleistocene:* Kepulauan Talaud (Umbgrove, 1938). *Recent:* ?South China Sea (Milne Edwards and Haime, 1848); Philippines (off Bohol; Tawi Tawi; Sulu Archipelago) (Faustino, 1927; Semper, 1872); 11-33 m.

38. *Truncatoflabellum crassum* (Milne Edwards and Haime, 1848), new combination

PLATE 32*d-f*

Flabellum crassum Milne Edwards and Haime, 1848:276-277, pl. 8: figs. 8, 8a; 1857:94-95.
Not *Flabellum crassum*.—Bourne, 1905:196-198, pl. 1, figs. 3, 3a.
Flabellum rubrum.—Faustino, 1927:50 [in part: pl. 3: figs. 8, 9].

DESCRIPTION OF HOLOTYPE.—Angle of rounded thecal edges 48°; inclination of lateral faces 18°. Corallum (anthocyathus) 27.8 × 15.1 mm in calicular diameter (GCD : LCD = 1.84) and 22.7 mm tall, with a basal scar of 6.5 × 4.2 mm. One pair of thecal spines originates 1-2.7 mm above basal scar. Anthocaulus unknown. Theca white and smooth. Septa hexamerally arranged in five cycles plus nine pairs of S_6 (114 septa), the S_6 pairs occurring in half-systems adjacent to two principal septa. S_{1-2} notched near calicular edge, slightly exsert, and have straight but highly granulated lower inner edges. S_3 about 0.9 width of S_{1-2}, with slightly less granular inner edges. S_{1-3} attain the columella. S_4 about 1/3 size of S_3 and have laciniate inner edges. S_5 and S_6 progressively smaller. Fossa deep. Columella rudimentary.

DISCUSSION.—Bourne's (1905) two specimens of *Flabellum crassum* reported from off Ceylon are similar to *T. crassum* only in very superficial ways, such as having a septal notch and similar septal symmetry. They are distinguished from the holotype of *F. crassum* by having a much smaller thecal edge angle (23° vs. 48°), a much taller corallum, a smaller basal scar, and three or four pairs of thecal spines. Furthermore, his specimens are not *T. irregulare*, which Bourne considered to be a junior synonym of *F. crassum*. Bourne's specimens probably represent an undescribed species.

Truncatoflabellum crassum is most similar to *T. aculeatum* and may, in fact, be an aberrant specimen of the latter. These species are similar in thecal and edge angles, lateral spines, septal arrangement, and presence of a septal notch. The holotype of *F. crassum*, however, differs in two characters: its basal scar is much smaller and its inner septal edges are straight and not closely adjacent as in *T. aculeatum*. In certain respects (e.g., inner septal edges, thecal spines), *T. crassum* is similar to *T. irregulare*, but can be distinguished by its different septal arrangement and wider thecal edge angle (Table 6).

MATERIAL EXAMINED.—Holotype; there have been no additional records.

TYPE.—The holotype is deposited at the BM (1981.5.12.2), Plate 32*d-f*. *Type Locality:* Philippines, depth unknown.

DISTRIBUTION.—Known only from type locality.

39. *Truncatoflabellum spheniscus* (Dana, 1846), new combination

PLATE 32*g-k*

Euphyllia spheniscus Dana, 1846:160-161, pl. 6: figs. 1a-e.
Flabellum debile Milne Edwards and Haime, 1848:270-271, pl. 8: fig. 2; 1857:88.
Flabellum affine Milne Edwards and Haime, 1848:274, pl. 8: fig. 10; 1857:93.—?Tenison-Woods, 1878b:310-311.
Flabellum spheniscus.—Milne Edwards and Haime, 1848:279-280.
Flabellum stokesii.—Faustino, 1927:54 [in part: pl. 3: fig. 20].
Flabellum rubrum stokesii.—Yabe and Eguchi, 1942a:98-99 [in part: Recent specimen, pl. 8: figs. 5a-c).
Flabellum rubrum debile.—?Yabe and Eguchi, 1941c:269, figs. 5, 6; 1942b:132-133 [in part: Recent specimen, pl. 11: figs. 15a-c].
?*Flabellum stokesi*.—Searle, 1956:25, pl. 40: fig. A.
?*Flabellum rubrum debile*.—Kikuchi, 1968:8, pl. 5: figs. 13a,b.

DIAGNOSIS BASED ON SYNTYPES.—Angle of thecal edges 82°-86°; inclination of thecal faces 20°-25°. Upper thecal faces strongly arched. Largest anthocyathus (USNM 92) 36.5 × 11.5 mm in calicular diameter and 28.1 mm tall, with a basal scar of 10.0 × 3.9 mm. Basal scar ranges from 10.0-11.2 × 3.9-4.8 mm in size. One or two pairs of thecal spines present on anthocyathus. Only known anthocaulus (USNM 93) 9.7 mm tall and 1.7 mm in pedicel diameter, with 56 septa; thecal spines lacking. Theca white and usually encrusted. Ratio of GCD : LCD high: 2.8-3.4. Septa arranged in four size classes, consisting of 40-44 primary, 40-44 secondary, 80-88 tertiary, and 2-7 pairs of quaternary septa, producing a total of up to 190 septa. Primary septa notched near calicular edge, slightly exsert; slightly concave midway down fossa. Inner edges of all septa straight; slightly sinuous in small specimens. Fossa deep. Columella well developed, about 1 mm wide.

DISCUSSION.—Based on the description and figure of Milne Edwards and Haime (1848), *F. affine* appears to be a junior synonym of *T. spheniscus*, a suggestion previously made by Milne Edwards and Haime (1857:93) and Brueggemann (fide Gardiner, 1929:309). Unfortunately, the holotype of *F. affine* is lost and this synonymy cannot be confirmed.

Flabellum debile is also synonymized with *T. spheniscus* based on a comparison of the syntypes (anthocauli) of *F. debile* with an anthocaulus and young anthocyathus of *T. spheniscus* (syntype, USNM 93). Compelling similarities include the same septal arrangement, absence of anthocaulus thecal spines, and corallum shape and size.

Truncatoflabellum spheniscus is distinctive among the *Truncatoflabellum* in having a very narrow, elongate calice (high GCD : LCD), and in having a high thecal edge angle. *Truncatoflabellum paripavoninum* has an even higher thecal edge angle (Table 6) but a considerably larger inclination of the lateral faces. The septal shape of *T. spheniscus* is also distinctive.

Truncatoflabellum spheniscus should also be compared to the Javanese Miocene fossil described as *F. variabile* by Gerth (1921) (see Plate 33*a*) and to the Recent specimens described as *F. stokesi* by Moseley (1881: *Challenger* 188, 190 (in part)) from the Arafura Sea. Both of these species have highly inclined lateral edges, a high GCD : LCD, and the same septal symmetry. *Truncatoflabellum spheniscus* is distinguished by having longer thecal edges, a smaller basal scar, and a white corallum (Table 6).

MATERIAL EXAMINED.—Syntypes of *F. spheniscus* and *F. debile*; *Sôyô-maru* 339 (1) TIUS 50228 (*F. rubrum debile* of Yabe and Eguchi, 1942b), Plate 32*h*; 1 specimen from Albany, Torres Strait (10°44′S, 142°37′E, 7-26 m), AM G11957; 3 specimens from off Roebuck Bay, Broome, Western Australia, AM G13343.

TYPES.—Four syntypes of *F. spheniscus* are deposited at the NMNH (USNM 89 (Plate 32*i-k*), 91, 92, 93). *Type Locality:* Singapore, 3-6 m.

The originally illustrated syntype of *F. debile* is 17.7 × 6.7 mm in calicular diameter, 18.3 mm tall, and 1.8 mm in pedicel diameter, consisting of an anthocaulus and firmly attached anthocyathus (Plate 32*g*). Angle of thecal edges 61°; inclination of lateral faces 19°. At corallum height of 12 mm there is a faint line indicative of a fracture plane, which would have produced a basal scar of 12.3 × 5.5 mm. One pair of downward-curved thecal spines present on anthocyathus, but none present on anthocaulus. Septa arranged in four size groups: 22 : 22 : 44 : 8, or 96 septa. Pairs of quaternaries present only in chambers directly adjacent to principal septa. Inner septal edges slightly sinuous. Columella fairly well developed, 1 mm wide. Three syntypes of *F. debile* are deposited at the BM (1855.12.27.2). *Type Locality:* Philippines, depth unknown.

The holotype of *F. affine* is not present at the BM or MNHNP and is therefore presumed to be lost. *Type Locality:* Sir Charles Hardy Island, Torres Strait, Australia, depth unknown.

DISTRIBUTION.—*?Neogene:* Java (Yabe and Eguchi, 1941e). *Recent:* Off Shikoko, Japan (Yabe and Eguchi, 1942b); off Singapore (Dana, 1846); Philippines (Milne Edwards and Haime, 1848); Sir Charles Hardy and Albany Islands, Torres Strait (Milne Edwards and Haime, 1848); Western Australia; 2–106 m.

40. *Truncatoflabellum stokesi* (Milne Edwards and Haime, 1848), new combination

PLATE 33*b–h,j*

Flabellum stokesii Milne Edwards and Haime, 1848:278, pl. 8: fig. 12.—Faustino, 1927:54 [in part: pl. 3: figs. 17, 21].
Flabellum owenii Milne Edwards and Haime, 1848:279, pl. 8: fig. 9.
Flabellum oweni.—Milne Edwards and Haime, 1857:96.
Flabellum stokesi.—Milne Edwards and Haime, 1857:96.—Moseley, 1881:172–173 [in part: only 2 of 7 specimens from *Challenger* 190; not *Challenger* 188].—Gerth, 1921:402, pl. 57: fig. 14.—Scheer and Pillai, 1974:62–63, pl. 29: figs. 1, 2.
Not *Flabellum rubrum stokesii.*—Yabe and Eguchi, 1942a:98–99, pl. 8: figs. 1–5 [mixed lot: *T. spheniscus* and another species].
Not *Flabellum stokesii.*—Umbgrove, 1950:640–641, pl. 8: figs. 3–4.
Not *Flabellum stokesi.*—Searle, 1956:25, pl. 40: fig. A [= *?T. spheniscus*].
?Flabellum Veron, 1986:603, fig.

DESCRIPTION.—Angle of rounded thecal edges 53°–67°; inclination of thecal faces 24°–29°. Upper thecal faces only slightly arched. Largest anthocyathus examined 31.7 × 13.1 mm in calicular diameter (*Challenger* 190); holotype 20.9 × 9.4 mm in calicular diameter and 11.3 mm tall. Basal scar quite large and V-shaped, 10.7–13.7 × 5.5–7.1 mm in size, that of the holotype being 13.7 × 7.1 mm. Three pairs of thecal spines generally present on anthocyathus, the lowest just above basal scar. The holotype, because of its small size, has only one pair of spines. Spines about 2 mm in basal diameter and up to 7 mm long. Anthocaulus unknown. Theca white and relatively smooth (not encrusted), bearing shallow longitudinal intercostal striae about 0.07 mm wide that delimit flat costae about 0.45 mm wide. Ratio of GCD : LCD = 1.9–2.4.

Holotype has 88 septa arranged in three size groups: 22 primary, 22 secondary, and 44 tertiary; however, largest corallum (*Challenger* 190) has hexameral symmetry according to the formula: $S_{1-3}>S_4>S_5$, with 7 additional pairs of S_6, for a total of 110 septa. S_{1-3} (or primary septa) slightly exsert but not notched near calicular edge. These septa have moderately sinuous inner edges that attain the columella. S_4 (or secondary septa) about half size of S_{1-3}, have straight inner edges and do not reach the columella. S_5 (tertiary septa) and S_6 progressively smaller to rudimentary.

Fossa deep; columella robust and elongate, 1–2 mm wide, and up to 12 mm long.

DISCUSSION.—Although the type of *F. owenii* was not examined, based on the description and figure of Milne Edwards and Haime (1848), it appears to be simply a younger anthocyathus of *T. stokesi*, an observation first made by Gerth (1921).

Gerth's (1921) Miocene specimen of *F. stokesi* from Java (Plate 33*b*) was examined and found to be almost identical to the holotype but poorly preserved.

The specimen reported by Scheer and Pillai (1974) from Great Nicobar, although not examined, fits precisely into the range of all characters of *T. stokesi* given in Table 6.

Truncatoflabellum stokesi is most similar to *T. aculeatum*, particularly regarding the size and shape of the basal scar and corallum. *Truncatoflabellum stokesi* differs markedly in having a broader fossa with a wider columella and unnotched septa near the calicular edge. The fossa of *T. aculeatum* is very narrow, the closely adjacent inner septal edges obscuring the rudimentary columella. *Truncatoflabellum stokesi* also differs in having less septa at a corresponding calicular diameter and a tendency toward hexameral symmetry in larger coralla. Milne Edwards and Haime (1848) distinguished *T. stokesi* from the other truncate species by its high GCD : H ratio, but this is an artificial distinction that changes as the anthocyathus grows upward.

MATERIAL EXAMINED.—Holotype of *F. stokesii*, BM; *Challenger* 190 (2) BM 1880.11.25.78 (in part) Moseley (1881) Plate 33*f–h;* Ngembok Boring, Java, #488 (1) RGM 3795 (Gerth, 1921), Plate 33*b;* supposed type of *Flabellum magnificum*, ZMB 5088, Plate 33*j*. *Reference Specimens: Flabellum rubrum stokesii* of Yabe and Eguchi (1942a) TIUS 43428, 43430, 50228; *F. stokesi* of Moseley (1881) *Challenger* 188, BM 1880.11.25.77, Plate 33*i*.

TYPES.—The holotype of *F. stokesii* is deposited at the BM (1981.5.12.1). *Type Locality:* Philippines, depth unknown.

The holotype of *F. owenii* is not present at the BM or MNHNP and is therefore presumed to be lost. *Type Locality:* Philippines, depth unknown.

DISTRIBUTION.—*Miocene:* Java (Gerth, 1921). *Recent:* Philippines (Milne Edwards and Haime, 1848); Arafura Sea (Moseley, 1881); Great Nicobar, Indian Ocean (Scheer and Pillai, 1974); 12–256 m.

41. *Truncatoflabellum bairdi* (Milne Edwards and Haime, 1848), new combination

PLATES 33*k*, 34*a–c*

Flabellum bairdi Milne Edwards and Haime, 1848:274–275; 1857:93.
?Flabellum sumatrense Milne Edwards and Haime, 1848:271; 1857:89.

DESCRIPTION OF HOLOTYPE.—Angle of rounded thecal edges 57°; inclination of lateral faces 20°. Corallum 25.9 × 8.9 mm in calicular diameter (GCD : LCD = 2.91) and 19.2 mm tall, with a basal scar 10.7 × 4.8 mm. One pair of thecal spines originates adjacent to basal scar on anthocyathus. Anthocaulus unknown (see "Discussion"). Theca black-brown and rough, with longitudinal costae as in *T. profundum*. Septa hexamerally arranged in five cycles plus 11 pairs of S_6 (118 septa). S_{1-3} slightly exsert, not notched near the calice, and have slightly sinuous lower, inner edges that fuse with the columella. S_4

about 3/4 size of S_{1-3} and usually do not attain the columella. S_5 1/4 size of S_4; S_6 rudimentary. All septa have large pointed granules aligned perpendicular to septal edge. Fossa deep and wide. Columella well developed, about 1.4 mm wide.

DISCUSSION.—Although not known from the Philippine Islands, *T. bairdi* is included in this revision for the sake of comparison to other Philippine and western Pacific congeners. *Truncatoflabellum bairdi* is most similar to *T. stokesi*, particularly in corallum shape, septal arrangement, and septal shape. The holotype, and only known specimen, of *T. bairdi* differs in having a larger basal scar, a more elongate calice (higher GCD : LCD), and a blackish color to the corallum. Any one of these characteristics could be interpreted as simply variation of *T. stokesi*, but taken together they imply a species distinction.

Superficially, *T. bairdi* resembles *T. profundum* in costal texture, thecal color, and columella and fossa shapes, but can be distinguished by septal symmetry and by having a smaller basal scar (Table 6).

Truncatoflabellum sumatrense may be the anthocaulus stage of *T. bairdi*, but more specimens of both stages are needed to confirm this correlation. The holotype of *F. sumatrense* (Plate 33*k*) has a calicular diameter of 10.5 × 5.2 mm (which is very similar to the basal scar diameter of *T. bairdi*), and light brown theca, another similarity to *T. bairdi*.

MATERIAL EXAMINED.—Holotypes of *F. bairdi* (Plate 34*a–c*) and *F. sumatrense* (Plate 33*k*).

TYPES.—The holotype of *F. bairdi* is deposited at the MNHNP (1019). *Type Locality:* Unknown.

The holotype of *F. sumatrense* is an anthocaulus with part of the anthocyathus still attached. The anthocaulus is 9.9 mm tall and has a pedicel diameter of 1.6 mm. Two flattened thecal spines originate from the basal part of the anthocyathus; the anthocaulus bears no spines. The theca is finely granular. Septa are hexamerally arranged in four cycles with 6 pairs of S_5 (60 septa). S_{1-3} have moderately sinuous inner edges. Columella well developed. Holotype deposited at the MNHNP (374). *Type Locality:* Off Sumatra.

DISTRIBUTION.—?Off Sumatra; depth unknown.

42. *Truncatoflabellum profundum* (Milne Edwards and Haime, 1848), new combination

PLATE 34*d–h*

Flabellum profundum Milne Edwards and Haime, 1848:276; 1857:93-94, pl. D1: figs. 5, 5a.

Flabellum crenulatum Milne Edwards and Haime, 1848:277; 1857:95.—?Yabe and Eguchi, 1942b:134.

DESCRIPTION.—Angle of sharp thecal edges 60°–71°; inclination of lateral faces 24°–29°. Upper thecal edges arched and peaked in small chevron-shaped apices, one corresponding to each primary and secondary septum. Largest anthocyathus (holotype of *F. profundum*) 50.0 × 21.0 mm in calicular diameter and 35.1 mm tall, with a basal scar of 13.5 × 7.3 mm. One pair of thecal spines present adjacent to basal scar. Anthocaulus unknown. Corallum light brown. Theca rough, with coarse longitudinal costae. Ratio of GCD : LCD = 2.4–2.7.

Septa decamerally arranged in four size classes: usually 20 primary, 20 secondary, 40 tertiary, and 80 quaternary septa, for 160 total septa; however, holotype of *F. profundum* lacks 2 pairs of quaternaries and has 5 pairs of quinaries, for a total of 166 septa. Primaries large and thick, their lower inner edges merging with a well-developed columella. Secondaries almost as large as primaries, especially in larger coralla, and also merge with columella. Tertiaries 1/3 to 1/2 width of secondaries, much thinner, but also merge with columella. Quaternaries 1/3 width of tertiaries; quinaries rudimentary. Inner edges of all septa straight to slightly sinuous. Damaged condition of all specimens examined did not allow observation of upper septal edges. Septal faces covered by large rounded granules about 0.25 mm in diameter arranged in discrete lines perpendicular to septal edge.

DISCUSSION.—Although this species is not known from the Philippine Islands, it has been collected "off China" and is included here for comparison with other Pacific species of *Truncatoflabellum*. *Truncatoflabellum profundum* is a fairly distinctive species within the genus (Table 6), distinguished by its septal symmetry, number of septa, scalloped calice margin, rough costae, and very large size. Comparisons to *T. bairdi* are made in the account of that species.

Flabellum profundum was chosen as the senior synonym instead of *F. crenulatum* for two reasons: *F. profundum* has page priority and is the only one of the two with a known type locality.

MATERIAL EXAMINED.—Holotypes of *F. profundum* and *F. crenulatum*; 5 additional specimens of *F. crenulatum* from an unknown locality (?syntypes), MNHNP 371.

TYPES.—The holotypes of *F. profundum* (Plate 34*d–f*) and *F. crenulatum* (Plate 34*g,h*) are deposited at the MNHNP (1026 and 1020, respectively). *Type Locality of* F. profundum: "Off China," depth unknown. *Type Locality of* F. crenulatum: Unknown.

DISTRIBUTION.—Off China; ?off Seto, Japan (Yabe and Eguchi, 1942b); depth unknown.

43. *Truncatoflabellum irregulare* (Semper, 1872), new combination

PLATES 34*i–k*, 35*a–c*

Flabellum irregulare Semper, 1872:242-245, figs. 1-3, pl. 16: figs. 7-17.—?Alcock, 1902a:32.

Not *Flabellum irregulare*.—Gerth, 1921:402, pl. 57: fig. 15.

Flabellum rubrum.—Faustino, 1927:50 [in part: pl. 3: figs. 1-5, not *Albatross* specimens].

DESCRIPTION.—Angle of rounded thecal edges 36°–43°; inclination of convex thecal faces only 19°–21°. Largest anthocyathus (ALB-5145) 42.8 mm tall with a calicular diameter of 27.5 × 16.8 mm, although most specimens examined were less than 30 mm tall with a greater calicular diameter less than 18 mm. A pair of downward-projecting thecal spines up to 2.5 mm long occur on lower thecal edges of anthocyathus; in one specimen a second pair of thecal spines occurs midway on thecal edge. Basal scar solid, about 4 × 3 mm in diameter; number of complete septa originating from basal scar not possible to determine because of worn or encrusted nature of scar. Anthocaulus stage unknown. Theca usually covered with encrusting organisms, i.e., bryozoa, bivalves, serpulids, and calcareous algae, but if theca is free of encrustation, it is white and somewhat porcelaneous. A low, rounded costa corresponds to each septum. All costae equal in width; no chevron-shaped markings on theca. Calice elliptical, GCD : LCD ranging from 1.6 to 2.0.

Septa arranged in a variety of symmetries (see Semper (1872) for more details); however, most common pattern consists of 18 primary, 18 secondary, and 36 tertiary septa, making a total of 72 septa. Other common variations include 16, 17, 19, and 12 primary septa (in order of frequency found in syntypes), with a corresponding number of higher-cycle septa. In addition to this variation in primary septal number, in elongate calices the two tertiary septa adjacent to each principal septa are enlarged and flanked by a pair of small quaternary septa, making a total of 80 septa (e.g., Semper, 1872, fig. 3 and pl. 16: fig. 13). Furthermore, some "quartets" of septa are lacking pairs of tertiary septa, thereby decreasing the total number of septa by 2, 4, 6, or 8 from the expected number. Primary septa wide, with a slightly exsert upper edge that is notched about 0.5 mm wide near calicular edge. Upper septal edge and notch area finely dentate. Secondary septa only slightly less wide than primaries, not exsert, and have only a slight septal notch near calice. Tertiary septa quite narrow, only $^{1}/_{6}$ to $^{1}/_{5}$ width of a primary, and rudimentary lower in fossa. Inner edges of all septa straight, those of primary septa quite thickened lower in fossa, contributing to the rudimentary columella. Septa covered by low pointed granules about 0.1 mm tall, particularly well developed on lower, inner edges of primary septa.

Fossa relatively narrow, crowded by the inner edges of the wide primary and secondary septa. Columella a porous fusion of lower inner edges of primary septa.

DISCUSSION.—Although not examined, Alcock's (1902a) *F. irregulare* from *Siboga* 253 is queried based on its much greater depth of capture of 304 m.

Gerth's (1921) *F. irregulare*, from the Miocene of Java, differs from typical *T. irregulare* by having regular hexameral symmetry, a larger basal scar, and a much more compressed corallum (Plate 37*f*). It is presented as a distinctive western Pacific species in Table 6.

Truncatoflabellum irregulare is similar to *T. cumingi* in corallum shape and size and septal arrangement (Table 6) but can be distinguished by its straight inner septal edges, discretely notched upper septal edges, and smaller basal scar. Comparisons to *T. incrustatum* are made in the account of that species.

The number of primary septa, and thus the total number of septa in a corallum, appears to be genetically fixed for a specimen, not a matter of increase in number with age, similar to the conclusion reached by Mori and Minoura (1983) for *Cylindrophyllia orientalis*. For instance, specimens with a greater calicular diameter of 13 mm may have 18 primary septa, whereas a larger specimen may have fewer primary septa.

Semper's (1872) text and figures pertaining to *T. irregulare* are misleading regarding the GCD : LCD ratio, which he stated was 2. This number is consistent with his figured specimens, but the calices of most of the other nonillustrated syntypes are not so compressed, having GCD : LCD ratios as low as 1.6. Furthermore, Semper only figured specimens with 18 primary septa (except for fig. 1). Although this is the most common symmetry among the syntypes, less than half of the specimens possess this number of primaries.

MATERIAL EXAMINED.—ALB-5145 (1) USNM 81975; syntypes of *F. irregulare* (19) NMW. *Reference Specimens: F. irregulare* (1) of Gerth (1921) RGM 3784.

TYPES.—Sixty-one syntypes of *F. irregulare* are deposited at the NMW (15507 (Plate 34*i,j*), 8199 (Plates 34*k*, 35*c*)). *Type Locality:* Lapinig Canal, Bohol, Philippines; 11–18 m.

DISTRIBUTION.—*Recent:* Philippines (off Bohol, Sulu Archipelago) (Semper, 1872); ?Kei Island, Banda Sea (Alcock, 1902a); 11–42 m.

44. *Truncatoflabellum incrustatum*, new species

PLATE 35*d,e*

Flabellum rubrum.—Faustino, 1927:53 [in part: ALB-5249, 5250, 5251, 5253].

DESCRIPTION.—Angle of rounded thecal edges 23°–32°; inclination of thecal faces 15°–19°. Thecal faces slightly convex in medium-sized specimens, becoming flat to slightly concave (i.e., constricted in center) in larger specimens with elongate calices. Largest anthocyathus known (ALB-5253) 28.0 × 13.5 mm in calicular diameter and 42 mm tall. A pair of downward-projecting thecal spines occurs on lower edges of anthocyathus. Basal scar solid, 5.0–6.0 × 3.5–4.0 mm in diameter; 12 complete septa originate from basal scar. Both spines and scar usually heavily encrusted or eroded, the spines rarely intact. Theca also heavily encrusted with sessile organisms, i.e., bryozoa, bivalves, foraminifera, serpulids, and calcareous algae. Beneath encrustation, theca is dark black-brown, especially apparent at upper thecal edges where encrustation has not yet occurred. Anthocaulus stage unknown. Calice elliptical, GCD : LCD ranging from 1.65–2.10 (with an average of 1.85), the higher values pertaining to larger specimens.

Septa hexamerally arranged in five cycles according to the formula: $S_{1-2}>S_3>S_4>S_5$, the fifth cycle complete at a greater calicular diameter of about 23 mm. S_{1-2} have slightly exsert, smooth upper edges that meet the calicular edge directly or with only a very slight septal notch. S_3 about $^3/_4$ width of S_{1-2}, slightly less exsert, and lack the septal notch. S_{4-5} nonexsert and progressively smaller, the S_5 becoming rudimentary lower in fossa. Inner edges of all septa straight to slightly sinuous, those of the S_{1-2} quite thickened and contributing to the columella. Septa covered by low blunt granules about 0.13 mm tall.

Fossa elongate and deep. Columella a spongy mass of trabeculae fused to the lower, inner edges of the S_{1-2}.

DISCUSSION.—Among the western Pacific species of *Truncatoflabellum, T. incrustatum* is most similar to *T. irregulare*, particularly in corallum size and shape, thecal encrustation, and GCD : LCD. Nonetheless, *T. incrustatum* can be distinguished by its hexameral symmetry and four different size classes of septa, i.e., $S_{1-2}>S_3>S_4>S_5$. *Truncatoflabellum irregulare* is not hexameral in septal arrangement and has only three size classes of septa. Furthermore, the relative size difference between the penultimate group of septa (S_4 of *T. incrustatum*, secondaries of *T. irregulare*) and the largest group of septa (S_{1-2} of *T. incrustatum*, primaries of *T. irregulare*) is very different, being much greater in *T. incrustatum*. Other characters distinguishing *T. incrustatum* from *T. irregulare* are its lack of a septal notch, smooth upper edges of S_{1-2}, brown-black thecal color, and slightly larger basal scar.

ETYMOLOGY.—The species name is from the Latin *incrustatum* (encrusted), and alludes to the condition common to all of the coralla of being heavily encrusted with epizoa.

MATERIAL EXAMINED.—Types.

TYPES.—*Holotype:* ALB-5251, USNM 40774, Plate 35*d,e*. *Paratypes:* ALB-5249 (1) USNM 40772; ALB-5250 (2) USNM 40773; ALB-5251 (1) USNM 81974; ALB-5253 (2) USNM 40776, (1) AM G15251; ALB-5265 (1) USNM 81973; ALB-5289 (1) USNM 40779. *Type Locality:* 7°05'12" 125°39'35"E (Davao Gulf, Mindanao, Philippines), 37 m.

DISTRIBUTION.—*Recent:* Endemic to Philippines: Verde Island Passage; Davao Gulf; 37–315 m.

45. *Truncatoflabellum cumingi* (Milne Edwards and Haime, 1848), new combination

PLATE 35*f–i*

Flabellum cumingii Milne Edwards and Haime, 1848:275, pl. 8: fig. 11.
Flabellum cumingi.—Milne Edwards and Haime, 1857:94.
Flabellum rubrum.—Faustino, 1927:50 [in part: pl. 3: fig. 6].

DESCRIPTION.—Angle of rounded thecal edges 31°–44°; inclination of thecal faces 18°–23°. Upper thecal faces only slightly arched. Largest anthocyathus examined (neotype) 19.8 × 10.5 mm in calicular diameter and 20.2 mm tall, with a basal scar of 8.4 × 4.7 mm. Two pairs of thecal spines present on anthocyathus, the lower pair adjacent to basal scar, the upper pair 5–8 mm above scar. Spines up to 10 mm long. Basal scar 7.6–9.0 × 4.2–4.9 mm. Anthocaulus unknown. Theca white and not encrusted. Ratio of GCD : LCD = 1.85–2.00.

Septa arranged in three size groups; total number of septa roughly a function of greater calicular diameter. Common ratios of primary, secondary, and tertiary septa are: 14 : 14 : 28, 16 : 16 : 32, and 18 : 18 : 36, the neotype have the last formula (72 septa). Primary septa slightly exsert, not notched, and have slightly sinuous inner margins that extend to the columella. Secondary septa about $^3/_4$ width of primaries and usually attain the columella. Tertiary septa about $^1/_4$ width of secondaries.

Fossa deep; columella robust, about 1.5 mm wide.

DISCUSSION.—Among the Pacific *Truncatoflabellum, T. cumingi* is most similar to *T. vanuatu* Wells, 1984 (see Plate 36*c*), particularly regarding septal symmetry and calice shape. *Truncatoflabellum cumingi* is distinguished by its larger basal scar, greater thecal edge angle, lesser number of thecal spines, and sinuous septal edges (Table 6).

Truncatoflabellum cumingi is also similar to *T. formosum* in corallum size and shape and presence of two pairs of thecal spines but can be distinguished by its larger basal scar, higher GCD : LCD, exsert primary septa (not attenuate), and lesser number of septa at a corresponding greater calicular diameter. Additional comparisons to *T. irregulare* are made in the account of that species.

MATERIAL EXAMINED.—Neotype; *Te Vega* 1-54 (13) USNM 81977.

TYPES.—The holotype of *F. cumingii* could not be found at the MNHNP or BM in 1987 and is presumed to be lost. Because of the high number of morphologically similar species of *Truncatoflabellum* in the western Pacific and the taxonomic confusion that has plagued this group of species, it was thought prudent to designate a neotype for this species. Accordingly, a neotype was chosen from *Te Vega* 1-54, USNM 81976 (Plate 35*f–h*). Although not from the original type locality of the Philippines, it is from the adjacent Molucca Passage off Halmahera, and the chosen neotype is virtually identical to Milne Edwards and Haime's (1848) illustrated holotype in corallum size and shape. *Type Locality:* 1°08.6'N, 128°01'E (Teluk Kau, Halmahera), 46–55 m.

DISTRIBUTION.—Philippines (Milne Edwards and Haime, 1848); Molucca Passage; 46–55 m.

46. *Truncatoflabellum formosum*, new species

PLATES 35*j,k*, 36*a,b*

Flabellum rubrum.—Faustino, 1927:53 [in part: ALB-5265, 5658].—Yabe and Eguchi, 1942a:96–98 [in part: pl. 8: fig. 14].

DESCRIPTION.—Angle of rounded thecal edges 37°–43°, although in the large specimen from ALB-4314, the thecal edges are crested above the second pair of thecal spines. Inclination of convex thecal faces 18°–21°. Near base of corallum, thecal faces slightly more compressed, having more acute thecal edges. Largest anthocyathus examined (ALB-5289) 23.0 × 13.4 mm in calicular diameter and 31.4 mm tall; holotype (ALB-5249) 19.8 × 11.8 mm in calicular diameter and 21.4 mm tall. One or two pair(s) of spines occur(s) on thecal edges of anthocyathus. Lower pair of spines cylindrical, about 1.3 mm in basal diameter, and 2-3 mm above basal scar. Upper pair, if present, has a wider triangular base about 2.7 mm in greater diameter, which occurs 5-7 mm above basal scar (almost midway on thecal edge of a large specimen). Basal scar 4.5-5.5 × 2.8-3.1 mm in diameter; 12 complete septa originate from scar, despite nonhexameral symmetry of septa. Anthocaulus stage unknown. Theca usually slightly encrusted with serpulids, bivalves, and calcareous algae, but nonetheless usually smooth; theca marked by fine, white, longitudinal costal striae and equally fine transverse epithecal corrugations. Theca light reddish brown. Calice elliptical, GCD : LCD = 1.42-1.85.

Septa of most specimens examined arranged in three size classes: 20 primary, 20 secondary, and 38-40 tertiary septa, resulting in a total of 78-80 septa. Below a greater calicular diameter of 20 mm, pairs of tertiary septa are often missing. Primary septa slightly exsert in small specimens but attenuate in larger specimens, meeting the thecal edge in a graceful concave arch (Plate 35*k*). Secondary septa always nonexsert and about half the width of primary septa. Tertiary septa quite small, only $^{1}/_{5}$ to $^{1}/_{4}$ width of secondary septa. Lower, inner edges of primary septa conspicuously sinuous. Septa covered by blunt granules about 0.1 mm tall, regularly aligned in oblique rows along septal undulations.

Fossa deep. Columella rudimentary, composed of the fusion of the lower inner edges of primary septa.

REMARKS.—Although most specimens have 20 primary septa the holotype has only 19, undoubtedly the result of a small injury and subsequent repair to one side of the upper corallum. The undamaged side of the calice contains the typical number of 10 primary septa. This slightly damaged specimen was chosen as the holotype because of its otherwise excellent preservation of septal structures.

The one specimen still preserved in alcohol (ALB-5658) has a polychaete completely encircling the theca just below the calicular edge.

DISCUSSION.—Only two species of Pacific *Truncatoflabellum* have attenuate larger septa: *T. formosum* and the delicate, deep-water *T. paripavoninum*, which are easily distinguished in Table 6. *Truncatoflabellum formosum* is also superficially similar to *T. cumingi* and is compared to it in the account of that species.

Truncatoflabellum formosum was previously illustrated as *F. rubrum* (in part) by Yabe and Eguchi (1942a). As discussed in the species account of *T. carinatum*, Yabe and Eguchi (1942a) confused at least four species as *F. rubrum*, only one of which was *T. formosum*.

ETYMOLOGY.—The species name is from the Latin *formosum* (beautifully formed), and alludes to the graceful arch of the upper edges of the primary septa.

MATERIAL EXAMINED.—Types; ALB-5137 (1) USNM 81956; ALB-5162 (1) USNM 81955; ALB-5483 (1) USNM 81957; ALB-5484 (1) USNM 81958; *Sôyô-maru* 465 (1 of 4 specimens) TIUS 50229 (*F. rubrum* of Yabe and Eguchi, 1942a), Plate 36*b*. The four *Albatross* specimens are expressly excluded from the type-series because of poor preservation.

TYPES.—*Holotype:* ALB-5249, USNM 81953, Plates 35*j,k*, 36*a*. *Paratypes:* ALB-5265 (3) USNM 40778; ALB-5289 (1) USNM 81954; ALB-5658 (1) USNM 40786.

DISTRIBUTION.—*Recent:* Korea Strait (Yabe and Eguchi, 1942a); Philippines (off Manila, Luzon; Leyte Gulf; Davao Gulf; Sulu Archipelago); Teluk Bone, Celebes; 37-933 m; 5.1°-17.8°C.

47. *Truncatoflabellum candeanum* (Milne Edwards and Haime, 1848), new combination

PLATE 36*d-h*

Flabellum candeanum Milne Edwards and Haime, 1848:278, pl. 8: fig. 13; 1857:95-96.—Marenzeller, 1889:46-48.

Flabellum elegans Milne Edwards and Haime, 1848:277.

Not *Flabellum candeanum*.—Duncan, 1870:300, pl. 20: figs. 1a-d [= undescribed species].—Tenison-Woods, 1878b:311.

Flabellum rubrum.—Yabe and Eguchi, 1942a:96-98 [in part: pl. 8: figs. 13-15, 21, 22].

Flabellum rubrum candeanum.—Yabe and Eguchi, 1942b:133-134.

DESCRIPTION.—Angle of rounded thecal edges 50°-80°; inclination of convex thecal faces 30°-41°. Largest anthocyathus examined (holotype of *F. elegans*) 32.3 × 16.5 mm in calicular diameter and 21.7 mm tall. Usually three pairs of thecal spines occur on anthocyathus, less commonly two pairs, but in one case four pairs. First pair of spines originates directly above basal scar, each spine up to 6 mm long, with a greater basal diameter of about 1.1 mm. Second pair massive, about 2.5 mm above basal scar, each spine up to 6 mm long with a greater basal diameter up to 2.3 mm. Third pair of spines smaller in diameter but longer, about 7 mm above basal scar, each spine up to 10 mm long, with a greater basal diameter of about 2.0 mm. Basal pair of spines directed downward, middle pair directed horizontally, and upper pair directed slightly upward. Basal scar 4.2-5.7 × 3.0-3.6 mm in diameter; approximately 20 complete septa originate from scar. Anthocaulus 4-5 mm tall at point of fracture, with a pedicel diameter of about 1.2 mm and a calicular diameter equal to that of anthocyathus basal scar. One pair of downward-projecting spines occur midway on thecal edge of anthocaulus. Before division, the fused anthocyathus and anthocaulus may be up to 7 mm tall, bearing a single pair of anthocaulus thecal spines and the basalmost pair of anthocyathus thecal spines. Anthocaulus contains 24 septa. Theca light reddish brown with slightly darker stripes corresponding to primary septa; specimens collected dead are occasionally bleached white. Theca usually not encrusted. Theca corresponding to primary septa often slightly raised, producing a slightly corrugated thecal face. Calice elliptical, GCD : LCD = 1.6-1.7. Upper thecal edge slightly scalloped, the apices of the margin corresponding to the primary septa.

Septa occur in three size classes, most commonly: 20 primary, 20 secondary, and 40 tertiary septa, resulting in 80 total septa. Number of primary septa, and thus total number of septa, roughly a function of greater calicular diameter, e.g., a corallum with a greater calicular diameter of 12 mm may have 16 primaries; 15 mm, 18 primaries; 16-18 mm, 20 primaries; 19 mm, 22 primaries; and 20-21 mm, 24 primaries. Primary septa moderately exsert, meeting the calicular edge at a right angle with no septal notch. Secondary septa slightly exsert, 1/3 to 1/2 size of primary septa. Tertiary septa not exsert and quite small, about 1/5 to 1/4 size of secondary septa. Inner edges of primary septa extremely sinuous and those of secondary septa also moderately sinuous. Tall pointed granules up to 0.15 mm high are aligned in rows perpendicular to septal edge. Lower, inner edges of primary septa bear large granules up to 0.25 mm tall.

Fossa relatively shallow. Columella robust, composed of a spongy trabecular mass bordered by lower, inner edges of primary septa.

DISCUSSION.—*Trucatoflabellum candeanum* is identified based on the original description and figure because the type specimen is not present at the BM or MNHNP and therefore presumed to be lost. It is one of the most distinctive species of *Truncatoflabellum*, distinguished by its three pairs of thecal spines, the uppermost being quite long; broad inclination of lateral faces, second only to that of *F. paripavoninum;* striped reddish brown theca; and slightly scalloped calicular margin (Table 6).

The specimen noted and illustrated by Duncan (1870) from the Australian Tertiaries as *F. candeanum* is clearly not the same species. It has a significantly larger corallum, a lesser thecal angle, a lower GCD : LCD, and beautifully attenuate septa with straight inner edges. A specimen in the NMNH collections (USNM MO 353592) from the Miocene of Victoria, Australia is virtually identical to Duncan's figure but has five pairs of thecal spines (Plate 36*i,j*) instead of three as figured by Duncan (1870). This Australian Tertiary form is believed to represent an undescribed species.

Truncatoflabellum candeanum was illustrated by Yabe and Eguchi (1942a) as *F. rubrum* (in part) and later (Yabe and Eguchi, 1942b) as the subspecies *Flabellum rubrum candeanum*. Although not all specimens were examined, Yabe and Eguchi's (1942a) specimens of *F. rubrum* represent at least four species, including *T. candeanum* (see discussion of *T. carinatum*).

MATERIAL EXAMINED.—ALB-5213 (21) USNM 81964; ALB-5311 (3) USNM 81965; ALB-5314 (4) USNM 81966; ALB-5369 (48) USNM 81967; ALB-5371 (10) USNM 81968; ALB-5376 (2) USNM 81969; ALB-5391 (1) USNM 81970; ALB-5393 (7) USNM 81971, (1) AM G15248; ALB-5593 (2) USNM 81972; ZMB 8194 (1) *F. candeanum* of Marenzeller (1889), Plate 36*h; Sôyô-maru* 422 (2) TIUS 50233 (*F. rubrum candeanum* of Yabe and Eguchi, 1942a); *Sôyô-maru* 465 (3 of 4 specimens) TIUS 50229 (*F. rubrum candeanum* of Yabe and Eguchi, 1942a); holotype of *F. elegans*. *Reference specimens:* USGS 10809 (1) USNM MO 353592, *F. candeanum* of Duncan, 1870.

TYPES.—The holotype of *F. candeanum* is presumed to be lost (see "Discussion"). Because the taxonomy of the numerous species of western Pacific *Truncatoflabellum* is confused, it was considered appropriate to designate a neotype (Plate 36*d,e*) for this species in order to stabilize the nomenclature. Accordingly, an anthocyathus from ALB-5369 (USNM 81963) was chosen as the neotype. It is 17.6 × 10.2 mm in calicular diameter and 12.7 mm tall, with a basal scar of 4.6 × 3.0 mm. It contains five full cycles of septa (96 septa), although several pairs of S_5 are rudimentary. *Type Locality:* 13°48'N, 121°43'E (Tayabas Bay, Luzon, Philippines), 194 m.

The holotype of *F. elegans* is deposited at the BM (1846.7.1.58), Plate 36*f,g*. *Type Locality:* "?Japan," according to the museum label.

DISTRIBUTION.—*Recent:* Off western Kyūshū, Japan (Yabe and Eguchi, 1942b; Marenzeller, 1889); South China Sea off Hong Kong (Milne Edwards and Haime, 1848); Philippines (Samar Sea; Tabayas Bay, Luzon); off Sabah, Celebes Sea; 70-249 m; 15.2°-17.8°C.

48. *Trucatoflabellum pusillum*, new species

PLATE 37*a-e*

DESCRIPTION.—Angle of rounded thecal edges 14°-18°; inclination of thecal faces about 18°. Largest anthocyathus (holotype) 6.9 × 4.2 mm in calicular diameter and 11.3 mm tall; corallum strongly compressed, especially lower half. Up to three pairs of thecal edge spines present on anthocyathus, the first pair curving downward and originating near basal scar; remaining pairs spaced at about 2.5 mm intervals along edge. Spines slender, about 0.5 mm in diameter, and up to 1.5 mm long. Basal scar elongate, 2.4-3.2 × 1.7-1.8 mm in diameter. Single known anthocaulus (ALB-5178) 3.5 × 2.0 mm in calicular diameter and 6.3 mm tall, with a nonreinforced, attached pedicel 0.9 mm in diameter. A pair of large, downward-curving edge spines present on anthocaulus, originating just below fracture plane. Anthocaulus contains 24 spiny septa arranged according to the formula: $S_{1-2}>S_3$. Theca smooth and porcelaneous, bearing longitudinal reddish brown stripes, a pair of stripes flanking each S_{1-2}. Ratio of GCD : LCD = 1.4-1.65.

Septa hexamerally arranged in three cycles plus four pairs of S_4, one pair in each half-system adjacent to the two principal septa, resulting in 32 septa. Inner edges of S_{1-2} vertical and highly sinuous, fusing lower in fossa to form a rudimentary columella. S_3 about 1/3 size of S_{1-2} and not sinuous. S_4 about 1/3 size of S_3. It is probable that additional S_4 are present in larger specimens, which would make a total of 48 septa for a large specimen. All septa bear pointed granules up to 0.12 mm tall. Details of relative septal exsertness and septal notches unknown because of damage to septa of upper calice of all specimens.

DISCUSSION.—*Truncatoflabellum pusillum* is very distinctive among Recent Pacific species of this genus in having the smallest adult corallum size and correspondingly smallest basal scar size, smallest corallum edge angle, and fewest number of septa (Table 6). It is most similar to *T. victoriae* (Duncan, 1864), described from the Miocene of South Australia, particularly in corallum shape and size, septal number and symmetry, and basal scar diameter (Plate 37*i*). *Truncatoflabellum pusillum* differs in having more than one pair of thecal edge spines and in having a more compressed corallum and correspondingly higher GCD : LCD (that of *T. victoriae* is about 1.2).

ETYMOLOGY.—The species name is from the Latin *pusillum* (very small), and refers to the small adult corallum size of this species.

MATERIAL EXAMINED.—Types. *Reference Specimens: T. victoriae* (9) USNM 353582.

TYPES.—*Holotype:* ALB-5178, USNM 81978, Plate 37*a,b*. *Paratypes:* ALB-5178 (2) USNM 81979; ALB-5162 (1) USNM 81980; ALB-5277 (1) USNM 81981. *Type Locality:* 12°43′N, 122°06′15″E (Sibuyan Sea, north of Romblon, Philippines), 143 m.

DISTRIBUTION.—*Recent:* Philippines (off Manila Bay, Luzon; north of Romblon, Sibuyan Sea; Tawi Tawi; Sulu Archipelago); 143-146 m; 14.7°C (one record).

49. *Truncatoflabellum paripavoninum* (Alcock, 1894), new combination

PLATES 37*j–l*, 38*a*

Flabellum pari-pavoninum Alcock, 1894:187.

Flabellum paripavoninum.—Alcock, 1898:21, pl. 2: figs. 3a,b.—Faustino, 1927:46–47, pl. 2: figs. 3, 4 [in part: ALB-5548, 5648, 5658, 5656, 5586, and USNM 40721].

Flabellum sp. Alcock, 1902a:31 [in part: *Siboga* 316].

Not *Flabellum pavoninum*.—Gardiner, 1902a:123–125.

Not *Flabellum pavoninum* var. *paripavoninum*.—Vaughan, 1907:59–62 [= *F. vaughani*].—Umbgrove, 1938:264 [= *Flabellum* sp.].—Yabe and Eguchi, 1942a:91–93, pl. 5: figs. 7, 8 [= *F. lamellulosum* and *F. politum*]; 1942b:129–130, pl. 11: fig. 9 [= *F. politum*].—Utinomi, 1965:255 [= *F. vaughani*].

Not *Flabellum paripavoninum*.—Vaughan, 1919, pl. 12: figs. 12, 12a [= *F. vaughani*].—Squires, 1964a:15 [= *F. vaughani*].—Wells, 1984:214–215, pl. 4: figs. 6, 7.

DESCRIPTION.—Angle of thecal edges variable, ranging from 65° to 135°; inclination of thecal faces 32°-62°. Largest anthocyathus examined (ALB-5283) 49.1 × 36.1 mm in calicular diameter and 41.0 mm tall. Upper calicular edge highly convex. Thecal edge spines absent; instead, the relatively short thecal edges meet at an acute angle, often producing a low edge carina. Basal scar variable in size, ranging from 6.8 × 4.1 to 14.5 × 6.8 mm. Anthocaulus 12.0 mm tall at point of fracture, with a pedicel diameter of about 1.7 mm, and a greater calicular diameter equal to that of the anthocyathus basal scar (in the single case known (ALB-5658), 11.5 mm). Illustrated fused anthocaulus plus anthocyathus (Plate 38*a*) 17.1 mm, the incipient line of fracture about 5 mm below calicular margin. Upper thecal edges of anthocaulus slightly carinate. Anthocyathus delicate, the theca a very light reddish brown. Lateral faces of living specimens often encrusted with barnacles, bivalves, and mollusk egg cases. Ratio of GCD : LCD = 1.4-2.0.

Septa hexamerally arranged in six cycles according to the formula: $S_{1-3}>S_4>S_5>S_6$ (192 septa). Sixth-cycle insertion begins at a greater calicular diameter of about 26 mm; pairs of S_7 occasionally present in half-systems adjacent to principal septa of large specimens. S_{1-3} have straight to slightly sinuous, vertical, thickened inner edges, which fuse and intermingle deep in the fossa to form a well-developed columella. S_4 about $^{3}/_{4}$ size of S_{1-3}, the inner edges of which only occasionally fuse with the columella. S_5 about $^{1}/_{2}$ size of S_4 and extend about $^{3}/_{4}$ distance down inner thecal edge. S_6 $^{1}/_{3}$ width of S_5 and extend only about $^{1}/_{3}$ to $^{1}/_{2}$ distance down inner theca. S_7, when present, rudimentary and only several mm long. Upper, outer septal edges attenuate, joining theca in a smooth concave curve. Granules small and sparse, aligned in curved rows following the contour of the inner septal edge.

DISCUSSION.—Although Alcock's (1898) subsequent description and figure of the holotype of *F. paripavoninum* indicate a basal scar, Gardiner (1902a) suggested that the scar was accidental and therefore synonymized this species with *F. pavoninum*. Gardiner (1929:304) later acknowledged that the type had a natural basal scar (as do all *Truncatoflabellum*) but still maintained *F. paripavoninum* as a form of *F. pavoninum*, a form he considered to be indistinguishable from the nominate subspecies by skeletal characters but distinguishable possibly by polyp characters. This philosophy influenced other coral systematists, including Vaughan (1907), Faustino (1927), Umbgrove (1938), and Squires (1964a), to identify nontruncate species as *F. paripavoninum*. Cairns (1984a) finally made the distinction between the truncate *F. paripavoninum* and the nontruncate *F. pavoninum*, the latter of which was renamed *F. vaughani* Cairns, 1984, in the case of Vaughan's (1907) Hawaiian records.

Only six of the 14 lots reported by Faustino (1927) are *T. paripavoninum*, the other lots being nontruncate species: *F. politum*, and *F. patens*. Conversely, he reported at least one lot of *F. paripavoninum* as *F. pavoninum* (see synonymy).

Umbgrove's (1938) Pleistocene-Holocene record of *F. pavoninum paripavoninum* from Talaud (RGM 35452) is not a *Truncatoflabellum*, lacking a truncate base and having nonspinose, sharp edges. It is too poorly preserved to properly identify.

The Japanese records of *F. pavoninum paripavoninum* of Yabe and Eguchi (1942a,b) are also nontruncate species: *F. lamellulosum* and *F. politum*.

Wells' (1984) Pleistocene specimen of *F. paripavoninum* from Vanuatu (Plate 37*g,h*) is compared to other Indo-Pacific species in Table 6. It is considered to be a separate species.

Only two species of Pacific *Truncatoflabellum* have nonspinose anthocyathi: *T. paripavoninum* and *T. trapezoideum*, the first having sharp thecal edges, the second having rounded thecal edges. *Truncatoflabellum paripavoninum* can be distinguished from all other *Truncatoflabellum* by its high thecal edge angle, very delicate corallum, and high number of septa (S_7 in larger coralla). Furthermore, it is one of only two species that occur in deep water and one of two species with attenuate larger septa (Table 6).

Although basal scar diameter is a fairly consistent and useful character to help diagnose species of *Truncatoflabellum*, in *T. paripavoninum* it is quite variable, the greater scar diameter ranging from 6–14 mm. Because this range of variation was found in a single lot of specimens, all other characters being equal, the range is assumed to be intraspecific and perhaps intrapopulational variation. *Truncatoflabellum paripavoninum* also varies strongly with regard to thecal edge angle, again, all other characters being similar in expression. Based on the specimens at hand, neither of these variable characters is considered to be of specific value. The holotype (illustrated specimen of Alcock, 1898) has a greater scar diameter of 7.5 mm and a 113° thecal edge angle (even though Alcock, 1898, stated the thecal edge angle to be 230°), which is consistent with the Philippine specimens collected at ALB-5283 and an unknown *Albatross* station in the Philippines (USNM 40721).

MATERIAL EXAMINED.—ALB-5283 (3) USNM 82006; ALB-5284 (1) USNM 82005; ALB-5527 (5) USNM 82007; ALB-5528 (1) USNM 40727; ALB-5529 (1) USNM 40750; ALB-5586 (1) USNM 40737; ALB-5589 (2) USNM 82008; ALB-5590 (2) USNM 82009; ALB-5648 (4) USNM 40728; ALB-5656 (1) USNM 40730; ALB-5658 (8) USNM 40729; unknown ALB station in Philippines (47) USNM 40721, (1) AM G15241; *Flabellum* sp. of Alcock (1902a), ZMA 1235, *Siboga* 316. *Reference Material: F. pavoninum paripavoninum* of Vaughan (1907) USNM; of Umbgrove (1938) RGM 35452; of Yabe and Eguchi (1942a) TIUS; *F. paripavoninum* of Wells (1984) USNM 71858.

TYPES.—The holotype is presumed to be deposited in the Indian Museum, Calcutta (fide Gardiner, 1902a). *Type Locality: Investigator* 177: 13°47′49″N, 73°07′E (off Pedro Bank, Luccadive Sea), 1163 m, 5 May 1894, 44.2°F.

DISTRIBUTION.—*Recent:* Luccadive Sea (Alcock, 1894); Philippines (Bohol Sea; off Manila, Luzon); Indonesia (off Sabah, Celebes Sea; Java Sea; Teluk Bone, Celebes); 476–1163 m; 4.0°–11.8°C.

50. *Truncatoflabellum carinatum*, new species

PLATE 38*b–e*

Flabellum rubrum.—Faustino, 1927:53 [in part: ALB-5311].—Yabe and Eguchi, 1942a:96–98, [in part: pl. 8; figs. 6–12, 20]; 1942b:131–132 [in part].—Umbgrove, 1950:641 [in part: pl. 81: figs. 5, 6].

?*Flabellum variabile* forma *alta* Gerth, 1921:40, pl. 57: fig. 16.

DESCRIPTION.—Angle of acute thecal edges 35°–50°; inclination of slightly convex thecal faces 18°–26°, anthocyathus quite compressed near base. Largest anthocyathus (holotype) examined 23.4 × 14.6 mm in calicular diameter and 26.8 mm tall, with a basal scar of 5.0 × 2.0 mm. Edges of lower half of corallum carinate, projecting as low, thin, continuous ridges up to 2 mm tall. Four pairs of thecal edge spines present on better-preserved specimens. Basal scar small, 4.5–5.2 × 1.7–2.0 mm in diameter. Anthocaulus unknown. Theca light reddish brown and free of encrustation. Theca smooth, marked by fine white longitudinal striae that delimit costae, which are equal in width, about 0.3 mm wide. Calice elliptical: GCD : LCD = 1.6–1.9.

Septa hexamerally arranged in five cycles according to the formula: $S_{1-3}>S_4>S_5$. Aspects of septal shape, relative septal exsertness, granulation, and presence of a septal notch unknown due to poor preservation of all specimens available. Inner edges of S_{1-3} vertical, thickened, and quite sinuous. Lower, inner edges of S_{1-3} form a loosely tangled columella deep in fossa.

DISCUSSION.—Among the Recent Pacific species of *Truncatoflabellum*, *T. carinatum* is most similar to *F. paripavoninum* of Wells, 1984, these being the only two species with acute thecal edges that bear 3 or 4 pairs of edge spines. *Truncatoflabellum carinatum* is distinguished by having a smaller thecal edge angle, smaller basal scar, and less septa arranged in a different symmetry (Table 6).

Truncatoflabellum carinatum is also very similar to the Javanese Miocene fossil described by Gerth (1921) as *F. variabile* forma *alta*. Gerth's specimen, although fragmentary (Plate 38*f*), is 15.9 × 6.3 mm in calicular diameter (broken) and 13–17 mm tall. It has acute thecal edges with evidence of three pairs of edge spines, an edge angle of 33°, face angle of 15°, and a septal formula of: $S_{1-3}>S_4>S_5$ (96 septa). Its thecal scar, however, is 7.8 × 3.7 mm, much larger than that of *T. carinatum*, but otherwise similar in size and shape to *T. carinatum*.

Truncatoflabellum carinatum was figured by Yabe and Eguchi (1942a) as *F. rubrum* (in part) as Pliocene fossils from Japan. Although I did not examine all of Yabe and Eguchi's specimens of *F. rubrum*, I did examine most of their figured specimens, concluding that their material consisted of at least four species, none of which are *F. rubrum*. In addition to *T. carinatum*, the species they figured in pl. 8: figs. 17–19, 23, 24, and pl. 11: fig. 14 is an undescribed *Truncatoflabellum* characterized by decameral symmetry (septal formula: 20 : 20 : 40), a very small basal scar, and 4 or 5 pairs of edge spines (Plate 38*g,h*). *Truncatoflabellum candeanum* and *T. formosum* are also included among the figured specimens (see respective synonymies of those species for details).

ETYMOLOGY.—The species name is from the Latin *carinatum* (keeled), and refers to the carinate thecal edges of the species.

MATERIAL EXAMINED.—Types; Gerth's (1921) *F. variabile* forma *alta*, RGM 3799; *F. rubrum* of Yabe and Eguchi

(1942a,b): TIUS 43434 (15) Tonahama, Pliocene, Plate 38*d;* TIUS 29233 (50) Tonbe; *F. rubrum* of Umbgrove (1950) RGM 77860, Plate 38*e*.

TYPES.—*Holotype:* ALB-5312, USNM 81959, Plate 38*b,c*. *Paratypes:* ALB-5312 (7) USNM 81960, (1) AM G15255; ALB-5313 (21) USNM 81961; ALB-5314 (3) USNM 81962. *Type Locality:* 21°30'N, 116°32'E (South China Sea off Hong Kong), 256 m.

DISTRIBUTION.—*?Miocene:* Java (Gerth, 1921). *Pliocene:* Japan (Yabe and Eguchi, 1942a). *Pleistocene:* Java (Umbgrove, 1950). *Recent:* South China Sea off Hong Kong; (not yet known from the Philippines but included in this revision because of proximity to Philippines and for comparative reasons); 223–274 m; 12.0°–15.3°C.

Blastotrochus Milne Edwards and Haime, 1848

Blastotrochus Milne Edwards and Haime, 1848:284–285; 1850:xviii; 1857:99.—Semper, 1872:237–238.—Alloiteau, 1952:653.—Cairns, in press a.
Flabellum (Blastotrochus).—Duncan, 1885:14.—Faustino, 1927:59–60.—Chevalier, 1961:379.
Flabellum.—Gardiner, 1902a:121 [in part].—Vaughan and Wells, 1943:226 [in part].—Wells, 1956:F432 [in part].—Zibrowius, 1974:19–20, 26 [in part: part of group 2].—Chevalier, 1987:752 [in part].

DIAGNOSIS.—Like *Truncatoflabellum*, but with additional asexual budding from lateral edges of corallum (anthoblast production).

DISCUSSION.—Milne Edwards and Haime (1848, 1857) originally distinguished *Blastotrochus* from the closely related species complex of truncate *Flabellum* (= *Truncatoflabellum*) by its budding from the lateral corallum edges; *Truncatoflabellum* reproduces asexually only by transverse division. Although some authors maintained *Blastotrochus* as a separate genus, most have treated it as a subgenus of *Flabellum* or simply as a junior synonym of *Flabellum*, in both cases allied with those species having transverse division (e.g., *"flabella truncata"* of Milne Edwards and Haime, 1848, or *Flabellum* group 2 of Zibrowius, 1974). Cairns (in press a) advocated the resurrection of *Blastotrochus* as a valid genus, distinguished from *Flabellum* by its asexual reproduction, and distinguished from *Truncatoflabellum* by its additional mode of asexual reproduction, termed anthoblast production (as opposed to the more simple transverse division of *Truncatoflabellum*). The anthoblast method differs from transverse division in several significant ways (Cairns, in press a) and leads to very different population strategies: the former allowing exponential increase of clonemates, the latter leading to a more gradual increase in clonemates. The morphological differences associated with anthoblast production (i.e., anthoblasts budding from the thecal edges), coupled with the potential adaptive advantage of exponential increase in clonemates, was considered to be a key innovation by Cairns (in press a) and therefore of generic importance.

Blastotrochus nutrix is the only Recent species known in this genus. Only one other species, appropriately named *B. proliferus* d'Archiardi, 1866, from the Miocene of Italy, has been attributed to this genus.

TYPE SPECIES.—*Blastotrochus nutrix* Milne Edwards and Haime, 1848, by monotypy.

DISTRIBUTION.—*Miocene:* Italy. *Recent:* Philippines; 11–18 m.

51. *Blastotrochus nutrix* Milne Edwards and Haime, 1848

PLATES 38*i–m*, 39*a,b*

Blastotrochus nutrix Milne Edwards and Haime, 1848:284–285, pl. 8: fig. 14; 1850:xviii; 1857:100.—Semper, 1872:238–241, pl. 16: figs. 1–6.—Zibrowius, 1974:20.—Cairns, in press a.
Not *Flabellum nutrix*.—Gardiner, 1902a:121.
?*Flabellum rubrum* var. *nutrix*.—Gardiner, 1902b:464–465.
Flabellum (Blastotrochus) nutrix.—Faustino, 1927:59–60, pl. 5: figs. 1–6.

DESCRIPTION.—Angle of rounded thecal edges 10°–16°; inclination of lateral faces 10°–12°. Corallum faces near base slightly more compressed, having more acute thecal edges. Largest specimen examined (1 of Semper's (1872) specimens, NMW 15500) 11.1 × 7.9 mm in calicular diameter and 33.3 mm tall. A pair of downward-projecting spines occurs 2–3 mm above basal scar, fully developed on anthoblasts still attached to parent corallum. Spines invariably broken or encrusted. Basal scar 2.8–3.3 × 2.3–2.5 mm in diameter; 12 complete septa originate from basal scar. Smaller coralla (anthoblasts) bud from each thecal edge, the buds separated by 3–4 mm. Anthoblasts attain three cycles of septa and some pairs of S_4 before detachment. Theca white, usually encrusted by bryozoans, bivalves, serpulids, and calcareous algae. Calice elliptical, GCD : LCD = 1.3–1.5.

Septa hexamerally arranged in four cycles according to the formula: $S_{1-2}>S_3>S_4$ (48 septa). Larger specimens have up to 56 septa, e.g., 14 primary, 14 secondary, and 28 tertiary septa, the extra quartets of septa usually developed in chambers adjacent to the principal septa by the process described for *T. aculeatum*. S_{1-2} slightly exsert, their upper, outer edges forming a distinct notch between theca and septa about 0.5 mm wide. S_3 about 3/4 width of S_{1-2}, and not exsert. S_4 small, about 1/4 width of S_3. Inner septal edges straight; lower, inner edges of S_{1-2} thickened. Septal faces very spiny, covered by tall, pointed granules about 0.08 mm high.

Columella rudimentary, formed by the loose fusion of lower, inner edges of S_{1-2}.

DISCUSSION.—*Blastotrochus nutrix* is known from only two collections: the six syntypes of Milne Edwards and Haime (1848), and 90 specimens reported by Semper (1872), both records from shallow water in the Philippines. Semper's meticulous analysis included observations on tissue color, septal insertion, and budding patterns.

Gardiner (1902a), based on a large suite of specimens from South Africa identified as *F. rubrum*, implied that lateral budding was typical for otherwise distally budding species and was perhaps an "accidental circumstance" (Gardiner, 1902a:121), leading him to synonymize *Blastotrochus* with *Flabellum* and name the laterally budding specimens *Flabellum rubrum* var. *nutrix*. He also noted that two syntypes of *B. nutrix* showed no evidence of lateral budding and implied that *F. irregulare* Semper, 1872, and *F. variabile* Semper, 1872, were probably synonymous with *B. nutrix*. Based on his illustrations, Gardiner's South African specimens clearly represent a mixed lot, including *F. inconstans, Rhizotrochus* sp., and other species, but not *F. rubrum* (see Squires, 1963).

Lateral budding is clearly a natural phenomenon that has been well explained and illustrated by Semper (1872), not an accidental circumstance. In fact, the presence or absence of lateral budding (anthoblast production) is interpreted as a basic difference in corallum morphology and physiology, significant at the generic level (Cairns, in press a), and is not seen as a variety of discontinuous variation as implied by Gardiner's position (1902b) (see also discussion of *Blastotrochus*). Consequently, contrary to Gardiner (1902a), *T. irregulare* is considered to be quite distinct from *B. nutrix*. Finally, also contrary to Gardiner (1902a), all six syntypes of *B. nutrix* have lateral buds or scars from detached buds.

Gardiner (1902b) reported *B. nutrix* from the Maldive Islands. Although not examined, this record is queried based on Gardiner's comment that it was similar to *F. rubrum* in corallum morphology; Gardiner's tendency to lump several species as one; and the great geographic separation from the known range.

Only one other species of *Blastotrochus* has been described, *B. proliferus* d'Archiardi, 1866, the types of which Chevalier (1961) was unable to find.

MATERIAL EXAMINED.—Syntypes; Semper's (1872) *B. nutrix* (4 of 90 specimens) NMW 15500, Plates 38*k-m*, 39*a,b*.

TYPES.—Six syntypes (Plate 38*i,j*) are deposited at the BM (1855.12.27.6), all from the Stokes Collection, the largest specimen matching the measurements and figure of Milne Edwards and Haime (1848). *Type Locality:* "Philippines," depth unknown.

DISTRIBUTION.—*Recent:* Known only from the Philippines (Lapinig Canal, north of Bohol); 11-18 m.

Placotrochus Milne Edwards and Haime, 1848

Placotrochus Milne Edwards and Haime, 1848:282; 1850:xviii; 1857:98.—Semper, 1872:251.—Duncan, 1885:16.—Vaughan and Wells, 1943:227 [in part: not fossil species].—Alloiteau, 1952:653.—Wells, 1956:F432.—Zibrowius, 1974:21, 26.—Chevalier, 1987:752, fig. 418,8.
Not *Placotrochus*.—Duncan, 1864:163-164.—Vaughan, 1907:66.
?*Microtrochus* Tenison-Woods, 1880b:101.—Wells, 1956:F432.

DIAGNOSIS.—Corallum compressed-flabellate; transverse division present, resulting in a frustum-shaped anthocyathus with a basal scar. Anthocaulus base simple, not stereome reinforced. One pair of thecal edge spines. Five cycles of septa; calicular edge smooth. Fossa deep; thin but prominent lamellar columella present.

DISCUSSION.—At least 12 species have been assigned to the genus *Placotrochus*. Seven of these 12, including six South Australian Tertiary species (*P. deltoideus* Duncan, 1864; *P. elongatus* Duncan, 1864; *P. corniculatus* Dennant, 1879; *P. pueblensis* Dennant, 1903; *P. inflatus* Dennant, 1903; and *P. magnus* Dennant, 1904) and the Recent *P. pedicellatus* Tenison-Woods, 1879 (from Princess Charlotte Bay, N.S.W.) are fundamentally different from the type species *P. laevis* in that they lack transverse division. Based on the same character that I used to distinguish *Truncatoflabellum* from *Flabellum* (the key innovation of transverse division), I also maintain that these seven species constitute a separate genus, for which there is currently no available name. *Microtrochus* Tenison-Woods, 1880b, considered by Wells (1956) to be a junior synonym of *Placotrochus*, is potentially available, but, based on the description of the columella and its apparent truncate base, it cannot be suggested as a name for this species complex, which is referred to as the *Placotrochus deltoideus* species complex in Table 4.

Vaughan (1907) described *P. fuscus* from Hawaii, but it differs from *Placotrochus* and *P. deltoideus* in having a firmly attached, sterome-reinforced base, much like that of *Javania*, but differing from *Javania* in having a lamellar columella (Table 4). Zibrowius (1974) used the character of a stereome-reinforced base to help distinguish *Javania* from *Flabellum*, and *Placotrochides* from *Truncatoflabellum*. There is no available name for a genus having the characters of *P. fuscus* (Table 4).

Of the four remaining species, *P. alveolus* Duncan, 1863, was transferred to *Meandrina* (see Cairns and Wells, 1987); *P. lonsdailei* Duncan, 1863, was made the type species of *Antillophyllia* Vaughan, 1932; and *P. candeanus* Milne Edwards and Haime, 1848, is considered to be a junior synonym of *P. leavis*—which results in *Placotrochus* being a monotypic genus; the sole species, *Placotrochus laevis*.

Placotrochus is distinguished from *Truncatoflabellum* by its lamellar columella, which is present even in very small specimens (Table 4). Zibrowius (1974) suggested that if this was the only difference between it and *Flabellum*, that it only be considered of subgeneric importance, but, because the presence or absence of a columella is usually interpreted as a generic level character, and because *Flabellum* has already been divided into subgenera based on other characters, I prefer to maintain *Placotrochus* as a separate genus.

TYPE SPECIES.—*Placotrochus laevis* Milne Edwards and Haime, 1848, by subsequent designation (Milne Edwards and Haime, 1850:xviii).

DISTRIBUTION.—*Recent:* Western Pacific; Gulf of Manaar; 22-69 m.

52. *Placotrochus laevis* Milne Edwards and Haime, 1848

PLATE 39*c-g*

Placotrochus laevis Milne Edwards and Haime, 1848:283, pl. 8: figs. 15, 15a; 1850:xviii; 1857:99.—Semper, 1872:251-252, pl. 18; figs. 11-13.—Bourne, 1905:200-201, pl. 1: fig. 5.—Folkeson, 1919:5-6.—Vaughan and

Wells, 1943:227.—Wells, 1956:F432, fig. 336,5a.—Zibrowius, 1974:21.
Placotrochus candeanus Milne Edwards and Haime, 1848:283-284; 1857:99.—Zibrowius, 1974:21.—?Alcock, 1902a:33.
Placotrochus sp. Veron, 1986:603, fig.

DESCRIPTION.—Angle of thecal edges 40°-72°; inclination of convex thecal faces 20°-33°. Corallum laterally compressed with acute, but not ridged, thecal edges. Largest anthocyathus examined (USNM 81994) 19.2 × 8.2 mm in calicular diameter and 17.7 mm tall, with a basal scar of 6.4 × 2.7 mm. A pair of downward-projecting thecal edge spines occurs near basal scar, but these spines are invariably broken early in ontogeny. A second pair of spines about 1 mm above the first occasionally present. Basal scar of fairly consistent dimensions, ranging from 5.4 × 2.7 to 7.0 × 3.4 mm. Anthocaulus even more compressed than anthocyathus, one 6.7 × 3.3 mm in calicular diameter, 5.6 mm tall, and 1.0 mm in pedicel diameter. Anthocaulus with acute, carinate thecal edges; no thecal spines; 48 septa arranged: $S_{1-3}>S_4$; and a rudimentary, trabecular to lamellar columella. Costae of anthocyathus white and porcelaneous; C_{1-3} often broader than C_{4-5} and slightly ridged. Ratio of GCD : LCD = 1.8-2.3; upper thecal faces arched.

Septa hexamerally arranged in five cycles according to the formula: $S_{1-3}>S_4>>S_5$. The fifth cycle begins to appear at a greater calicular diameter of about 9.5 mm and is fully attained by a greater calicular diameter of about 11.5 mm. S_{1-3} highly exsert, with very sinuous inner edges, the lower, inner edges firmly fused to the columella through a tangle of digitiform processes. S_4 half width of S_{1-3}, less exsert, and have straight, laciniate inner edges that do not attain the columella. S_5 rudimentary, spiny ridges about $^1/_5$ width of S_4, only 3-5 mm long, and not exsert. Septal granules large and triangular, about 0.14 mm tall, with a base of 0.15 mm.

Columella lamellar, thin (0.15-0.20 mm), and straight. In small coralla, columella composed of 12-15 closely adjacent, slender, flattened elements, which, as the corallum increases in size, fuse laterally into a solid, almost rectangular plate. Upper edge of columella often irregular, reflecting the individual columellar elements present prior to fusion.

DISCUSSION.—Based on the original descriptions of *P. laevis* and *P. candeanus*, the latter appears to be simply a smaller specimen of the former, having a greater calicular diameter consistent with a calice of only four cycles of septa. Alcock's (1902a) report of *P. candeanus* from the Java Sea is queried because of its small basal scar (3.8 × 2.1 mm) and incipient third pair of thecal spines on an anthocyathus of 6.5 × 3.8 mm in calicular diameter. In these characters, it is similar to Folkeson's (1919) specimen number 5 from off Cape Jaubert, Western Australia.

MATERIAL EXAMINED.—ALB-5106 (1) USNM 81990; ALB-5107 (19, including 2 anthocauli) USNM 81989; ALB-5133 (3, including 1 anthocaulus) USNM 81991; ALB-5134 (1) USNM 81992; ALB-5144 (1) USNM 81993; *Alpha Helix* 79-M-14 (15) USNM 81995; Great Barrier Reef (1) USNM 81994; *Siboga* 12 (1) ZMA 1309 (*P. candeanus* of Alcock, 1902a).

TYPES.—The holotype of *Placotrochus laevis* was not traced. *Type Locality:* "Philippines," depth unknown.

The holotype of *Placotrochus candeanus* was not traced. *Type Locality:* "Les mers de la Chine," depth unknown.

DISTRIBUTION.—*Recent:* South China Sea (Milne Edwards and Haime, 1848); Philippines (Luzon; Mindanao; Basilan; Sulu Archipelago); ?Java Sea (Alcock, 1902a); Arafura Sea, off Wessel Island, Arnhem Land, Australia; off Queensland, Australia; off southern Australia (Folkeson, 1919); Gulf of Manaar (Bourne, 1905); 22-69 m.

Javania Duncan, 1876

Desmophyllum.—Michelotti, 1871:341 [in part: *D. clavatum, D. subturbibatum*].—Vaughan and Wells, 1943:214 [in part].—Wells, 1956:F426 [in part].
Javania Duncan, 1876:434-435.—Chevalier, 1961:402.—Zibrowius, 1974:3-7, 23, 26; 1980:156.—Chevalier, 1987:753, fig. 418, 6 [in part: not *Placotrochides*].
Desmophyllum (Javania).—Duncan, 1885:11-12.

DIAGNOSIS.—Corallum ceratoid to trochoid and straight, often with a flared upper calice. Corallum firmly attached by a stereome-reinforced base; transverse division lacking. Three to five cycles of moderately to highly exsert septa; calicular edge jagged. Fossa deep; columella rudimentary or absent.

DISCUSSION.—Following its original description, *Javania* was considered as a subgenus or junior synonym of *Desmophyllum* until Chevalier (1961) correctly transferred it from the Caryophylliidae to a separate genus in the Flabellidae. Zibrowius (1974), in his preliminary revision of the Flabellidae, reviewed the genus *Javania*, listing six Recent species. Further progress on the taxonomy of this genus was made by Zibrowius (1980) and Cairns (1979, 1982, 1984a).

Javania is one of three flabellid genera having a stereome-reinforced base (Table 4). It differs from *Placotrochides* in lacking transverse division and in having a jagged calicular margin. It differs from *"Placotrochus" fuscus* in lacking a columella (but see below).

Currently the genus contains five Recent and three exclusively fossil species: *J. insignis* Duncan 1876 (Indo-West Pacific); *J. antarctica* (Gravier, 1914) (Antarctica); *J. lamprotichum* (Moseley, 1880) (Hawaii); *J. cailleti* (Duchassaing and Michelotti, 1864) (widespread distribution, with junior synonyms of *Desmophyllum eburnem* Moseley, 1881; *D. nobile* Verrill, 1885; *D. vitreum* Alcock, 1898; *D. galapagense* Vaughan, 1906; and *D. delicatum* Yabe and Eguchi, 1942b); *J. pseudoalabastra* Zibrowius, 1974 (North Atlantic); *J. duncani* Wells, 1977 (Eocene of Tonga); *J. clavatum* (Michelotti, 1871) (Miocene of Italy); and *J. subturbinatum* (Michelotti, 1871) (Miocene of Italy). In addition to these described species are two undescribed species in the collections of the NMNH: one from the Kermadec Islands (USNM 82014) and one from the Bering Sea (USNM 82019). Characters of diagnostic value at the species level include number of septal cycles, corallum size and shape; and relative exsertness of septal cycles.

Placotrochus fuscus Vaughan, 1907, from Hawaii, may possibly be yet another species of *Javania*. It was based on three specimens, only one of which has a lamellar columella (USNM 20734); no additional specimens have been reported. The two specimens without a columella (USNM 20732, 20733) are very similar to *J. duncani* and the undescribed species from the Kermadecs. More specimens are needed from Hawaii to resolve the placement of *P. fuscus*.

TYPE SPECIES.—*Javania insignis* Duncan, 1876, by monotypy.

DISTRIBUTION.—*Eocene:* Java. *Miocene:* Italy. *Recent:* Worldwide, including Antarctica; 52–3165 m.

53. *Javania insignis* Duncan, 1876

PLATE 40*d,e,g,h,j,k*

Javania insignis Duncan, 1876:435, pl. 39: figs. 11–13.—Marenzeller, 1907:23, pl. 2; fig. 6.—Zibrowius, 1974:8–9, pl. 1: figs. 1–6.—Fricke and Schuhmacher, 1983:184.—Scheer and Pillai, 1983:165–166, fig. 4, pl. 37: figs. 9–12.—Cairns, 1984a:23, pl. 4: figs. F–H.

Desmophyllum cf. *insigne*.—Yabe and Eguchi, 1942b:115, pl. 9: figs. 5, 6.

Desmophyllum insignis.—Eguchi, 1965:290, fig. 427; 1968:C-41, pl. C9: figs. 4–9.

?*Desmophyllum alabastrum* Alcock, 1902a:28–29, pl. 4: figs. 27, 27a.—Faustino, 1927:64, pl. 5: figs. 11, 12.—Zibrowius, 1974:23.—Van Soest, 1979:112.—Zibrowius, 1980:159.

Not *Desmophyllum alabastrum*.—Yabe and Eguchi, 1942b:115, pl. 9: fig. 4 [= *Desmophyllum cristagalli]*.

DESCRIPTION.—Corallum ceratoid, usually expanding into a flared elliptical calice with a GCD : LCD of 1.3–1.7. Coralla rarely larger than 25 × 18 mm in calicular diameter and about 43 mm tall; however, largest reported specimen (Cairns, 1984a: specimen from Christmas Island) 43 × 27 mm in calicular diameter and 53.8 mm tall. Pedicel periodically reinforced with layers of stereome, becoming thicker with age. Ratio of pedicel diameter (measured at narrowest pedicel diameter) to greater calicular diameter, 0.40–0.55. Theca robust; theca and septa milky white, the theca usually very smooth, almost porcelaneous. C_{1-3} sometimes expressed as short low ridges on upper third of corallum. Calicular edge jagged, the calice rising to small apices at S_{1-3}. Jagged calicular margin less apparent in larger coralla.

Septa hexamerally arranged in five cycles according to the formula: $S_1 > S_2 > S_3 >> S_4 > S_5$, the fifth cycle usually complete at a greater calicular diameter of about 15–17 mm. S_1 highly exsert (up to 5 mm) and quite thick, with vertical, straight inner edges. S_2 only slightly smaller and less exsert, with slightly sinuous inner edges that extend equally as far into the fossa as do the S_1. S_3 1/3 to 1/2 width of S_2 but also quite exsert; inner edges slightly sinuous. S_4 considerably smaller than S_3 (only about 1/5 size) and nonexsert. In larger coralla, the upper margins of the S_4 terminate 1–2 mm below calicular edge. S_5 rudimentary, about 1/2 width of S_4. Large, blunt granules about 0.10 mm tall cover septal faces.

Fossa elongate and very deep. Columella absent.

DISCUSSION.—Duncan's (1876) original description of *J. insignis* and the first subsequent report by Marenzeller (1907) were both based on relatively small specimens of about 15 mm greater calicular diameter having only an incomplete fifth cycle of septa. Specimens slightly above this size have a full five cycles (96) of septa, an important point of differentiation from *J. cailleti*.

Among the described species of *Javania*, *J. insignis* is most similar to *J. antarctica* (Gravier, 1914), another species with five cycles of septa, a white corallum, and a massively reinforced pedicel. *Javania antarctica* is distinguished by its less exsert septa, larger corallum size, and more delicate theca. Furthermore, it is known only from Antarctica and the Scotia Ridge (Cairns, 1982).

In the collections of the ZMA (1232) is a specimen of *J. insignis* labeled as a manuscript type of *Flabellum weberi* (Plate 40*g,h*), which Alcock apparently intended to describe in his *Siboga* report. For some reason, it was omitted from the *Siboga* report as a new species or even as a record of another species.

Alcock (1902a) described *Desmophyllum alabastrum* from two small specimens, the larger of which (Alcock's figured specimen from *Siboga* 105) is lost (Van Soest, 1979). The larger specimen had a greater calicular diameter of 8 mm, a thick pedicel, and four cycles of septa. The smaller specimen (*Siboga* 95, Plate 40*f,i*) has a greater calicular diameter of only 4.0 mm, a thickened pedicel, and only three cycles of septa. Zibrowius (1974, 1980:159) suggested that these specimens might be the anthocaulus stage of a species of *Placotrochides*. Unfortunately, juvenile specimens of *Javania* are virtually indistinguishable from the anthocaulus stage of a *Placotrochides*, the major difference being that the latter subsequently divides transversely, the former does not. Young stages (anthocauli) of both genera are poorly known, especially those of *Placotrochides*, and therefore Alcock's specimens cannot be definitively identified; however, its circular calice and recessed higher-cycle septa are more indicative of a juvenile *Javania* than of *Placotrochides*. If, however, following subsequent study, *D. alabastrum* proves to be the anthocaulus stage of *P. scaphula*, it could have nomenclatural priority due to page precedence. Gardiner (1904:98) assigned Alcock's *D. alabastrum* to *Flabellum*, making it a junior secondary homonym of *Flabellum alabastrum* Moseley, 1873. To resolve this homonymy, he created the new name *Flabellum sibogae* for *D. alabastrum* Alcock, 1902, which was unnecessary as long as *D. alabastrum* remains in either *Javania* or *Placotrochides*. Ironically, the South African specimens that Gardiner reported as *F. sibogae* are not *D. alabastrum* Alcock, 1902, but probably a legitimate undescribed species of *Flabellum*.

MATERIAL EXAMINED.—ALB-5255 (1) USNM 81986; ALB-5357 (5) USNM 81987; ALB-5580 (1) USNM 81988; Izu Oceanic Park, Japan, 46 m (1) USNM 81985; *Anton Bruun* 371-F (10) USNM 77200; specimens of Cairns (1984a) from Hawaiian and Christmas Islands, Bishop Museum, Honolulu; *Siboga* 310 (1) ZMA 1232 (manuscript type of *F. weberi*) (Plate 40*g,h*). *Reference Material:* Syntype of *D. alabastrum*, *Siboga* 95, Plate 40*f,i*.

TYPES.—The holotype of *Javania insignis* is deposited at the BM (1973.2.20.1). *Type Locality:* 34°13′N, 136°13′E (Owase, off southeastern Honshu), 88 m.

Of the two syntypes of *Desmophyllum alabastrum* Alcock, 1902, one (*Siboga* 105) is lost and the other (*Siboga* 95) is deposited at the ZMA (1252) (Van Soest, 1979). *Type Locality:* Sulu Archipelago, Philippines, 275–522 m.

DISTRIBUTION.—*Recent:* Off Japan (Duncan, 1876; Yabe and Eguchi, 1942b); Philippines (Palawan; Davao Gulf); Indonesia (off Sabah, Celebes Sea; Savu Sea); Hawaiian and Line Islands (Cairns, 1984a); Red Sea (Marenzeller, 1907; Fricke and Schuhmacher, 1983; Scheer and Pillai, 1983); Madagascar (Zibrowius, 1974); Mozambique; 46–825 m.

Placotrochides Alcock, 1902

Placotrochides Alcock, 1902a:33 [in part: not *P. dentiformis*].—Zibrowius, 1974:20, 23, 26.—Cairns, 1979:151.—Zibrowius, 1980:159.

Flabellum.—Vaughan and Wells, 1943:226 [in part].—Wells, 1956:F432 [in part].—Chevalier, 1961:379 [in part].

DIAGNOSIS.—Corallum compressed-cylindrical; transverse division present, resulting in an anthocyathus with a basal scar almost as large as calicular diameter. Anthocaulus base reinforced with stereome. Lateral thecal spines absent. Three to four cycles of nonexsert septa; calicular edge smooth. Fossa moderately deep, containing a robust, trabecular columella.

DISCUSSION.—*Placotrochides* has customarily been considered as a junior synonym of *Flabellum*, along with other truncate flabellids, such as *Blastotrochus* and *Truncatoflabellum*. Zibrowius (1974) resurrected *Placotrochides* to accommodate those species with the character combination of transverse division, stereome-reinforced anthocaulus base, and a trabecular columella; however, Chevalier (1987) still considered it to be a junior synonym of *Javania*. *Placotrochides* is distinguished from *Javania* by having transverse division, a smooth calicular edge, nonexsert septa, and a trabecular columella (Table 4). It is distinguished from *Truncatoflabellum* by its trabecular columella, stereome-reinforced anthocaulus base, and cylindrical corallum shape.

Five species have been attributed to *Placotrochides*, but three of them have been subsequently transferred to other genera: *P. dentifomis* Alcock, 1902a, was transferred to *Premocyathus* by Zibrowius (1980); *P. kikutii* Yabe and Eguchi, 1941, is transferred in this revision to the turbinoliid genus *Idiotrochus;* and *D. alabastrum* Alcock, 1902a, placed in *Placotrochides* by Zibrowius (1974, 1980), is probably a species of *Javania* (see discussion of *J. insignis*). Two species remain: *P. scaphula* Alcock, 1902a, type species of the genus, and *P. frusta* Cairns, 1979.

TYPE SPECIES.—*Placotrochides scaphula* Alcock, 1902a, by subsequent designation (Wells, 1936).

DISTRIBUTION.—*Recent:* Caribbean; off Morocco; Philippines; Indonesia; 476–1628 m.

54. *Placotrochides scaphula* Alcock, 1902

PLATES 40*l*, 41*a–e*

Placotrochides scaphula Alcock, 1902a:34, pl. 4: figs. 32, 32a.—Wells, 1936:124.—Zibrowius, 1974:23.—Van Soest, 1979:113.—Zibrowius, 1980:159.

?*Desmophyllum alabastrum* Alcock, 1902a:28–29 [see discussion of *Javania insignis*].—Faustino, 1927:64, pl. 5: figs. 11–12.—Van Soest, 1979:112.

Not *Desmophyllum alabastrum*.—Yabe and Eguchi, 1942b:115, pl. 9: fig. 4 [= *Desmophyllum cristagalli*].

DESCRIPTION.—Corallum a laterally compressed cylinder with subacute, but not ridged, thecal edges. Thecal edges virtually parallel, diverging at 0°–3°; inclination of convex lateral faces 8°–10°. Largest anthocyathus examined (ALB-5582) 13.0 × 7.4 mm in calicular diameter, 12.0 mm tall, and 12.0 × 6.3 mm in basal scar diameter, almost twice the size of Alcock's holotype. Basal scar V-shaped and massive, invariably almost as large as the calicular diameter, ranging from 6.5 × 3.2 to 12.0 × 6.3 mm in diameter. Anthocaulus unknown, but assumed to have a stereome-reinforced base. Theca white, bearing fine, white, vertical intercostal striae about 0.05 mm wide that delimit broad, flat, equal costae 0.55–0.70 mm wide. Theca ringed with fine, chevron-shaped epithecal markings, each vertical row of chevrons peaking at a major (C_{1-3}) intercostal stria. Ratio of GCD : LCD = 1.55–2.0; however, one aberrant specimen (MUSORSTOM 2-25) has a ratio of 1.2.

Septal symmetry sometimes difficult to distinguish due to unequal development of septal cycles or analysis of immature specimens. Largest known specimen contains 42 septa hexamerally arranged accordingly: S_{1-2}>S_3>S_4; however, four pairs of S_4 are missing from thecal face half-systems, and one half-system adjacent to a principal septum has not only its full complement of S_4 but also a pair of S_5. In this particular half-system, the S_3 was accelerated to a size equivalent to that of the S_{1-2}. S_{1-2} slightly exsert, have slightly sinuous inner edges, and do not have septal notches. S_3 about half width of S_{1-2}; S_4 1/4 width of S_3; and S_5, if present, rudimentary. Lower edges of S_{1-2} contribute to the columella, and often the lower, inner edges of S_3 join the columella deep in the fossa. Septal faces smooth, bearing sparse, low granules about 0.07 mm tall.

Columella large: elongate and about 1/3 width of lesser calicular diameter. Columella composed of a loose fusion of crispate laths interconnected with protuberances from the lower, inner edges of the S_{1-2} and occasionally the S_3.

DISCUSSION.—Despite several previous references to this species (see synonymy), it was known from only one specimen—the holotype. Additional records reported herein therefore add to our knowledge of its variation and geographic distribution.

The only other species in this genus, *P. frusta* Cairns, 1979, is known exclusively from 357–1300 m in the Atlantic Ocean. *Placotrochides scaphula* is distinguished by its larger corallum size (including a larger basal scar), greater number of septa, and higher GCD : LCD. Aside from these size and shape differences, they are very similar species.

MATERIAL EXAMINED.—ALB-5582 (2) USNM 81886; ALB-5586 (4) USNM 81997; ALB-5589 (5) USNM 81998; ALB-5591 (1) USNM 81999; MUSORSTOM 2-25 (2) MNHNP; holotype.

TYPES.—The holotype (Plate 41*a,b*) is deposited at the ZMA (1094) (Van Soest, 1979). *Type Locality:* 5°54.5'S, 120°19.2'E (Flores Sea, off southeastern Celebes), 462 m.

DISTRIBUTION.—*Recent:* Philippines (Verde Island Passage; ?Sulu Archipelago (Alcock, 1902a)); Indonesia (Darvel Bay, off Sabah; Flores Sea (Alcock, 1902a)); 476–1628 m; 3.4°–7.6°.

Rhizotrochus Milne Edwards and Haime, 1848

Rhizotrochus Milne Edwards and Haime, 1848:281; 1850:xviii; 1857:97–98.—Duncan, 1885:14–15 [in part].—Yabe and Sugiyama, 1936:346–347.—Scheer and Pillai, 1983:164–165.

Not *Rhizotrochus*.—Pourtalès, 1868:134 [= *Polymyces*].

Vasillum Tenison-Woods, 1879b:93.

Monomyces.—Vaughan and Wells, 1943:227 [in part].—Alloiteau, 1952:653 [in part].—Wells, 1956:F432.—Zibrowius, 1974:21–22, 26 [in part]; 1980:154 [in part].

DIAGNOSIS.—Corallum turbinate. Transverse division lacking; pedicel small, not reinforced with stereome. No thecal spines; however, 2–20 discrete, slender, hollow rootlets anchor corallum base, tending to be concentrically arranged in groups of 6 or 12 at different levels. Three to six cycles of nonexsert septa; lower cycle septa notched near smooth calicular margin. Fossa deep; columella rudimentary.

DISCUSSION.—All recent higher-level revisions of the Scleractinia place *Rhizotrochus* in synonymy with *Monomyces* Ehrenberg, 1834: the type species of *Rhizotrochus* having more than one (usually six or more) rootlets; *Monomyces* having but one or two rootlets intimately fused with the adjacent pedicel, called a secondary pedicel or basal talon by Chevalier (1987:533). In his revision of the Flabellidae, Zibrowius (1974) stated that the number of rootlets did not justify generic separation. Squires (1966) also concluded that the position and number of rootlets did not have taxonomic significance for *Monomyces radiatus*, but occurred instead in response to the microenvironment in order to better stabilize the corallum. On the other hand, as early as 1936, Yabe and Sugiyama questioned this generic synonymy, asserting that the rootlets of *Rhizotrochus* were quite different from those of *Monomyces*, and used the name *Rhizotrochus* for their multirootlet species. More recently, Scheer and Pillai (1983) distinguished the two genera and implied that Zibrowius would now agree with that distinction. I, too, agree that the genera should be separate: *Monomyces* having species with one massive, irregularly shaped rootlet or group of rootlets that eventually fuses inseparably to one side of the pedicel; *Rhizotrochus* having numerous (≥2) slender, discrete rootlets that do not fuse to the pedicel. I also agree with Squires (1966) that the number of rootlets per corallum is variable and often environmentally controlled within species, but, the difference between the single massive root of *Monomyces* and the multiple discrete rootlets of *Rhizotrochus* is a more basic difference.

As redefined, *Monomyces* contains only two or three species: *M. pygmaea* (Risso, 1826), *M. rubrum* (Quoy and Gaimard, 1833), new combination (= *F. nobile* Holdsworth, 1862; *F. latum* Studer, 1877 (not Alcock, 1902a); *F. harmeri* Gardiner, 1929), and *M. deperditus* (Michelotti, 1871)(Miocene of Italy). The latter species is only tentatively included in *Monomyces* based on its variable presence of the rootlet structure. When present, which is dependent on the need to stabilize the corallum in a high-energy environment (Squires, 1966), the rootlet is identical in construction to that of *M. pygmaea*, and, in fact, the two species are very similar in most other characters.

Rhizotrochus contains four or five species: *R. typus* Milne Edwards and Haime, 1848; *R. levidensis* Gardiner, 1899; *R. radiatus* Dennant, 1904 (= *?R. levidensis; =?Vasillum tuberculatum* Tenison-Woods, 1879); *R. niinoi* Yabe and Eguchi, 1942; and *R. flabelliformis*, new species. Comparison of the two syntypes of *R. levidensis* (BM 1970.1.26.9-10) with topotypic *R. radiatus* (USNM 82094, 82095) reveals no differences that could not be explained by the small size of the former. Pairs of incipient S_4 are present in *R. levidensis* (S_4 are present in *R. radiatus*), and the size and position of rootlets are the same as in *R. radiatus;* however, more specimens are needed from throughout the South Pacific to verify this tentative synonymy. Characters of specific diagnostic value in the genus are number of septal cycles, number and placement of rootlets, pedicel diameter, and corallum size.

Although not examined, the description and illustration of *Vasillum tuberculatum* Tenison-Woods, 1879, from Port Phillip or Bass Strait, suggest a synonymy with *R. radiatus* Dennant, 1904, and, if the same, would have nomenclatural priority over both *R. radiatus* and *R. levidensis*.

TYPE SPECIES.—*Rhizotrochus typus* Milne Edwards and Haime, 1848, by monotypy.

DISTRIBUTION.—*Recent:* Indo-West Pacific; 20–1048 m.

55. *Rhizotrochus typus* Milne Edwards and Haime, 1848

PLATE 41*f–j*

Rhizotrochus typus Milne Edwards and Haime, 1848:282, pl. 8: fig. 16; 1850:xviii; 1857:98.—Marenzeller, 1907:23, pl. 2: fig. 5.—Fricke and Schuhmacher, 1983:184, fig. 14e.—Scheer and Pillai, 1983:165, pl. 38: figs. 1–4.

Rhizotrochus worsleyi Wood-Mason and Alcock, 1891a:5–6.

Rhizotrochus crateriformis Alcock, 1893b:170–171, pl. 8, figs. 1–2; 1894:187; 1898:24.

Flabellum magnificum.—Harrison, 1911: 1020–1021, pl. 57: figs. 1–3.

Rhizotrochus cf. *typus*.—Yabe and Sugiyama, 1936:347–348, figs. 3, 3a.

Flabellum (Rhizotrochus) crateriformis.—Gardiner and Waugh, 1938:174–175.

Rhizotrochus palaoensis Yabe and Eguchi, 1942b:155.

Flabellum transversale.—Nishimura and Suzuki, 1971:11, pl. 4: fig. 1.

Monomyces typica.—Eguchi, 1968:C49.

Monomyces uchiuraensis Eguchi, 1972:160, pl. 1: figs. 1-7; 1973:83, pl. 1: figs. 1, 2.
Monomyces typus.—Zibrowius, 1974:22.
Flabellum crateriformis.—Scheer and Pillai, 1983:164.

DESCRIPTION.—Corallum turbinate, expanding into a flared, irregularly elliptical calice with a GCD : LCD of 1.3–1.45. Angle of evenly rounded lateral edges about 90°; inclination of lateral faces about 65°. Largest specimen examined (ALB-5357) 57.2 × 40.1 mm in calicular diameter and 38.3 mm tall; however, Scheer and Pillai (1983) reported a specimen from the Gulf of Aqaba measuring 68 × 47 mm in calicular diameter and 35 mm tall. Pedicel tiny and unreinforced, 1.0–1.5 mm in diameter, and often obscured from view by descending rootlets. Theca thin and delicate. Corallum white; epitheca marked by numerous very fine horizontal growth lines. Theca often encrusted by foraminifera, serpulids, bryozoa, sponges, and bivalves. Calicular edge smooth; upper thecal faces strongly arched. Rootlets circular in cross section (1.0–2.5 mm in diameter) and hollow, directly communicating with polyp inside corallum. A ring (cycle) of 5 or 6 rootlets usually occurs about 6 mm above the pedicel. In larger specimens, a second irregular cycle of 10–12 rootlets appears about 14 mm above the pedicel. Additional rootlets may occur higher on the theca in an irregular arrangement but rarely higher than 20 mm above the pedicel. Twenty rootlets, some up to 36 mm long, not uncommon on large specimens. Rootlets irregular in length and shape, conforming to presence and shape of substrate. Rootlets often laterally fused in large specimens but still maintain their integrity from other rootlets and from the pedicel.

Septa hexamerally arranged in six cycles according to the formula: $S_{1-2}>S_3>S_4>S_5>S_6$; however, sixth cycle rarely complete, and fifth cycle complete only at a greater calicular diameter of 25–27 mm. S_{1-2} have straight, almost vertical inner edges that attain the columella. S_3 about 3/4 width of S_{1-2} and also reach columella. Upper 6–8 mm of S_{1-3} (near the calice) quite narrow, after which each septum forms a prominent septal lobe before descending into the fossa. A septal notch is formed at the inflection point transitional between the narrow upper septa and the lower septal lobe. S_4 about 3/4 width of S_3 and do not have septal notches. S_5 about half width of S_4 and extend only about 1/3 distance down fossa. S_6 rudimentary, often missing from various half-systems. Septal faces bear large blunt granules about 0.15 mm tall.

Fossa elongate and deep. Columella elongate and trabecular, not massive, but better developed than in most species of *Flabellum*.

DISCUSSION.—*Rhizotrochus typus* is a widely distributed and morphologically variable species, particularly regarding corallum shape, columella expression, and number of rootlets, which has resulted in its having been described under five different names from localities throughout the Indo-West Pacific. Although never illustrated or even cited after its original description, *R. worsleyi* Wood-Mason and Alcock, 1891, from the Gaspar Straits, Indian Ocean, is quite similar to typical *R. typus*. The holotype of *R. worsleyi* is relatively small (greater calicular diameter = 24 mm) and therefore would be expected to have only five cycles of septa. Also, the great inequality in sizes of the S_2 and S_3 described by Wood-Mason and Alcock for *R. worsleyi* is not unusual in specimens of *R. typus* of that size range; e.g., an equal-sized specimen of *R. typus* from the Andaman Islands (*Anton Bruun* 1-28A) shows the same variation.

Likewise, Alcock's (1893b) description and illustration of *R. crateriformis* from off southeastern India are also consistent with *R. typus*. The holotype of *R. crateriformis* is 32 mm in greater calicular diameter with 90 septa.

Rhizotrochus palaoensis Yabe and Eguchi, 1942b, originally described from one specimen from the Palau Islands (110 m) by Yabe and Sugiyama (1936) as *R.* cf. *typus*, was distinguished from *R. typus* only by the presence of a rudimentary columella. It is now known that a rudimentary columella is well within the range of variation of *R. typus*.

Finally, Eguchi (1972) distinguished *R. uchiuraensis* (collected from Uchiura Bay, Izu Peninsula, Japan) from *R. typus* by its larger size and irregularity of rootlets; however, *R. typus* is now known to grow much larger than the largest *R. uchiuraensis* (see Scheer and Pillai, 1983) and the irregular arrangement of rootlets is a variable character. Eguchi's description and illustration of *R. uchiuraensis* are perfectly compatible with *R. typus*.

Rhizotrochus typus is distinguished from the other valid species in the genus by its greater size and correspondingly higher number of septal cycles (5–6 vs. 3–4) and rootlets (15–20 vs. 3–6). In addition, it differs from *R. levidensis* and *R. niinoi* in having equal-sized S_{1-2} (in the other two species the S_1 are larger than the S_2). *Rhizotrochus typus* differs from *R. radiatus* and *R. levidensis* in having a smaller pedicel (1.0–1.5 vs 2.0–2.3 mm in diameter).

MATERIAL EXAMINED.—ALB-5357 (1) USNM 82000; ALB-5580 (1) USNM 40712; ALB-5593 (1) USNM 82001; *Anton Bruun* 1-28A (2) USNM 77204; BM 1851.2.19.2 (1), Plate 41*i,j*.

TYPES.—The two syntypes of *R. typus* figured by Milne Edwards and Haime (1848) are deposited at the MNHNP. *Type Locality:* Singapore, depth unknown.

The holotype of *R. worsleyi* is presumed to be deposited at the Indian Museum, Calcutta. *Type Locality:* Gaspar Straits, Indian Ocean.

The holotype of *R. crateriformis* is presumed to be deposited at the Indian Museum, Calcutta. *Type Locality: Investigator* 142: 14°13′08″N, 80°24′02″E (Madras coast, Bay of Bengal), 1048 m.

The holotype of *R. palaoaensis* is deposited at the TIUS (60633). *Type Locality:* West channel of Palau, barrier reef, 110 m (see Yabe and Sugiyama, 1936).

The deposition of the three syntypes of *R. uchiuraensis* is unknown. Eguchi (1973) designated a lectotype from the syntype series. *Type Locality:* Near Awashima, Uchiura Bay, Izu Peninsula, Japan, 20 m.

DISTRIBUTION.—*Recent:* Off Honshū, Japan (Eguchi, 1972); Palau (Yabe and Sugiyama, 1936); Philippines (Balabac Island, Sulu Sea); Indonesia (Darvel Bay, off Sabah); Singapore (Milne Edwards and Haime, 1848); Andaman Islands; Bay of Bengal (Alcock, 1893b; Wood-Mason and Alcock, 1891a); Persian Gulf (Harrison, 1911); Red Sea (Marenzeller, 1907; Gardiner and Waugh, 1938; Fricke and Schuhmacher, 1983; Scheer and Pillai, 1983); 20–1048 m (dead coralla collected at 1135 m (Scheer and Pillai, 1983)); 7.4°–13.2°C (based on only two records).

56. *Rhizotrochus flabelliformis*, new species

PLATES 41*k,l*, 42*b,d*

Flabellum latum.—Alcock, 1902a:31.

DESCRIPTION OF HOLOTYPE.—Corallum flabellate, with an S-shaped elongate calice 61.5 mm long and 18.2 mm wide (GCD : LCD = 3.38). Angle of rounded lateral edges 90°; inclination of straight to slightly concave thecal faces 18°. Holotype 35.6 mm tall, with a tiny unreinforced pedicel 1.2 mm in diameter. Corallum dense; theca worn and heavily encrusted with foraminifera, serpulids, and bryozoa, although original thecal color appears to have been reddish brown. Upper thecal faces arched and only slightly damaged. Two symmetrically arranged bundles of rootlets present, one on each lower thecal edge. Rootlets tightly fused into bundles 6–7 mm in diameter.

Septa hexamerally arranged in seven cycles according to the formula: $S_{1-4}>S_5>S_6>S_7$, the seventh cycle incomplete, having only 46 pairs of septa (284 septa total). S_{1-4} not exsert and have highly sinuous lower, inner edges. As in *R. typus*, the upper edges of the larger septa are very narrow near the calicular edge, forming a concave notch before widening into a broad septal lobe toward the center of the fossa. S_5 not notched or sinuous, about $^{3}/_{4}$ width of S_{1-4}. S_6 about half width of S_5; S_7, when present, rudimentary. Septal granules large, about 0.1 mm tall.

Fossa deep and narrow, obscuring view of rudimentary columella.

DISCUSSION.—Alcock (1902a) originally identified the holotype of this species as *F. latum* Studer, 1878, based on its admittedly similar corallum and calice shape and size, the two species (specimens) even agreeing in the aberrant S-shaped calice. Squires (1963) later synonymized *F. latum* with *F. rubrum*, but, because the specimen was unavailable to him, Squires (1963:11, 15) did not suggest an identification of *F. latum* reported by Alcock (1902a). He did questionably enter it in the synonymy of *F. rubrum*, despite its occurrence in deep water and far from New Zealand.

Rhizotrochus flabelliformis is remarkably similar to *Monomyces rubrum*, particularly to those flabellate specimens of *M. rubrum* with reinforced bases. The main differences are that *R. flabelliformis* has (1) two rootlet structures that are not fused to the pedicel, (2) a smaller pedicel: 1.2 mm vs. 1.8–2.5 mm of *M. rubrum*, and (3) more septa (*M. rubrum* never has a complete sixth cycle). Another difference concerns the geographic and bathymetric distribution. According to Squires (1963) and Squires and Keyes (1967), *M. rubrum* is endemic to New Zealand from 0–201 m; *R. flabelliformis* is known only from the Philippines from 275 m. If more specimens of *R. flabelliformis* are collected, they should once again be compared to *M. rubrum*, particularly regarding variation in rootlet structure.

Rhizotrochus flabelliformis is easily distinguished from other congeners by its highly compressed corallum, two symmetrical rootlets, and greater number of septa.

ETYMOLOGY.—The species name is from the Latin *flabelliformis* ("a small fan" plus "form"), and alludes to the flabellate shape of the corallum.

MATERIAL EXAMINED.—Holotype.

TYPE.—*Holotype: Siboga* 105, ZMA 1216 (*Flabellum latum* of Alcock, 1902a), Plates 41*k,l*, 42*b,d*. *Type Locality:* 6°08'N, 121°19'E (north of Jolo Island, Sulu Archipelago, Philippines), 275 m.

DISTRIBUTION.—Known only from the type locality.

Gardineria Vaughan, 1907

Haplophyllia Pourtalès, 1868:140 [name preoccupied by *Haplophyllia* Fromentel, 1865].—Duncan, 1885:32–33.

Duncania Pourtalès, 1874:44 [name preoccupied by *Duncania* De Koninck, 1872].—Duncan, 1885:32.

Gardineria Vaughan, 1907:65.—Vaughan and Wells, 1943:227.—Alloiteau, 1952:654.—Wells, 1956:F432.—Zibrowius, 1974:23–24, 26.—Cairns, 1979:160; 1982:50.—Chevalier, 1987:753.

DIAGNOSIS.—Corallum turbinate. Transverse division lacking but parricidal rejuvenescence and secondary lateral attachment via massive rootlet common. Thecal spines lacking; epitheca transversely wrinkled. Exsert septa in three to four cycles, each separated from the smooth calicular edge by a deep notch. Fossa shallow; paliform lobes present, usually before S_2; columella papillose.

DISCUSSION.—*Gardineria* is distinguished from other flabellid genera by its well-developed, papillose columella and presence of paliform lobes (Table 4). Vaughan and Wells (1943) further diagnosed the genus as often having basal rootlets. In the course of examining the species of this genus, I discovered that four of the seven valid species (*G. paradoxa* (Pourtalès, 1874); *G. minor* Wells, 1973; *G. simplex* (Pourtalès, 1878); and *G. philippinensis*, new species) do have one massive irregularly shaped accessory rootlet very similar in shape and position to that of *Monomyces*. Of the three remaining species, type specimens of *G. hawaiiensis* Vaughan, 1907, were not sufficiently well-preserved to allow examination of this structure, and *G. capensis* (Gardiner, 1904) and *G. musorstomica*, new species, appear not to have rootlet structures.

Contrary to the opinions of Zibrowius (1974) and Cairns (1982), I choose to remove *G. antarctica* Gardiner, 1929, from the genus based on its nonepithecate (septothecate), costate wall; nondiscrete paliform lobes; and relatively high (i.e., 5) number of septal cycles. It is more closely allied to the caryophylliid genera *Crispatotrochus*, *Conotrochus*, or *Labyrinthocyathus*. Following a similar reevaluation, *Gardineria capensis* may also be grouped with *G. antarctica*.

Characters of diagnostic value in species identification include symmetry and number of septa; arrangement of paliform lobes; and relative septal exsertness.

TYPE SPECIES.—*Gardineria hawaiiensis* Vaughan, 1907, by original designation.

DISTRIBUTION.—*Recent:* Caribbean, Antarctic, South Africa, Philippines, Hawaiian Islands; 2-700 m. The new species reported herein represent the first records of this genus in the western Pacific. The report of *Gardineria* from the Philippines (Vaughan and Wells, 1943) was probably based on the unpublished observations of specimens of *G. philippinensis* in the NMNH collections.

57. *Gardineria philippinensis*, new species

PLATE 42*a*

DESCRIPTION.—Corallum initially turbinate, rapidly expanding from a pedicel diameter of about 2.0 mm to a cylindrical corallum 11-17 mm in calicular diameter. Calice circular; calicular edge smooth. Holotype 12.6 mm in calicular diameter and 16.4 mm tall; however, the parent corallum from which it originated is 17.0 mm in calicular diameter. Smaller paratype 11.4 mm in calicular diameter and 9.2 mm tall. Corallum white; epitheca marked by numerous very fine transverse growth lines, and heavily encrusted with serpulids, sponges, and foraminifera. Pedicel augmented by a single, large, irregularly shaped lateral rootlet that substantially increases the base of attachment.

Septa hexamerally arranged in four incomplete cycles according to the formula: $S_1>=S_2>S_3>S_4$, only five pairs of rudimentary S_4 present in the holotype (34 total septa). S_{1-2} of holotype equal in size and exsertness, all attaining the columella. S_1 of paratype highly exsert and have straight inner edges that reach the columella. S_2 of paratype smaller than S_1 but also exsert, each bearing a small paliform lobe that joins the columella. S_3 of both specimens half width of S_2 and do not reach columella. S_4 rudimentary when present. Septal notches occur between the upper edges of S_{1-2} and the calice. In the holotype, only those S_3 flanked by pairs of S_4 bear paliform lobes (P_3); the P_2, if ever present, merge indistinguishably with the columella. To summarize, paliform lobes occur before the second septal cycle through the penultimate septal cycle but are sometimes indistinguishable from the columella.

Fossa relatively shallow, containing a columella composed of a field of 12-15 granulated papillae. Columellar elements similar in size and shape to paliform lobes.

DISCUSSION.—Among the five valid species of *Gardineria*, *G. philippinensis* is most similar to *G. paradoxa* (Pourtalès, 1874), known only from 91-700 m from the Caribbean (Cairns, 1979). These two species are similar in corallum shape and size, relative septal exsertness and shape, columella morphology, presence of a lateral rootlet, and tendency for rejuvenescence from the parent corallum. *G. philippinensis* is distinguished solely by its hexameral symmetry and very different geographic occurrence. Even though there are three other species of *Gardineria* having hexameral symmetry (*G. capensis*, *G. minor*, *G. simplex*), *G. philippinensis* is distinguished from them by characteristics of septal shape, corallum size, and/or number of septal cycles.

ETYMOLOGY.—This species is named after its type locality, the Philippine Islands, which, in turn, were named for the crown prince of Spain, later to become King Philip II (1527-1598).

MATERIAL EXAMINED.—Types; ALB-5508 (1) USNM 82004.

TYPES.—*Holotype:* ALB-5217, USNM 82002, Plate 42*a*. *Paratype:* ALB-5217 (1) USNM 82003. The specimen from ALB-5508 is not designated as a paratype because of its fragmentary condition and slightly uncertain identification. *Type Locality:* 13°20′N, 123°14′15″E (Burias Pass, Burias Island, Sibuyan Sea, Philippines), 192 m.

DISTRIBUTION.—Philippines: Burias Island; Iligan Bay, Mindanao; 192-494 m; 11.8°-17.2°C.

58. *Gardineria musorstomica*, new species

PLATE 42*c,e-g*

DESCRIPTION OF HOLOTYPE.—Corallum ceratoid; angle of thecal edges constant at about 34°. Calice circular; calicular edge smooth. Corallum 13.5 mm in calicular diameter, 18.3 mm tall, and 4.8 mm in pedicel diameter. Corallum white; epitheca marked by numerous fine transverse growth lines; no encrusting organisms attached. Accessory rootlets absent.

Septa hexamerally arranged in three cycles according to the formula: $S_1>>S_2>S_3$. S_1 small and not exsert; in fact, upper edges of S_1 terminate 2-3 mm below calicular edge and do not have septal notches. Inner edges of S_1 straight, merging with columella. S_2 about $^1/_5$ width and $^1/_2$ thickness of S_1, each bearing a robust, tuberculate paliform lobe that joins the septum to the columella. S_3 smaller than S_2 and even more recessed from the calicular edge, but, at the level of the columella S_3 are about the same width as the S_2 (without its paliform lobe). Inner margins of all septa entire. Septal faces covered by very low granules not aligned in rows.

Fossa relatively deep, 5 mm in the holotype. Columella composed of 3 tuberculate elements, which are surrounded by 6 equally sized and shaped P_2.

DISCUSSION.—*Gardineria musorstomica* is easily distinguished from the other valid congeners by its ceratoid corallum, thick pedicel with no accessory rootlets, and deeply recessed septa. It is so distinctive that it may not belong to this genus, but it is undoubtedly most closely allied to *Gardineria* based on its papillose columella and paliform lobes before the penultimate septal cycle.

ETYMOLOGY.—This species is named in honor of the French MUSORSTOM Philippine cruises.

MATERIAL EXAMINED.—Holotype.

TYPE.—*Holotype:* MUSORSTOM 2-32, MNHNP. *Type Locality:* 13°40.5'N, 120°53.9'E (Balayan Bay, Luzon, Philippines), 192-220 m.

DISTRIBUTION.—Known only from the type locality.

Distribution

As noted in the Epigraph (Alcock, 1902a; Vaughan and Wells, 1943) of this revision, the East Indies, more specifically Indonesia and the Sulu Sea, appear to be the center of deep-water coral species diversity. As examples of the richness of this area, Alcock (1902a) cited *Siboga* 95 (Sulu Sea, Sulu Archipelago, Philippines, 521 m), from which 22 ahermatypic species from 14 genera were collected. As another example, Vaughan and Wells (1943) cited *Albatross* 5133 (Sulu Sea, off Mindanao, 69 m), from which 12 ahermatypic species from 11 genera were collected. Vaughan and Wells (1943) estimated that there are 152 species and varieties of ahermatypic coral in the East Indies, 51 of which occurred in the Philippines. In this study alone, which reviews only half of the ahermatypic species known from the Philippines, 53 species are reported from the Philippines and 110 species are estimated to occur in the island group. This further supports the claim that the Indonesian-Philippine region has the highest species diversity of deep-water corals of any place in the world, the second highest diversity probably occurring in the Antilles of the Caribbean (Cairns, 1979).

Zoogeographic conclusions based on deep-water coral distributions are always tentative for a number of reasons: e.g., the number of collection sites is usually low compared to the vast geographic area; the taxonomy of the species may be confused, especially if not all previous records have been verified; collections from adjacent regions may be uneven; and, in this case, only half of the ahermatypic species are being considered. Notwithstanding these disclaimers, some remarks follow.

Of the 53 species of ahermatypic Scleractinia occurring in the Philippine Islands that pertain to this revision (Table 7), the highest diversity occurs off the western and southern coasts of Luzon (36 species), followed closely by 34 species known from the much smaller geographic area of the Sulu Archipelago. Sixteen species occur off Mindanao, and only five species are known from the Sulu Sea off Palawan. Thirteen species are as yet known only from the Philippine Islands (Table 7); however, it is premature to conclude that any of these species are endemic to this island group. Except for Davao Gulf, no ahermatypic corals have been reported from the eastern oceanic coasts of the Philippines, but this is probably largely due to meager collecting effort on these coasts.

Not surprisingly, 16-17 of the 53 Philippine species (30%-32%) are also known from the northwestern South China Sea in the vicinity of Hong Kong and the Formosa Strait, and 19-20 species (36%-38%) are known from off Japan, primarily off Kyūshū. It may seem ironic that Japan, which is farther away from the Philippines than Hong Kong, has a higher number of shared species, but this is probably caused by uneven collecting effort: the South China Sea records are based on only a few *Albatross* stations, whereas the Japanese records are based on extensive collections, followed by the major systematic revisions of Yabe and Eguchi (1942a,b).

The geographic area with the highest species affinity with the Philippines is the Indonesian region directly to the south, with which it probably forms a natural zoogegraphic unit. Twenty-five to 27 species (47%-51%) of the 53 Philippine species are shared with Indonesia, a number that will undoubtedly increase when the Indonesian fauna is better known (e.g., examination of the specimens from the *Snellius* expeditions). Only 5-8 Philippine species (9%-15%) are shared with the Australian/New Zealand region south of Indonesia.

To the west of Indonesia, 13-14 of the 53 Philippine species are also found in the Indian Ocean: 7 in the eastern Indian Ocean and 10-11 in the western Indian Ocean. The higher number of shared species from the more remote western Indian Ocean is probably also a result of uneven collecting effort. Alcock (1902a:1) lamented the fact that Indonesia and the Indian Ocean had less than 10% of their species in common, but now that both faunas are better known, that percentage is much higher: 13-14/53, or 25%-26%, and likely to increase.

The ahermatypic fauna of the eastern and central Pacific (except for the Hawaiian Islands) is poorly known. However, thanks to the reports of Moseley (1881) and Wells (1977, 1984) from mid-Pacific islands, at least 11 of the 53 Philippine species (21%) are known to be shared with this vast region.

Three of the 53 Philippine species (6%) are also known from the Atlantic, having broad circumtropical distributions: *Peponocyathus australiensis, Peponocyathus folliculus,* and *Guynia annulata.*

To summarize, the nucleus of 53 species known from the Philippines is most diverse in the Sulu Sea, especially the Sulu Archipelago. Away from the Sulu Sea the number of species held in common with other areas quickly attenuates, most noticeable longitudinally, i.e., to the east (Pacific Ocean) and west (Indian Ocean). Latitudinally, the Philippines share a relatively high percentage of their species with the seas off China (30%-32%) and Japan (36%-38%) but has its greatest affinity (47%-51%) with Indonesia to the south.

Vaughan and Wells (1943:83) analyzed the bathymetric distribution of the 51 ahermatypic species then known from the

TABLE 7.—Geographic distribution and bathymetric ranges of species described in this revision. (Key to areas: 1 = off Luzon, 2 = central Philippine Islands, 3 = off Mindanao, 4 = Sulu Archipelago, 5 = Palawan, 6 = off Japan, 7 = South China Sea off mainland, 8 = Indonesia, 9 = Australia/New Zealand, 10 = eastern Indian Ocean, 11 = western Indian Ocean, 12 = Atlantic Ocean, and 13 = eastern and central Pacific Ocean).

Species	Philippines					Pacific				Indian Ocean		Other areas		Bathymetric range (m)	Temperature range (°C)
	1	2	3	4	5	6	7	8	9	10	11	12	13		
*1. _F. (F.) stephanus_	X	X	X		X			X		X	X			245–1977	3.5–15.0
2. _F. (F.) paliferus_		X		X		†		X	?		X		†	90–522	11.6–13.7
3. _F. (B.) sibogae_				X				X						411–1914	
!*4. _F. (B.) granulosus_	X	X		X										390–567	6.1–10.8
*5. _F. (B.) variegatus_	X	X					X						†	187–333	13.1–15.3
*6. _F. (B.) turbinolioides_				X			X							622–635	
!*7. _Leptopenus_ sp. A				X										871	5.1
8. _L. formosissima_	X	X		X		X		X	?				X	97–470	9.3–21.7
!9. _R. squiresi_		X	X											622–929	9.7–11.6
10. _R. niphada_	X			X		X								424–715	8.2–11.9
11. _S. fungulus_				X		X	X				?			15–635	6.7–21.2
*12. _S. neglecta_	X	X		X	X			X					†?	49–555	
*13. _N. venustus_	X			X		†	X	X					†?	70–555	11.1–14.1
14. _N. conicus_	X	X	X	X		X		X						34–923	6.7–17.5
15. _P. australiensis_	X	X	X	X		X	X	X	X†		X	X	X	44–635	6.2–17.3
*16. _P. folliculus_	X			X		X	X		†			X		50–582	6.8–17.2
*17. _T. lessoni_	X	X	X	X			X	X			X			68–421	11.7–26.3
18. _T. pileus_	X	X	X	X		X	X		X	X	X			123–522	10.3–15.5
*19. _I. kikutii_	X	X		X		X	X		?					143–645	6.7–11.6
*20. _T. multilobatus_	X			X			X							130–507	10.3–17.2
*21. _S. (S.) hancocki_				X			X						†	18–274	12.4–14.1
!*22. _E. laticostatus_			X											46–70	
*23. _G. annulata_	X							X			X	X	X	28–653	
‡24. _T. irregularis_							X							161	
‡25. _F. (F.) pavoninum_						X	X						X	223–271	14.2
26. _F. (F.) magnificum_	X	X		X		X				X				291–700	6.7–13.9
27. _F. (F.) patens_	X			X		X	X	X						256–439	9.1–12.4
28. _F. (F.) lamellulosum_	X	X	X			?		X						198–402	10.1–15.5
29. _F. (F.) politum_	X	X	X	X		X	X	X						40–402	9.6–15.5
!30. _F. (F.) dens_				X										522	
31. _F. (U.) deludens_	X	X	X			X				X	X			106–1035	4.3–18.4
32. _F. (U.) japonicum_	X	X	X	X		X		?						365–550	8.0–12.2
!*33. _F. (U.) marenzelleri_	X													247–315	
*34. _F. (U.) messum_	X			X				X						368–949	5.1–10.2
!*35. _F. (U.) sexcostatum_	X													772	5.7
*36. _F. (U.) conuis_					X								X	1994–2021	9.7
37. _T. aculeatum_		X		X			?	†						11–33	
!38. _T. crassum_	X													?	
*39. _T. spheniscus_	X					X		X	X					3–106	
40. _T. stokesi_	X							†		X				12–256	
‡41. _T. bairdi_								?						?	
‡42. _T. profundum_						?	X							?	
43. _T. irregulare_		X		X				X						11–42	
!*44. _T. incrustatum_	X		X											37–315	
45. _T. cumingi_	X							X						46–55	
*46. _T. formosum_	X	X	X	X			X	X						37–933	5.1–17.8
*47. _T. candeanum_	X	X				X	X	X						70–249	15.2–17.8
*48. _T. pusillum_	X	X		X										143–146	14.7
49. _T. paripavoninum_	X	X		X				X			X			476–1163	4.0–11.8
‡50. _T. carinatum_						†	X	†?						223–274	12.0–15.3
!51. _B. nutrix_		X												11–18	
52. _P. laevis_	X		X	X			X	?	X	X				22–69	
53. _J. insignis_			X	X	X	X		X			X		X	46–825	
*54. _P. scaphula_	X			X				X						476–1628	3.4–7.6
*55. _R. typus_				X	X	X		X		X	X		X	20–1048	7.4–13.2
!56. _R. flabelliformis_				X										275	
!*57. _G. philippinensis_		X	X											192–494	11.8–17.2
!*58. _G. musorstomica_	X													192–220	
Totals for 58 species	36	25	16	34	5	21–23	20–21	26–29	5–8	7	10–11	3	12		
Totals for 53 Philippine species	36	25	16	34	5	19–20	16–17	25–27	5–8	7	10–11	3	11		

* New record for the Philippine Islands (27 species).

! Thus far known only from the Philippine Islands (13 species).

† Fossil record.

‡ Thus far not known from the Philippine Islands (5 species).

? Questionable record (see pertinent text).

Philippines, noting that the greatest diversity (27/51 species) occurred between 200-300 fathoms (366–549 m). This kind of analysis was not performed on the species in this revision, but depth ranges are given for each species in Table 7. Some bathymetric trends are apparent from the list for certain taxonomic groups. For instance, species of *Flabellum (Ulocyathus)* are, in general, found deeper than their counterparts of *Flabellum (Flabellum):* averages of 800 m vs. 350 m, respectively. The deepest recorded scleractinian from the Philippines is *Flabellum (Ulocyathus) conuis* at 2021 m. On the other hand, the previously synonymous and morphologically similar *Truncatoflabellum* is characteristic of much shallower depths: as shallow as 3 m and, except for *T. paripavoninum*, most common between 50-150 m (continental shelf). Species of both fungiacyathids and micrabaciids are found in moderately deep water on the upper continental slope, averaging 650 and 520 m, respectively. The bathymetric range of the Turbinoliinae ranges from the upper continental shelf (18 m) to the upper continental slope (645 m), but are most common between 200 and 500 m.

Appendix

Station List

Station	Latitude (°N)	Longitude (°E)	Depth (m)	Date	Bottom temp. (°C)
	U.S. Fish Commission Steamer *Albatross* (ALB)				
3698	35°08′	139°10′	280	5 May 1900	
3999	Ukula Point, Kauai, Hawaiian Islands		13-271	16 Jun 1902	
4101	Pailolo Channel, Hawaiian Islands		223-262	23 Jul 1902	
4911	31°38′30″	129°19′00″	715	12 Aug 1906	9.5
4915	31°33′00″	129°25′30″	783	12 Aug	
4960	32°34′00″	132°21′45″	1057	23 Aug	
5054	34°52′45″	138°42′20″	516	12 Oct	
5083	34°04′20″	137°57′30″	1141	20 Oct	3.4
5086	35°08′15″	139°20′00″	534	23 Oct	
5091	35°04′10″	139°38′12″	360	26 Oct	8.7
5092	35°04′50″	139°38′18″	128	26 Oct	13.5
5094	35°04′42″	139°38′20″	161	26 Oct	12.7
5106	14°23′55″	120°32′33″	68	9 Jan 1908	
5107	14°24′30″	120°33′40″	51	9 Jan	
5110	13°59′20″	120°15′45″	247	15 Jan	15.0
5113	13°51′30″	120°50′30″	291	17 Jan	
5116	13°41′00″	120°47′05″	366	19 Jan	10.1
5117	13°52′22″	120°46′22″	216	21 Jan	
5118	13°48′45″	120°41′51″	291	21 Jan	
5124	12°52′00″	121°48′30″	514	2 Feb	
5133	7°41′00″	122°01′00″	70	6 Feb	
5134	6°44′45″	121°48′00″	46	7 Feb	
5136	6°04′20″	120°59′20″	40	14 Feb	
5137	6°04′25″	120°58′30″	37	14 Feb	
5144	6°05′50″	121°02′15″	34	15 Feb	
5145	6°04′30″	120°59′30″	42	15 Feb	
5146	5°46′40″	120°48′50″	44	16 Feb	
5152	5°22′55″	120°15′45″	62	18 Feb	
5153	5°18′10″	120°02′55″	90	19 Feb	
5156	5°12′50″	119°55′55″	33	21 Feb	
5161	5°10′15″	119°53′00″	29	22 Feb	
5162	5°10′00″	119°47′30″	421	22 Feb	11.6
5164	5°01′40″	119°52′20″	33	24 Feb	
5172	6°03′15″	120°35′30″	581	5 Mar	
5173	6°02′55″	120°53′00″	340	5 Mar	
5177	13°35′00″	120°54′36″	476	24 Mar	
5178	12°43′00″	122°06′15″	134-143	25 Mar	
5179	12°38′15″	122°12′30″	68	25 Mar	24.3
5197	9°52′30″	123°40′45″	318	9 Apr	12.4
5198	9°40′50″	123°39′45″	402	9 Apr	12.2
5202	10°12′00″	125°04′10″	918	10 Apr	
5212	12°04′15″	124°04′36″	198	20 Apr	15.5
5213	12°15′00″	123°57′30″	146	20 Apr	
5217	13°20′00″	123°14′15″	192	22 Apr	17.3
5221	13°38′15″	121°48′15″	353	24 Apr	11.3
5222	13°38′30″	121°42′45″	357	24 Apr	11.6
5249	7°06′06″	125°40′08″	42	18 May	

Station	Latitude (°N)	Longitude (°E)	Depth (m)	Date	Bottom temp. (°C)
	U.S. Fish Commission Steamer *Albatross* (ALB).—Continued.				
5250	7°05′07″	125°39′45″	42	18 May	
5251	7°05′12″	125°39′35″	37	18 May	
5253	7°04′48″	125°39′38″	51	18 May	
5255	7°03′00″	125°39′00″	183	18 May	
5256	7°21′45″	124°07′15″	289	22 May	
5260	12°25′35″	121°31′35″	428	3 Jun	10.8
5265	13°41′15″	120°00′50″	247	6 Jun	
5268	13°42′00″	120°57′15″	311	8 Jun	
5272	14°00′00″	122°20′30″	216	14 Jul	14.1
5273	13°58′45″	120°35′21″	208	14 Jul	
5277	13°56′55″	120°13′45″	146	17 Jul	14.8
5278	14°00′10″	120°17′15″	186	17 Jul	15.3
5280	13°55′20″	120°25′55″	353	17 Jul	9.8
5281	13°52′45″	120°25′00″	368	18 Jul	10.2
5283	13°48′30″	120°28′40″	512	18 Jul	8.2
5284	13°42′05″	120°30′45″	772	20 Jul	5.7
5285	13°39′36″	120°32′55″	497	20 Jul	8.1
5289	13°41′50″	120°58′30″	314	22 Jul	
5291	13°29′40″	121°00′25″	302	23 Jul	10.8
5298	13°43′25″	120°57′40″	256	24 Jul	
5301	20°37′00″	115°43′00″	380	8 Aug	10.3
5311	21°33′00″	116°15′00″	161	4 Nov	
5312	21°30′00″	116°32′00″	256	4 Nov	14.2
5313	21°30′00″	116°43′00″	274	4 Nov	12.0
5314	21°41′00″	116°46′00″	223	5 Nov	15.3
5315	21°40′00″	116°58′00″	271	5 Nov	12.4
5317	21°36′00″	117°27′00″	421	5 Nov	10.3
5318	21°32′00″	117°46′00″	622	5 Nov	
5348	10°57′45″	118°37′15″	686	27 Dec	13.6
5349	10°54′00″	118°26′20″	1335	27 Dec	4.8
5357	8°06′00″	117°17′10″	124	5 Jan 1909	
5369	13°48′00″	121°43′00″	194	24 Feb	
5371	13°49′40″	121°40′15″	152	24 Feb	
5372	13°49′12″	121°36′09″	274	24 Feb	
5373	13°40′00″	121°31′10″	618	2 Mar	11.0
5374	13°46′45″	121°35′08″	347	2 Mar	
5376	13°42′50″	121°51′30″	165	2 Mar	
5380	13°02′45″	122°29′00″	?	4 Mar	
5381	13°14′15″	122°45′30″	234	6 Mar	
5387	12°54′40″	123°20′30″	382	11 Mar	11.3
5388	12°51′30″	123°26′15″	413	11 Mar	10.8
5391	12°13′15″	124°05′03″	216	13 Mar	
5392	12°12′35″	124°02′48″	247	13 Mar	
5393	12°03′30″	124°03′36″	249	13 Mar	
5398	11°35′12″	124°13′48″	208	15 Mar	
5403	11°10′00″	124°17′15″	333	16 Mar	13.2
5408	10°40′15″	124°15′00″	291	18 Mar	13.0
5411	10°10′30″	123°51′15″	265	23 Mar	12.9
5412	10°09′15″	123°52′00″	296	23 Mar	12.7
5417	10°10′00″	123°53′15″	302	25 Mar	12.4
5418	10°08′50″	123°52′30″	291	25 Mar	
5419	9°58′30″	123°46′00″	320	25 Mar	12.5
5423	9°38′30″	121°11′00″	929	31 Mar	9.9
5424	9°37′50″	121°12′37″	622	31 Mar	10.2
5425	9°37′45″	121°11′00″	907	31 Mar	9.7
5426	9°12′00″	118°28′00″	49	3 Apr	
5428	9°13′00″	118°51′15″	2021	3 Apr	9.8
5445	12°44′42″	124°59′50″	699	3 Jun	6.8
5453	13°12′00″	123°49′18″	267	7 Jun	
5454	13°12′00″	123°50′30″	280	7 Jun	

Station	Latitude (°N)	Longitude (°E)	Depth (m)	Date	Bottom temp. (°C)
U.S. Fish Commission Steamer *Albatross* (ALB).—Continued.					
5483	10°27′30″	125°19′15″	135	30 Jul	
5484	10°28′00″	125°20′00″	125	30 Jul	
5505	8°37′15″	124°36′00″	402	5 Aug	
5506	8°40′00″	124°31′45″	479	5 Aug	11.8
5508	8°17′24″	124°11′42″	494	5 Aug	
5510	8°16′00″	124°03′50″	774	7 Aug	11.7
5513	8°16′45″	124°06′48″	923	7 Aug	11.6
5523	8°48′44″	123°27′35″	?	10 Aug	
5527	9°22′30″	123°42′40″	717	11 Aug	11.8
5528	9°24′45″	123°39′15″	620	11 Aug	
5529	9°23′45″	123°39′30″	807	11 Aug	11.7
5535	9°20′30″	123°23′45″	567	19 Aug	11.8
5536	9°15′45″	123°22′00″	510	19 Aug	11.9
5537	9°11′00″	123°23′00″	464	19 Aug	11.9
5538	9°08′15″	123°23′20″	468	19 Aug	11.8
5541	8°49′38″	123°34′30″	385	20 Aug	11.8
5564	5°50′00″	120°31′00″	432	21 Sep	11.3
5565	5°51′42″	120°30′30″	444	21 Sep	
5567	5°48′00″	120°33′45″	490	21 Sep	11.1
5569	5°33′15″	120°15′30″	555	22 Sep	11.3
5576	5°25′56″	120°03′39″	507	23 Sep	11.8
5577	5°20′36″	119°58′51″	439	23 Sep	12.4
5579	4°54′15″	119°09′52″	320	25 Sep	12.9
5580	4°52′45″	119°06′45″	296	25 Sep	13.2
5582	4°19′54″	118°58′38″	1624	26 Sep	3.5
5584	4°17′40″	118°57′42″	534	27 Sep	6.8
5585	4°07′00″	118°49′54″	871	28 Sep	5.1
5586	4°06′50″	118°47′20″	616	28 Sep	6.7
5587	4°10′35″	118°37′12″	759	28 Sep	5.7
5589	4°12′10″	118°38′08″	476	29 Sep	7.6
5590	4°10′50″	118°39′35″	567	29 Sep	6.8
5591	4°11′48″	118°38′20″	475	29 Sep	
5592	4°12′44″	118°27′44″	558	29 Sep	6.3
5593	4°02′40″	118°11′20″	70	29 Sep	
5605	0°21′33″	121°34′10″	1183	16 Nov	
5618	0°37′00″	127°15′00″	764	27 Nov	
5619	0°35′00″	127°14′40″	798	27 Nov	
5630	0°56′30″S	128°05′00″	1040	2 Dec	
5647	5°34′00″S	122°18′15″	949	16 Dec	
5648	5°35′00″S	122°20′00″	1022	16 Dec	4.0
5656	3°17′40″S	120°36′45″	885	19 Dec	5.1
5658	3°32′40″S	120°31′30″	933	19 Dec	5.1
5668	2°28′15″S	118°49′00″	1648	29 Dec	3.4
5670	1°19′00″S	118°43′00″	2159	30 Dec	3.4
R/V *Anton Bruun*					
1-28	11°49′N	92°53′E	87	27 Mar 1962	26.0
7-371	24°42′S	35°23′E	190	18 Aug 1964	15.6
7-372	24°48′S	34°59′E	45.7	19 Aug 1964	21.6
9-453	11°11′N	51°14′E	47-49	17 Dec 1964	20.2
CH-5	2°38′S	40°43′E	155		
USNS *Eltanin*					
598	58°13′S	25°50′W	2384-2416	3 May 1963	
1545	61°04′S	39°55′W	2355-2897	11 Feb 1966	
1926	74°53′S	175°10′W	2117-2150	27 Jan 1967	
2002	72°18′S	177°35′E	2005-2010	11 Jan 1968	
2108	74°55′S	174°12′W	2022-2060	7 Feb 1968	

Station	Latitude (°N)	Longitude (°E)	Depth (m)	Date	Bottom temp. (°C)
		MUSORSTOM			
1-64	14°00.5′N	120°16.3′E	194-195	27 Mar 1976	
2-11	14°00.4′	120°19.7′	194-196	2 Nov 1980	
2-25	13°39′	120°43′	520-550	23 Nov 1980	
2-32	13°40.5′	120°53.9′	192-220	24 Nov 1980	
2-33	13°32.3′	121°07.5′	130-137	24 Nov 1980	
2-66	14°00.6′	120°20.3′	190-204	29 Nov 1980	
3-88	14°00.5′	120°17.4′	183-187	31 May 1985	
3-91	14°01.1′	120°17.8′	190-203	31 May 1985	
3-96	14°00.3′	120°17.3′	190-194	1 Jun 1985	
3-102	14°00.8′	120°17.8′	192	1 Jun 1985	
3-108	14°01.1′	120°17.9′	188-195	2 Jun 1985	
3-109	14°00.2′	120°17.9′	188-190	2 Jun 1985	
3-131	11°36.6′	121°43.0′	120-122	5 Jun 1985	
3-143	11°28.3′	124°11.6′	205-214	7 Jun 1985	
		Cordin			
2-235	0°04.6′S	119°48.4′E	1110	Nov 1980	
		Alpha Helix			
79-M-14	11°33′S	135°53′E	22	1979	
		Kimbla			
3(2634)	23°33.7′S	152°37′E	338-348	17 Nov 1977	
		Marion Dufresne			
27-4-CP06	8°11′N	79°03′E	1035	28 Jul 1981	
27-4-CP07	8°29′N	79°19′E	1095	28 Jul 1981	
32-128	20°51′S	55°36′E	280-340	2 Sep 1982	
		Nimbus			
12	26°32′S	153°45′E	?	?	
		Te Vega			
1-54	1°08.6′N	128°01′E	46-55	?	

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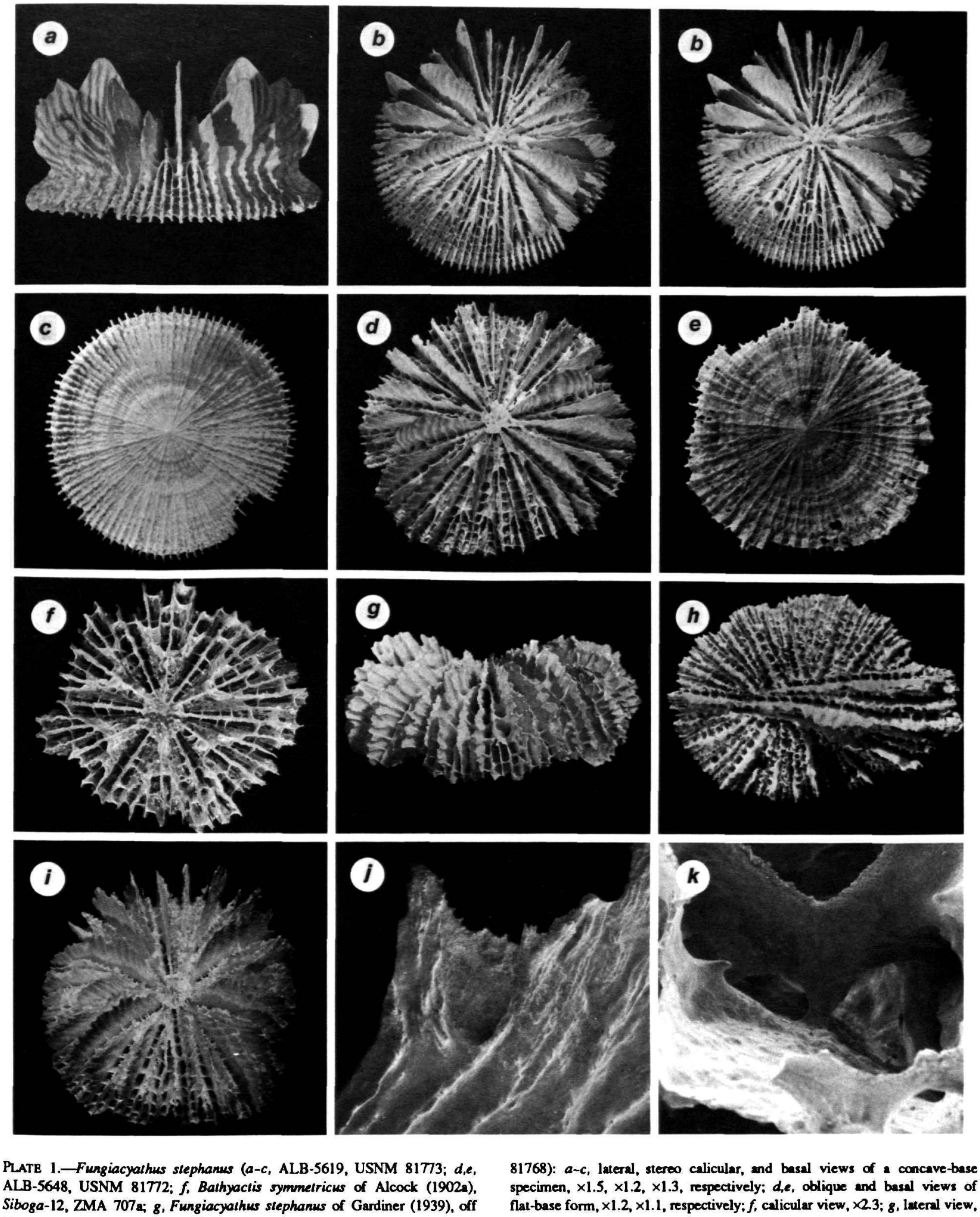

PLATE 1.—*Fungiacyathus stephanus* (*a–c*, ALB-5619, USNM 81773; *d,e*, ALB-5648, USNM 81772; *f*, *Bathyactis symmetricus* of Alcock (1902a), *Siboga*-12, ZMA 707a; *g*, *Fungiacyathus stephanus* of Gardiner (1939), off Natal, BM 1939.7.20.121; *h*, ALB-5198, USNM 81777; *i*, *Bathyactis stephanus* of Alcock (1902), *Siboga*-88, ZMA 705; *j,k*, ALB-5110, USNM 81768): *a–c*, lateral, stereo calicular, and basal views of a concave-base specimen, ×1.5, ×1.2, ×1.3, respectively; *d,e*, oblique and basal views of flat-base form, ×1.2, ×1.1, respectively; *f*, calicular view, ×2.3; *g*, lateral view, ×1.8; *h*, calicular view of regenerating corallum, ×2.8; *i*, oblique calicular view, ×1.5; *j*, P_2, ×18; *k*, Y-shaped trabecular plate joining septa, ×60.

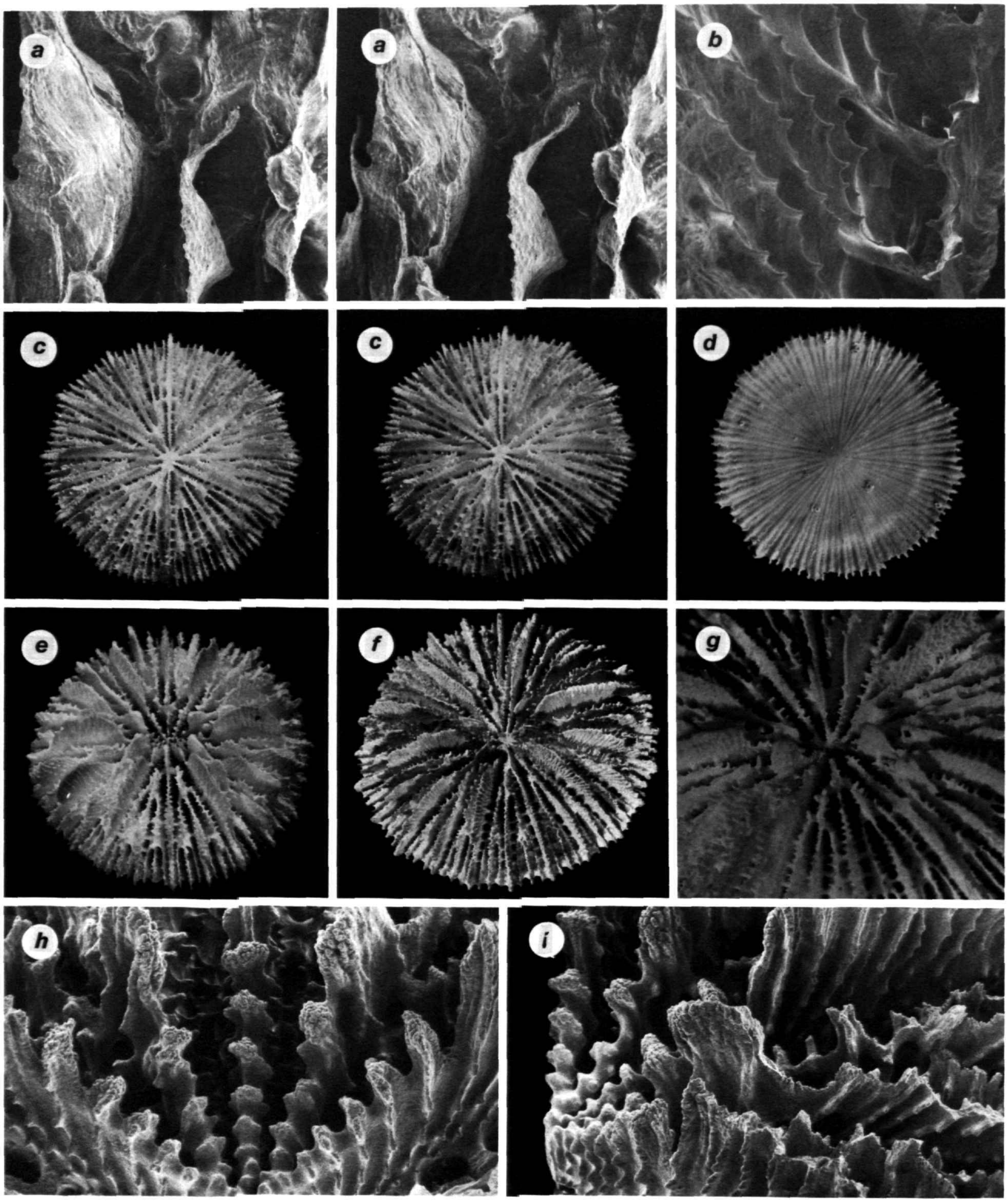

PLATE 2.—*Fungiacyathus stephanus* (*a*, ALB-5648, USNM 81770; *b*, ALB-5110, USNM 81768): *a*, edge of base showing tall, thin costal ridges, ×16 (stereo pair); *b*, oblique view of septal face showing dentate trabeculae and synapticular plates, ×18.9. *Fungiacyathus paliferus* (*c,d,g*, syntype, *Siboga*-153, ZMA 1171; *e*, specimen reported by Yabe and Eguchi (1942a), sta 412, TIUS 58913; *f,h,i*, MD32-128, MNHNP): *c,d*, calicular and basal views of largest syntype, both ×2.7 (*c* is a stereo pair); *e*, oblique calicular view illustrating pali, ×3.1; *f*, oblique calicular view, ×2.6; *g*, higher magnification of syntype illustrated in *c,d*, showing pali, ×5.2; *h*, two half-systems viewed obliquely, ×25; *i*, lateral view of specimen illustrated in *h* accentuating P_2, ×21.

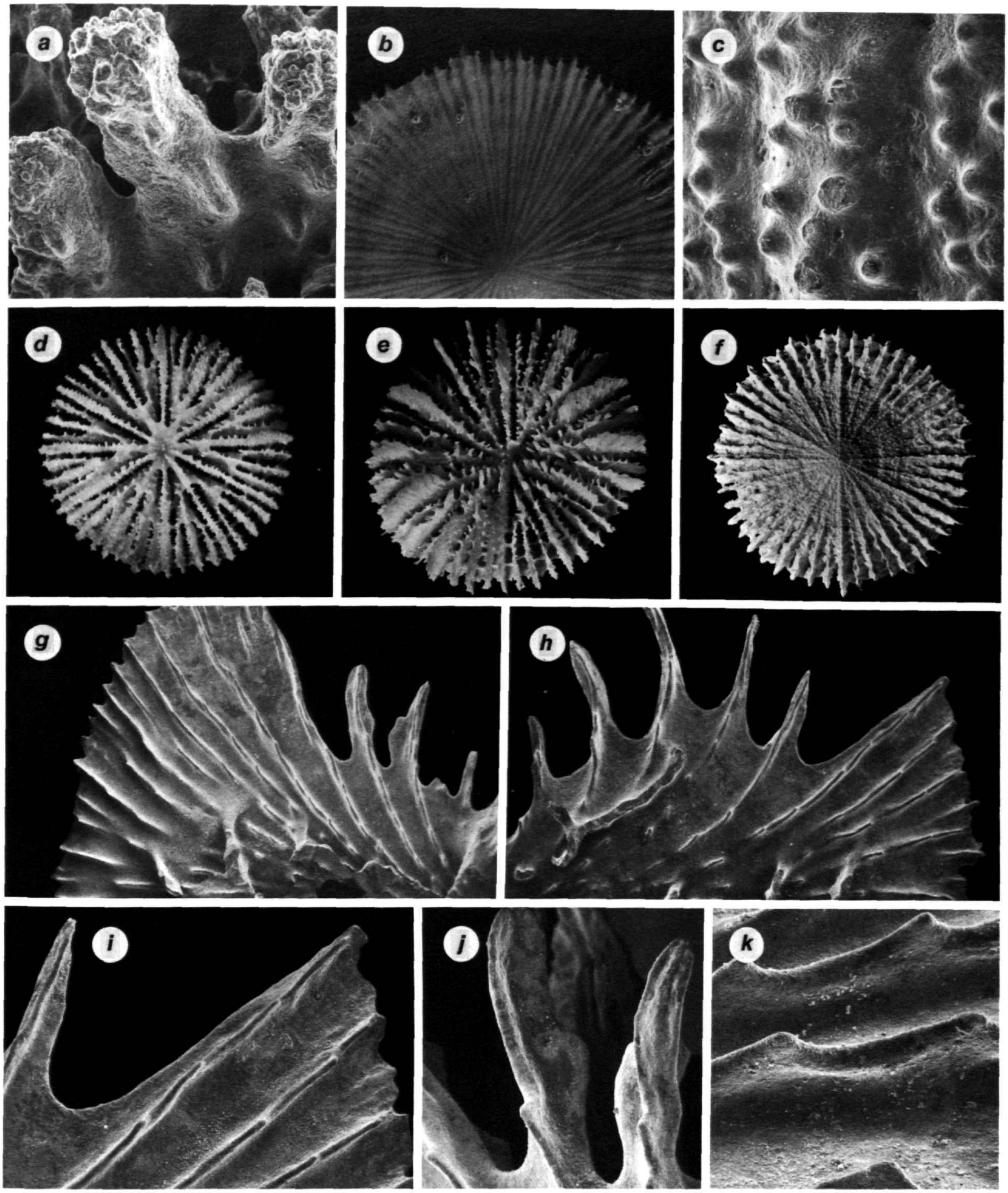

PLATE 3.—*Fungiacyathus paliferus* (*a*, ALB-5178, USNM 81759; *b*, syntype, *Siboga*-153, ZMA 1171; *c*, MD32-128, MNHNP): *a*, compound inner trabecular spines, ×81; *b,c*, granular base, ×45, ×79, respectively. *Fungiacyathus sibogae* (*d*, lectotype, *Siboga*-175, ZMA 1173; *e,f*, ALB-5619, USNM 81767; *g-k*, ALB-5618, USNM 81766): *d*, calicular view, ×3.5; *e,f*, oblique calicular and basal views of two specimens, ×3.7; *g*, lateral view of an S_1, illustrating outer septal lobe and inner trabecular spines, ×12.8; *h*, lateral view of an S_1 showing inner trabecular spines and outer septal lobe, ×17; *i*, outer lobe of S_1, ×34; *j*, inner trabecular lobes of an S_1, ×37; *k*, dentate septal face, ×66.

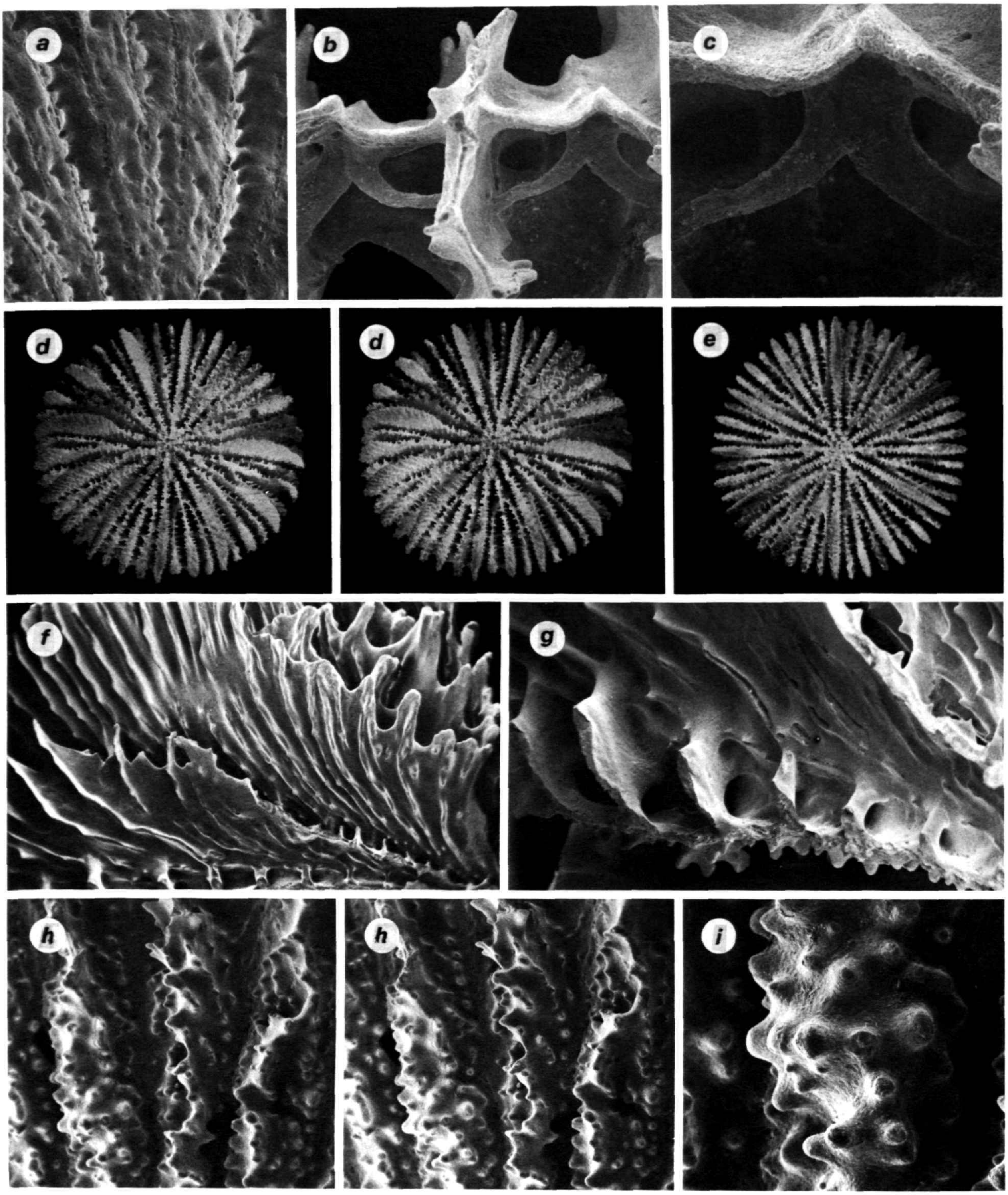

PLATE 4.—*Fungiacyathus sibogae* (*a–c*, ALB-5618, USNM 81766): ***a***, dentate costae, ×22.5; ***b,c***, Y-shaped synapticular plates, ×44, ×88, respectively. *Fungiacyathus granulosus* (*d,e*, holotype; *f–i*, paratype from ALB-5592, USNM 81753): ***d,e***, calicular views of holotype, ×2.2, ×2.0, respectively (*d* is a stereo pair); ***f***, lateral view of several septa, ×8.9; ***g***, view of a series of synapticular plates (columella to right), ×18.5; ***h***, stereo view of costae near outer edge of calice, ×14.5; ***i***, granular costa, ×42.

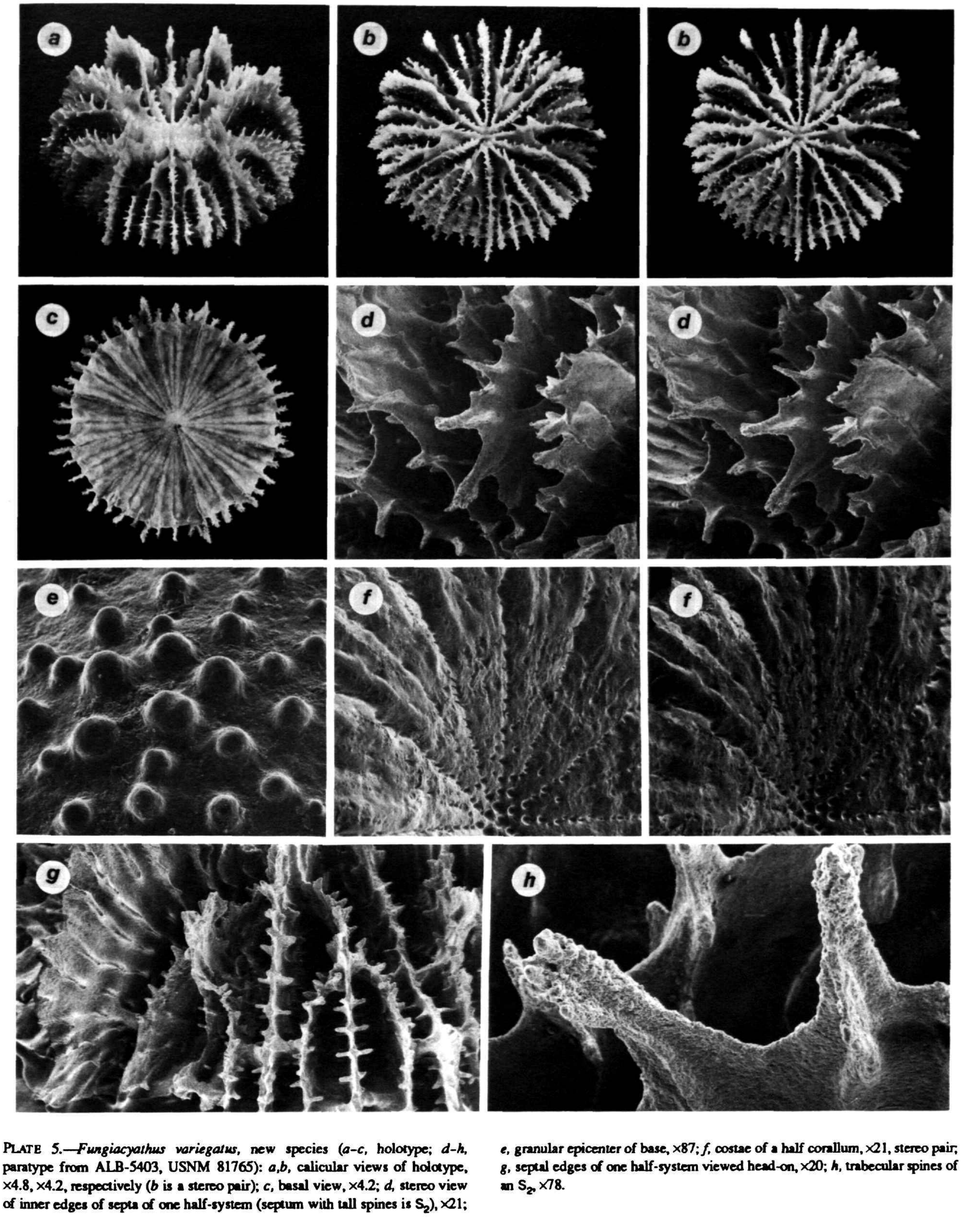

PLATE 5.—*Fungiacyathus variegatus*, new species (*a–c*, holotype; *d–h*, paratype from ALB-5403, USNM 81765): *a,b*, calicular views of holotype, ×4.8, ×4.2, respectively (*b* is a stereo pair); *c*, basal view, ×4.2; *d*, stereo view of inner edges of septa of one half-system (septum with tall spines is S_2), ×21; *e*, granular epicenter of base, ×87; *f*, costae of a half corallum, ×21, stereo pair; *g*, septal edges of one half-system viewed head-on, ×20; *h*, trabecular spines of an S_2, ×78.

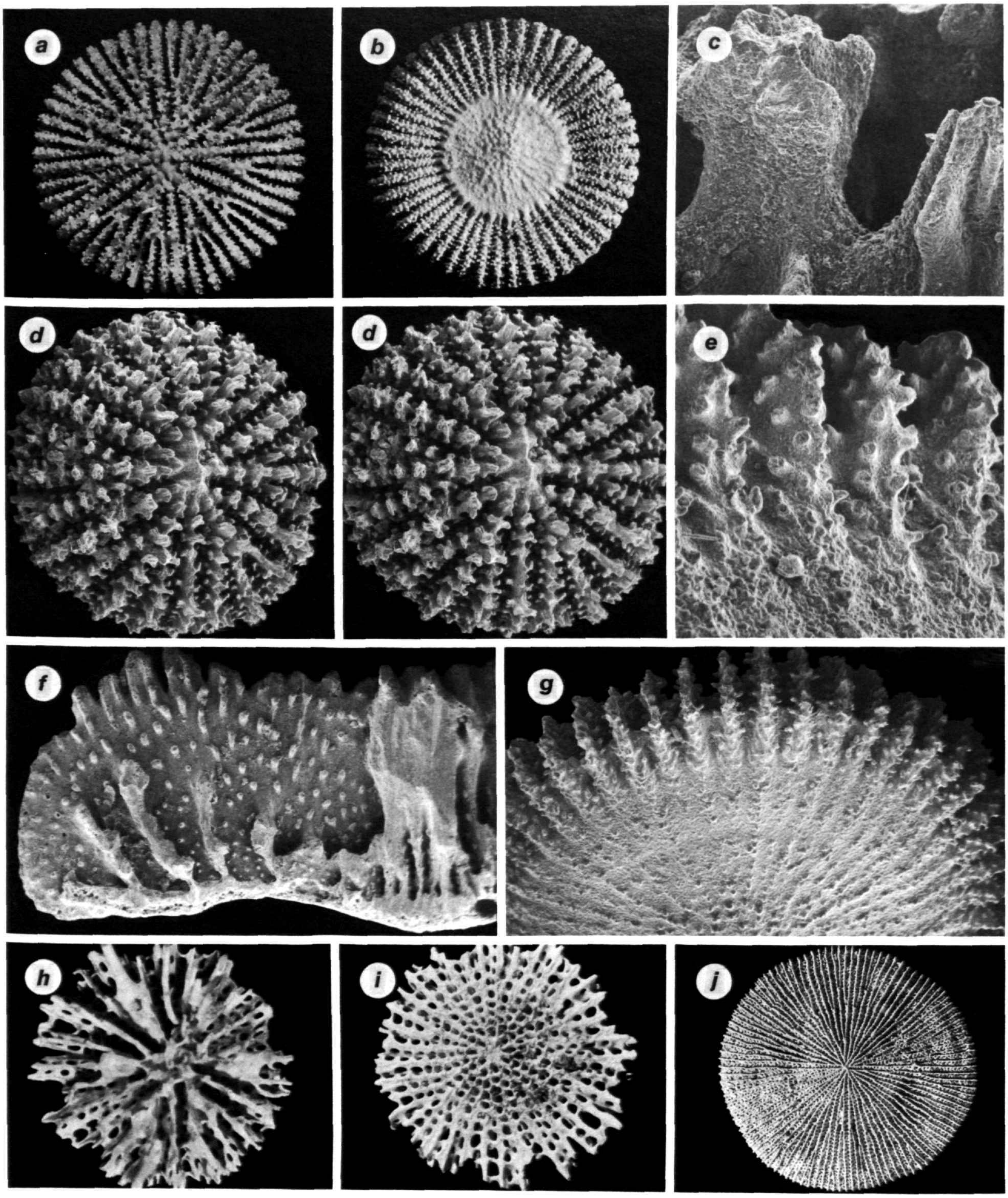

PLATE 6.—*Fungiacyathus turbinolioides*, new species (*a*, holotype; *b*, paratype from ALB-5318, USNM 81749; *c-g*, paratype from ALB-5586, USNM 81748): *a,b*, calicular and basal views of holotype and a paratype, ×6.0, ×6.2, respectively; *c*, compound trabecular spine, ×114; *d*, stereo calicular view of a paratype, ×20; *e,g*, views of costal edges ×51, ×16, respectively; *f*, lateral view of S_1 showing trabecular spines and synapticular plates, ×16. *Leptopenus* sp.: *h,i*, *Galathea*-453, ZMC, calicular and basal views of specimen reported by Squires (1965), both ×10.2. *Letepsammia formosissima*: *j*, base of syntype from *Challenger*-209, BM 1880.11.25.156, × 2.2.

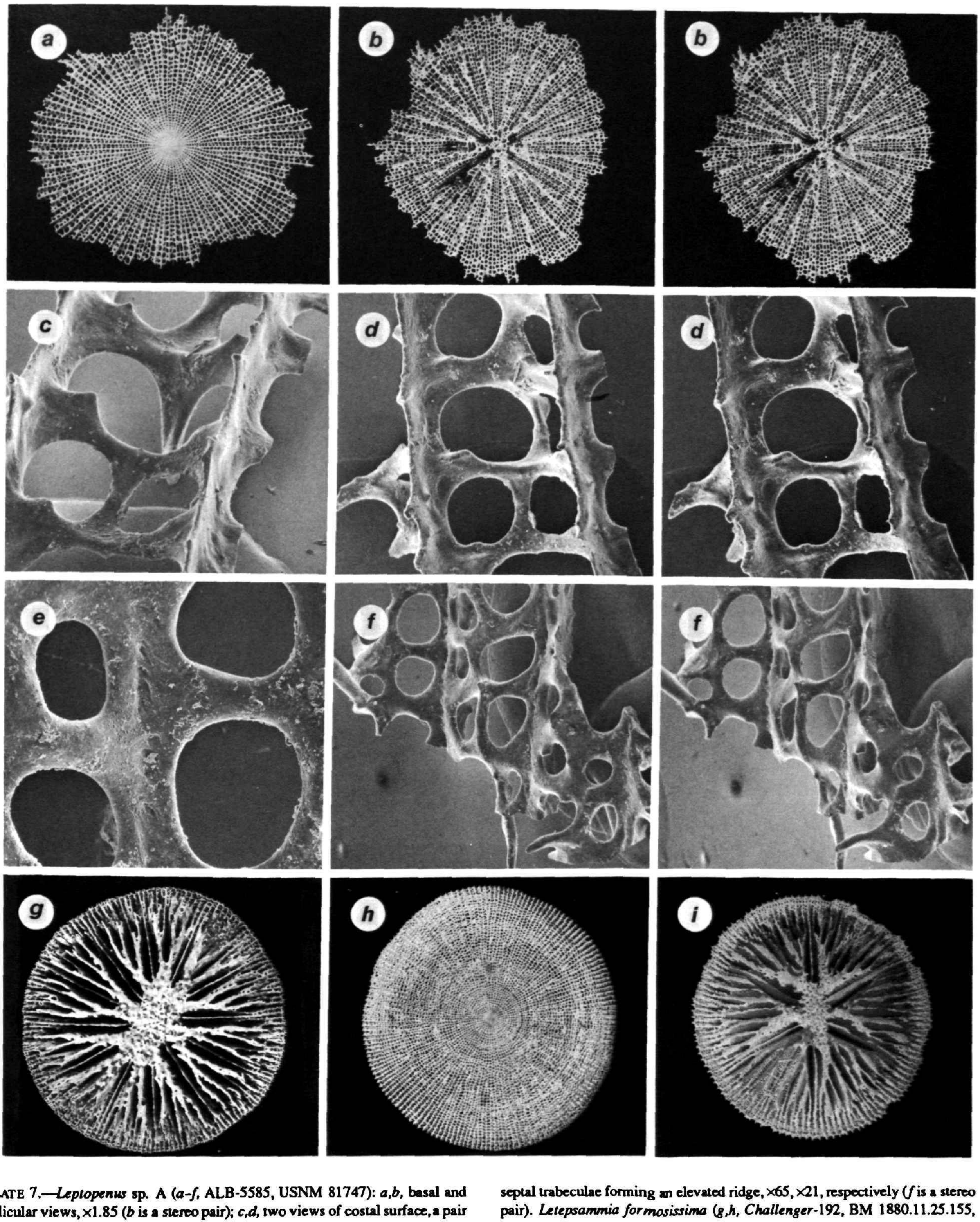

PLATE 7.—*Leptopenus* sp. A (*a–f*, ALB-5585, USNM 81747): *a,b*, basal and calicular views, ×1.85 (*b* is a stereo pair); *c,d*, two views of costal surface, a pair of spinose costae flanking a septum, the septum seen from beneath, ×38, ×30, respectively (*d* is a stereo pair); *e,f*, two views of upper "septal" surface, the septal trabeculae forming an elevated ridge, ×65, ×21, respectively (*f* is a stereo pair). *Letepsammia formosissima* (*g,h*, *Challenger*-192, BM 1880.11.25.155, syntype; *i*, MUSORSTOM 3-108, USNM 81877): *g,h*, calicular and basal views of largest syntype, ×1.25; *i*, calicular view, ×1.2.

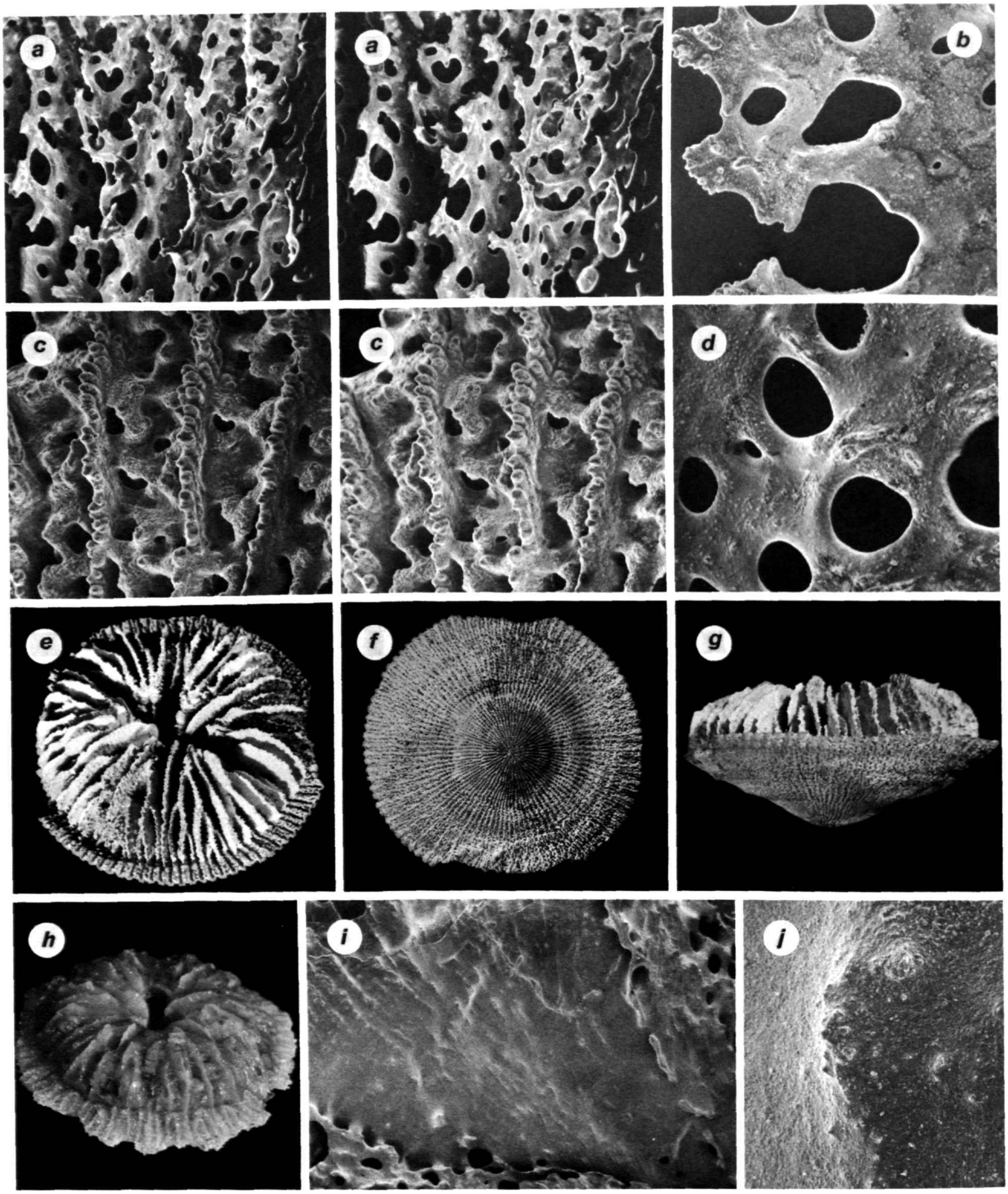

PLATE 8.—*Letepsammia formosissima* (*a–d*, ALB-5369, USNM 81881): *a,b,d*, three views of septa illustrating septal porosity and formation of septal pores (*b*), ×9, ×27, ×26, respectively (*a* is a stereo pair); *c*, stereo view of costae, ×22. *Rhombopsammia squiresi* (*e–g*, holotype; *h*, *Stephanophyllia formosissima* of Alcock (1902a), *Siboga*-284, ZMA 1163; *i,j*, ALB-5425, USNM 72800, paratype): *e–g*, calicular, basal, and lateral views of holotype, ×1.85, ×1.85, ×1.95, respectively; *h*, alcohol-preserved specimen with some tissue still intact, ×2.0; *i*, relatively smooth septal face, ×10; *j*, enlargement of septal granulation, ×153.

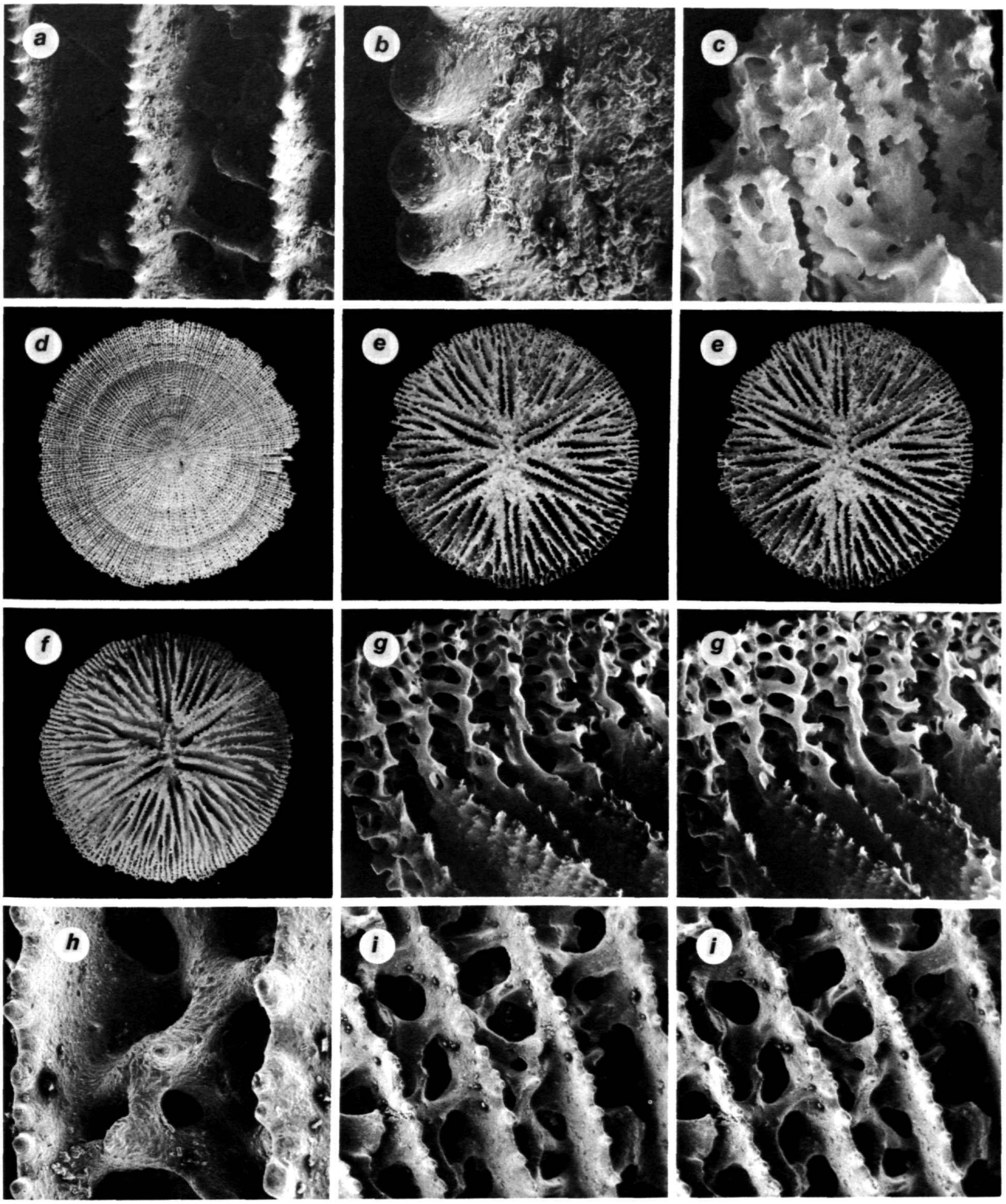

PLATE 9.—*Rhombopsammia squiresi: a,b,* ALB-5425, USNM 72800, paratype, costal granulation, ×33, ×182, respectively; *c,* marginal shelf, ×14.5. *Rhombopsammia niphada* (*d,e,* holotype; *f,* specimen from off Mi Sake, Japan, USNM 81867; *g-i,* unknown ALB station from Philippines, USNM 72805, paratype): *d,e,* basal and calicular views of holotype, ×1.6 (*e* is a stereo pair); *f,* calicular view of a nontype specimen, ×1.5; *g,* stereo view of marginal shelf, ×9.4; *h,i,* costal granulation, ×55, ×21, respectively (*i* is a stereo pair).

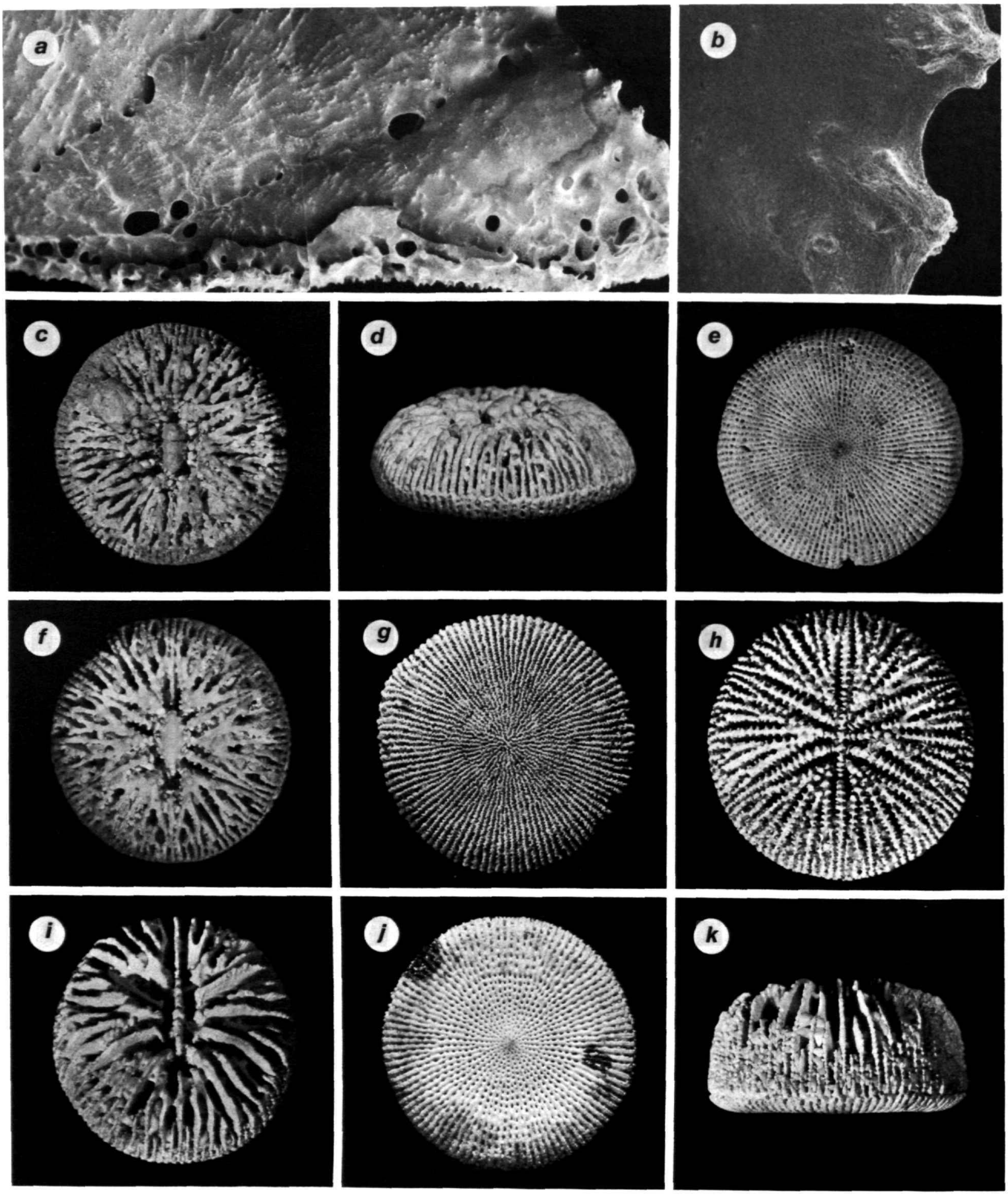

PLATE 10.—*Rhombopsammia niphada* (*a,b,* unknown ALB station from Philippines, USNM 72805, paratype): *a,* lateral view of several septa illustrating their junction at lines of bifurcation, ×8.7; *b,* lateral view of septal edge, ×67. *Stephanophyllia fungulus* (*c–f,* syntypes of *Stephanophyllia fungulus, Siboga*-100, ZMA 1321; *g,* ALB-5311, USNM 81855; *h,* BM 1939.7.20.408, specimen from "off Natal"; *i–k, Stephanophyllia complicata* of Alcock (1902a), *Siboga*-59, ZMA 1453b): *c–e,* calicular, lateral, and basal views of a syntype, ×2.8, ×3.1, ×2.9, respectively; *f,* calicular view of another syntype, ×3.3; *g,* basal view, ×3.6; *h,* calicular view, ×4.8; *i–k,* calicular, basal, and lateral views of Alcock's *S. complicata,* ×3.5.

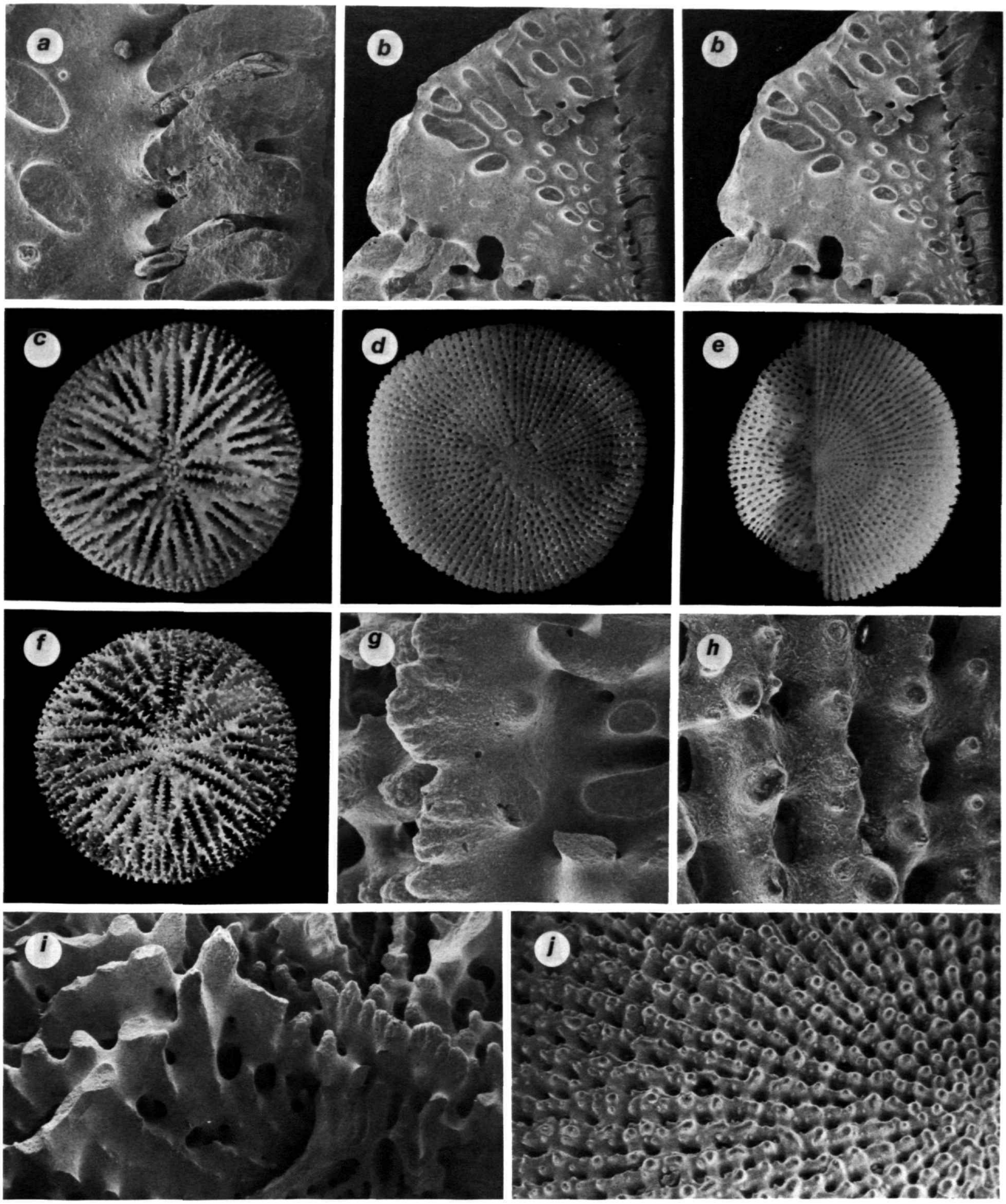

PLATE 11.—*Stephanophyllia fungulus* (*a,b*, Pleistocene specimen from Ryūkyū Islands, USNM 81858): *a*, massive costal synapticulae, ×45; *b*, stereo view of septal face showing costal and septal synapticular plates, ×11.8. *Stephanophyllia neglecta* (*c–e*, syntypes from *Siboga*-260, ZMA 1102; *f*, MUSORSTOM 3-131, USNM 81864; *g-j*, ALB-5213, USNM 81863): *c,d*, calicular and basal views of largest syntype, ×6.0; *e*, regenerating syntype, ×5.1; *f*, calicular view, ×4.7; *g,i*, lamellar columella, ×43, ×18, respectively; *h,j*, costal granulation, ×69, ×18, respectively.

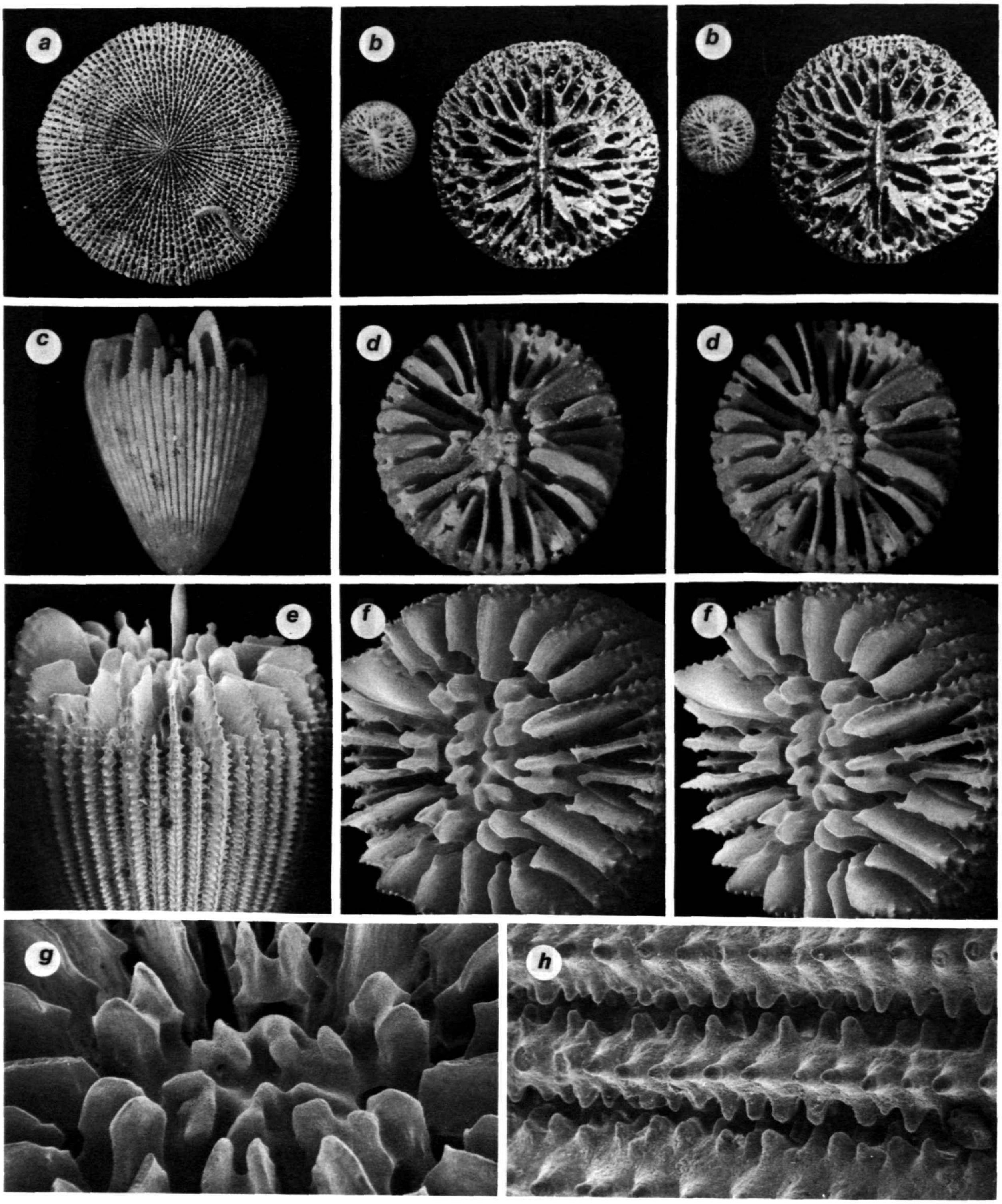

PLATE 12.—*Stephanophyllia complicata: a,b,* syntypes, *Challenger*-192, BM 1880.11.25.155a,b, basal and calicular views, ×3.0, ×2.7, respectively (*b* is a stereo pair). *Notocyathus venustus* (*c,d,* one of three syntypes from *Siboga*-59, ZMA 1244; *e-h,* ALB-5576, USNM 81785): *c,d,* lateral and calicular views of a syntype, ×5.5, ×6.9, respectively (*d* is a stereo pair); *e,* lateral view of upper calicular margin illustrating highly exsert S_{1-3} and very small S_4, ×10.3; *f,* oblique stereo view of calice, ×10.9; *g,* columella surrounded by palar crown, ×21.3; *h,* granular costae, ×59.

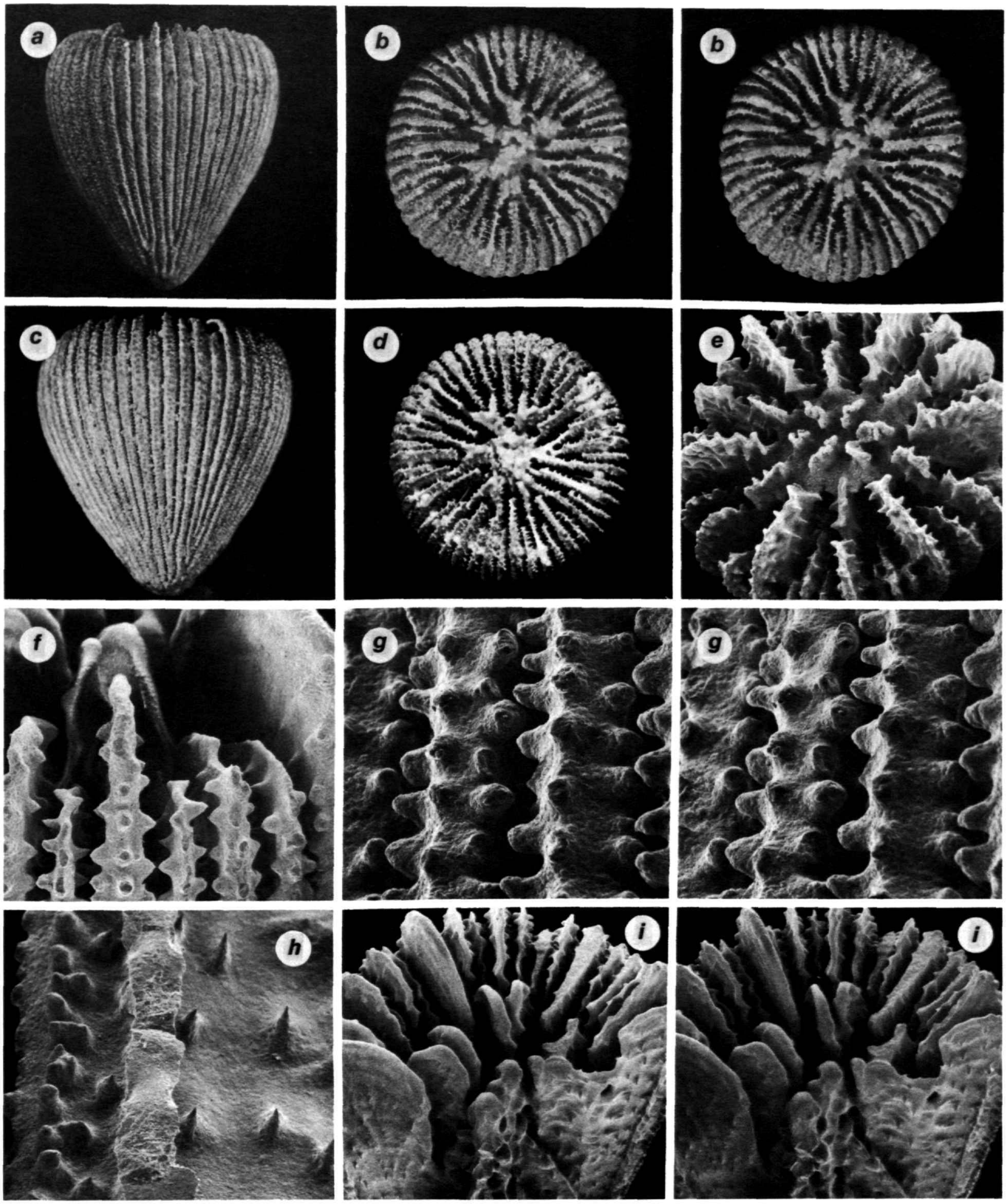

PLATE 13.—*Notocyathus conicus* (*a–e*, syntypes, *Siboga*-95, ZMA 1185; *f–i*, MUSORSTOM 2-33, USNM 81801): *a,b*, lateral and calicular views of larger syntype, ×5.8, ×6.3, respectively (*b* is a stereo pair); *c,d*, lateral and calicular views of slightly smaller syntype, ×6.8, ×7.1, respectively; *e*, juvenile specimen showing P_1 and P_2, ×22.5; *f*, lateral view of upper calicular edge showing relative exsertness of septal cycles (S_2 photographed head-on), ×32; *g*, stereo view of costae, ×76; *h*, lateral view of septum illustrating, from left to right: lateral edge of costa, longitudinal section of broken theca, and septal face granulation, ×74; *i*, stereo view of broken corallum illustrating columella, pali, and septal granulation, ×17.5.

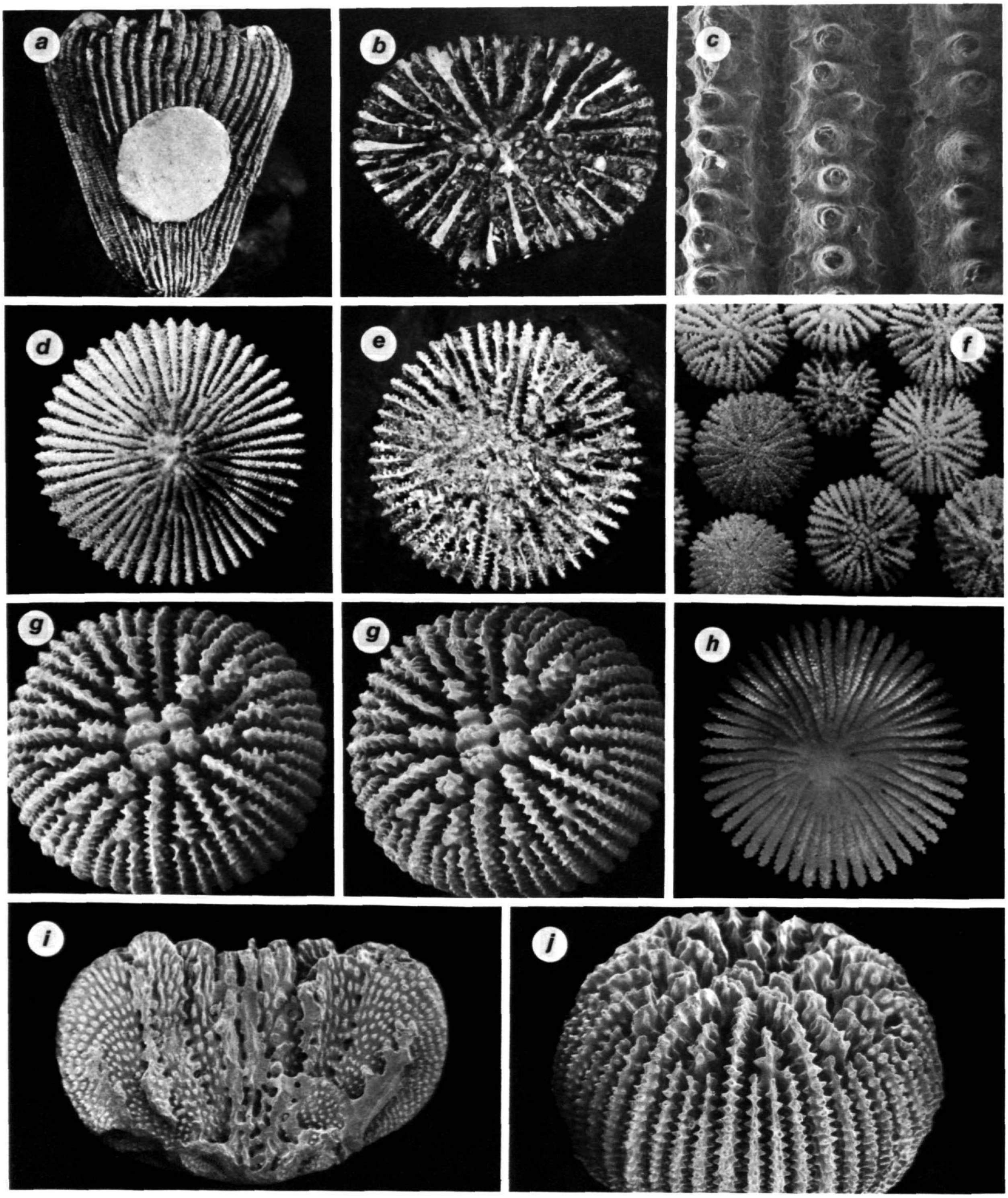

PLATE 14.—*Notocyathus viola* (*a,b*, holotype; *c*, specimen from Muddy Creek, Victoria, Australia, Miocene, USNM 77067): *a,b*, lateral and calicular views of holotype, ×5.4, ×7.7, respectively; *c*, costal granulation, ×62. *Peponocyathus australiensis* (*d,e*, holotype of *Deltocyathus italicus* var. *australiensis*; *f*, syntypes of *Deltocyathus minutus*, JM-206, BM 1950.1.9.1190–1219; *g,j*, MUSORSTOM 2-33, USNM 81836; *h*, syntype of *Deltocyathus lens*, *Siboga*-275, ZMA 5444; *i*, ALB-5577, USNM 81834): *d,e*, basal and calicular views of Miocene holotype, both ×8.8; *f*, cluster of several syntypes of *D. minutus*, ×6.3; *g*, stereo view of calice, ×12.2; *h*, basal view of syntype of *D. lens*, ×14.7; *i*, longitudinal fracture of specimen illustrating costae, septal and palar faces, theca, and columella, ×11.2; *j*, oblique view of corallum, ×15.3.

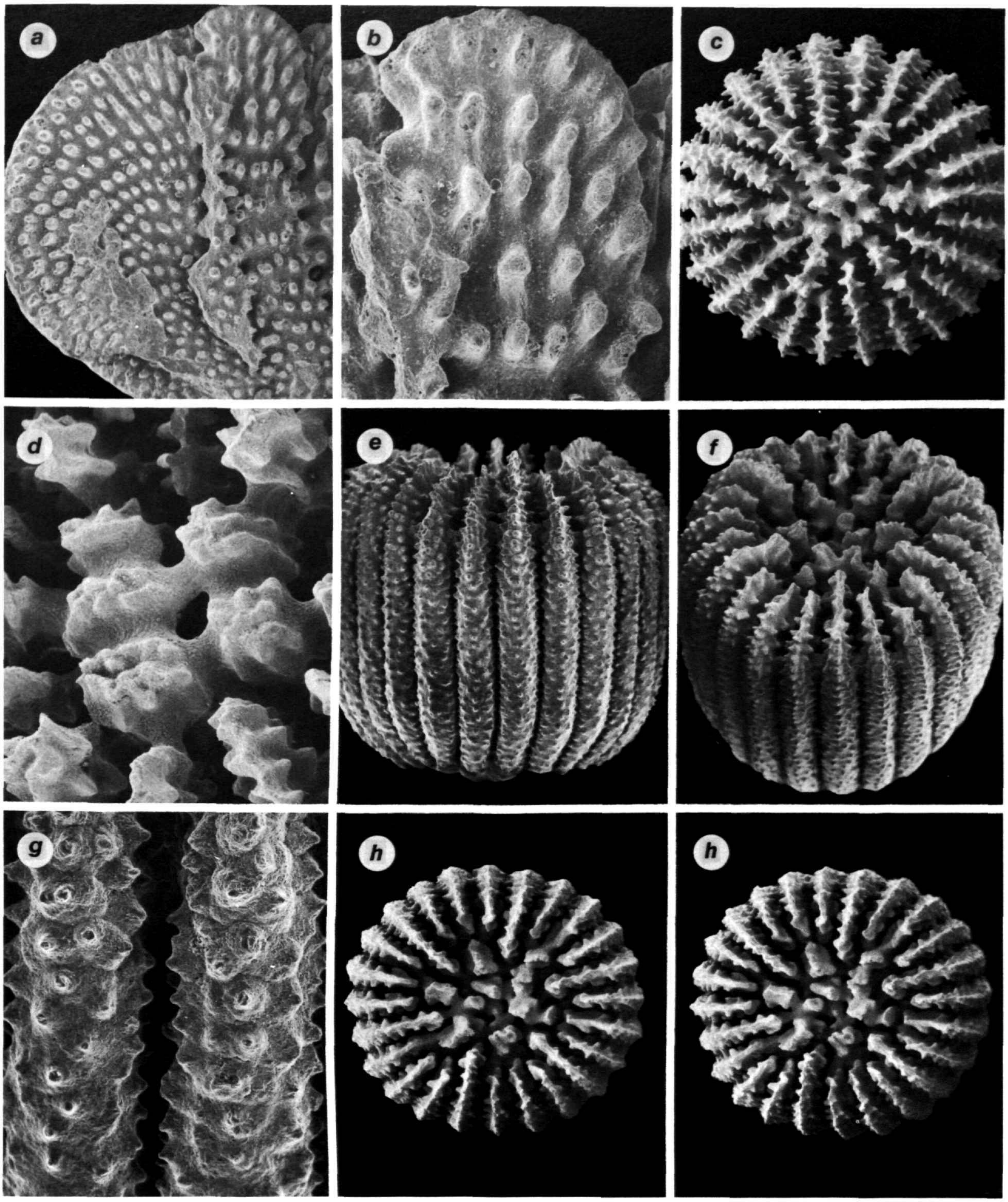

PLATE 15.—*Peponocyathus australiensis* (*a,b*, ALB-5577, USNM 81834; *c,d*, MUSORSTOM 2-33, USNM 81836): *a*, lateral view of costal, septal, and palar faces (longitudinal fracture of theca also visible), ×22; *b*, enlargement of palar face of *a*, ×55; *c*, juvenile specimen, ×24; *d*, columella composed of five elements flanked by several pali, ×39. *Peponocyathus folliculus* (*e-h*, ALB-5217, USNM 81839): *e,f, h*, lateral, oblique, and calicular views of same specimen, ×17.5, ×18, ×15, respectively (*h* is a stereo pair); *g*, enlargement of costal granulation, ×68.

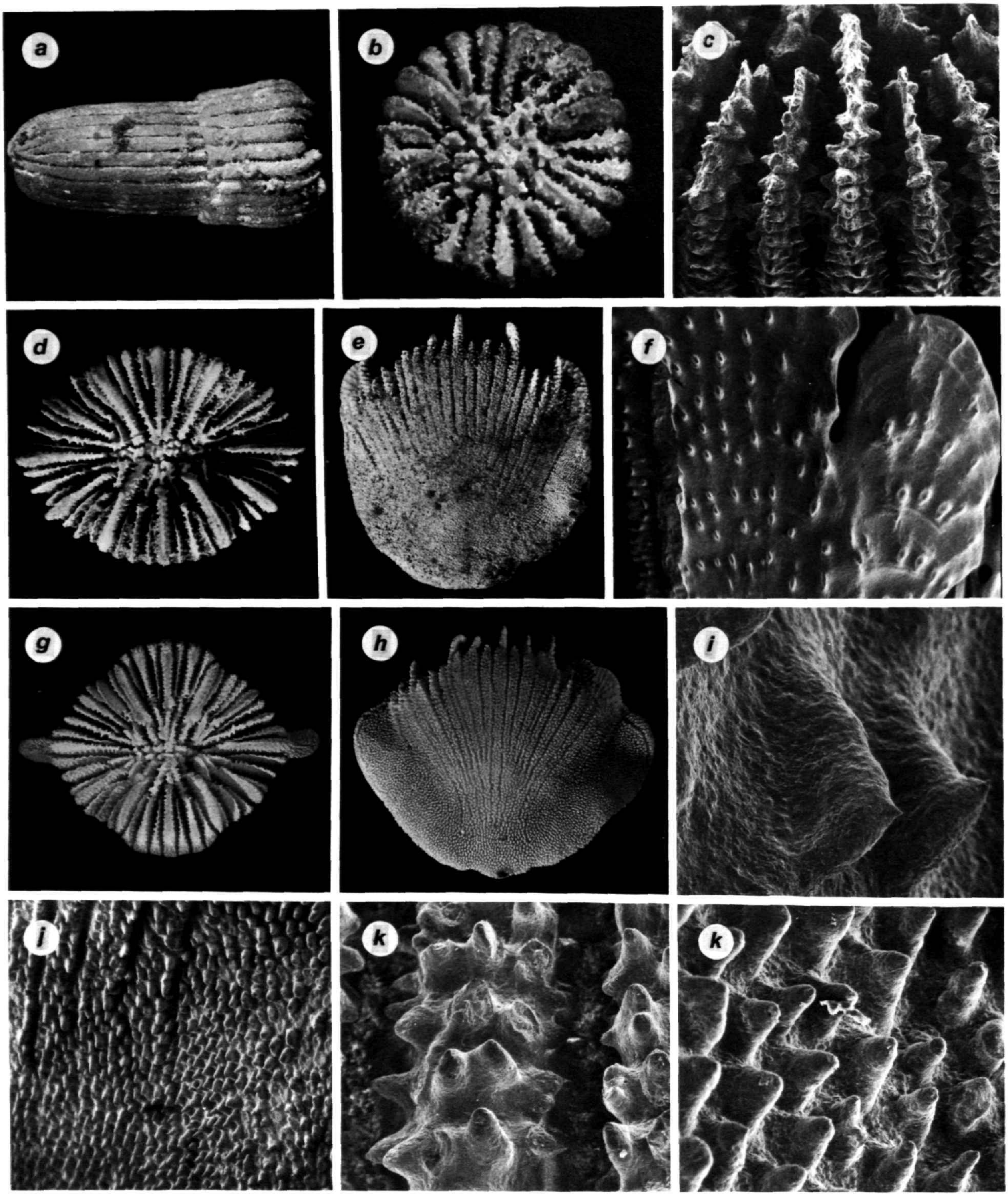

PLATE 16.—*Peponocyathus folliculus* (*a,b*, ALB-5277, USNM 81840; *c*, ALB-5217, USNM 81839): *a,b*, lateral and calicular views of same specimen, ×6.3, ×11, respectively; *c*, costal granulation near calicular edge, ×33. *Tropidocyathus lessoni* (*d,e*, MUSORSTOM 3-108, MNHNP; *f,i-l*, *Anton Bruun*-CH-5, USNM 78582; *g,h*, ALB-5178, USNM 81845): *d,e*, calicular and oblique lateral views of same corallum, both ×3.5; *f*, lateral faces of costa, septum, and palus (longitudinal fracture of theca also shown on left), ×17.5; *g,h*, calicular and lateral views of same corallum, ×4.3, ×4.0, respectively; *i*, enlargement of septal granules, ×150; *j,l*, costal granulation on edge crest, ×14.2, ×78, respectively; *k*, granulation on a distinct costa near calicular margin, ×61.

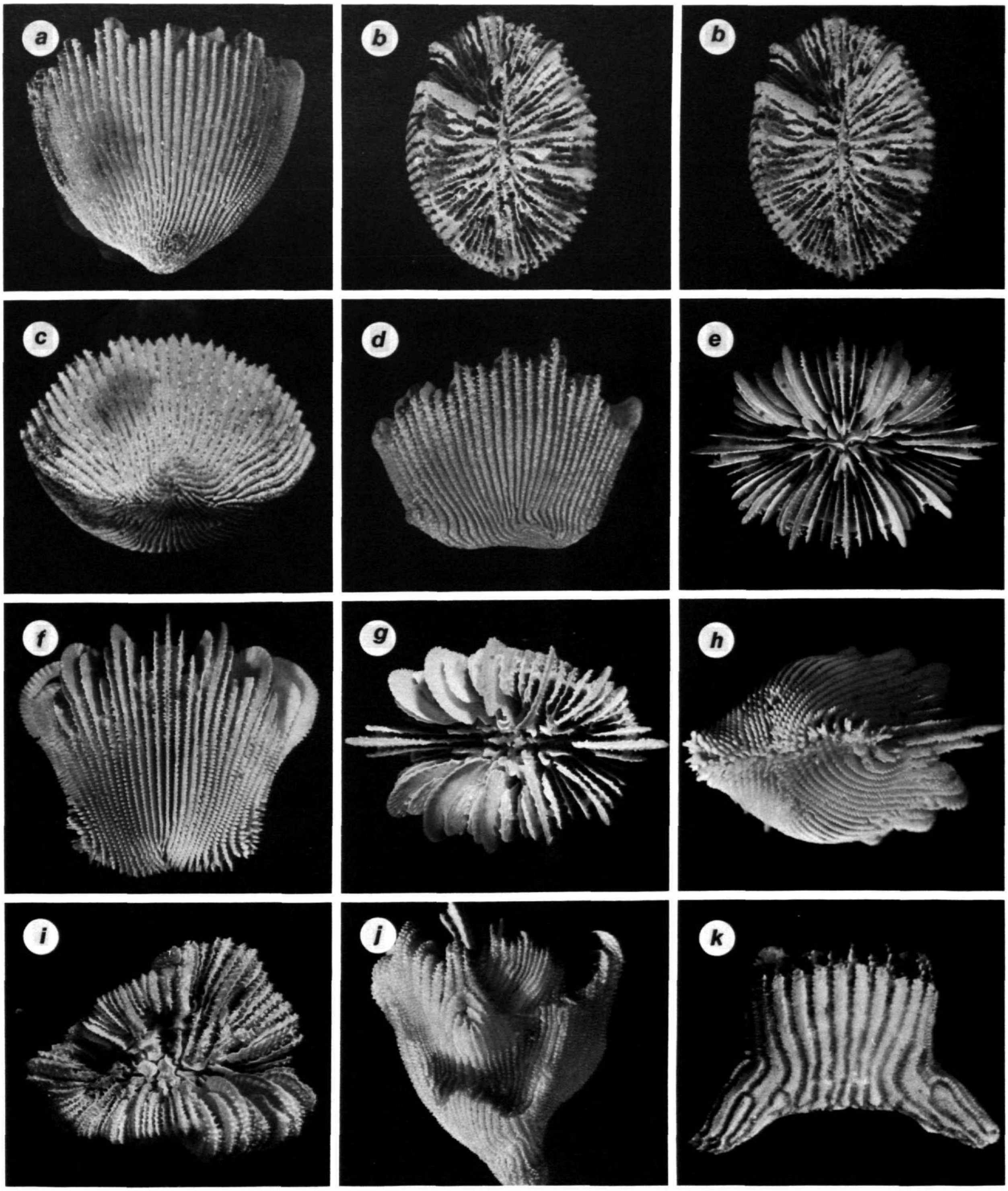

PLATE 17.—*Tropidocyathus pileus* (*a–c*, largest syntype, *Siboga*-95, ZMA 7352; *d*, another syntype, *Siboga*-95, ZMA 1326; *e*, ALB-5506, USNM 81848; *f–h*, ALB-5508, USNM 81854): *a–c*, lateral, calicular, and basal views of largest syntype, ×3.5, ×3.9, ×4.1, respectively (*b* is a stereo pair); *d*, lateral view of smaller syntype, ×3.5; *e*, calicular view, ×2.2; *f–h*, lateral, calicular, and oblique basal views of same specimen, all ×2.5. *Tropidocyathus nascornatus*: *i,j*, syntype from JM-104, BM 1950.1.9.1262–1264, calicular and lateral views, both ×3.6. *Idiotrochus australis*: *k*, lateral view of specimen from USGS 10820 (Muddy Creek, Victoria, Australia, Miocene), USNM 77059, ×7.0.

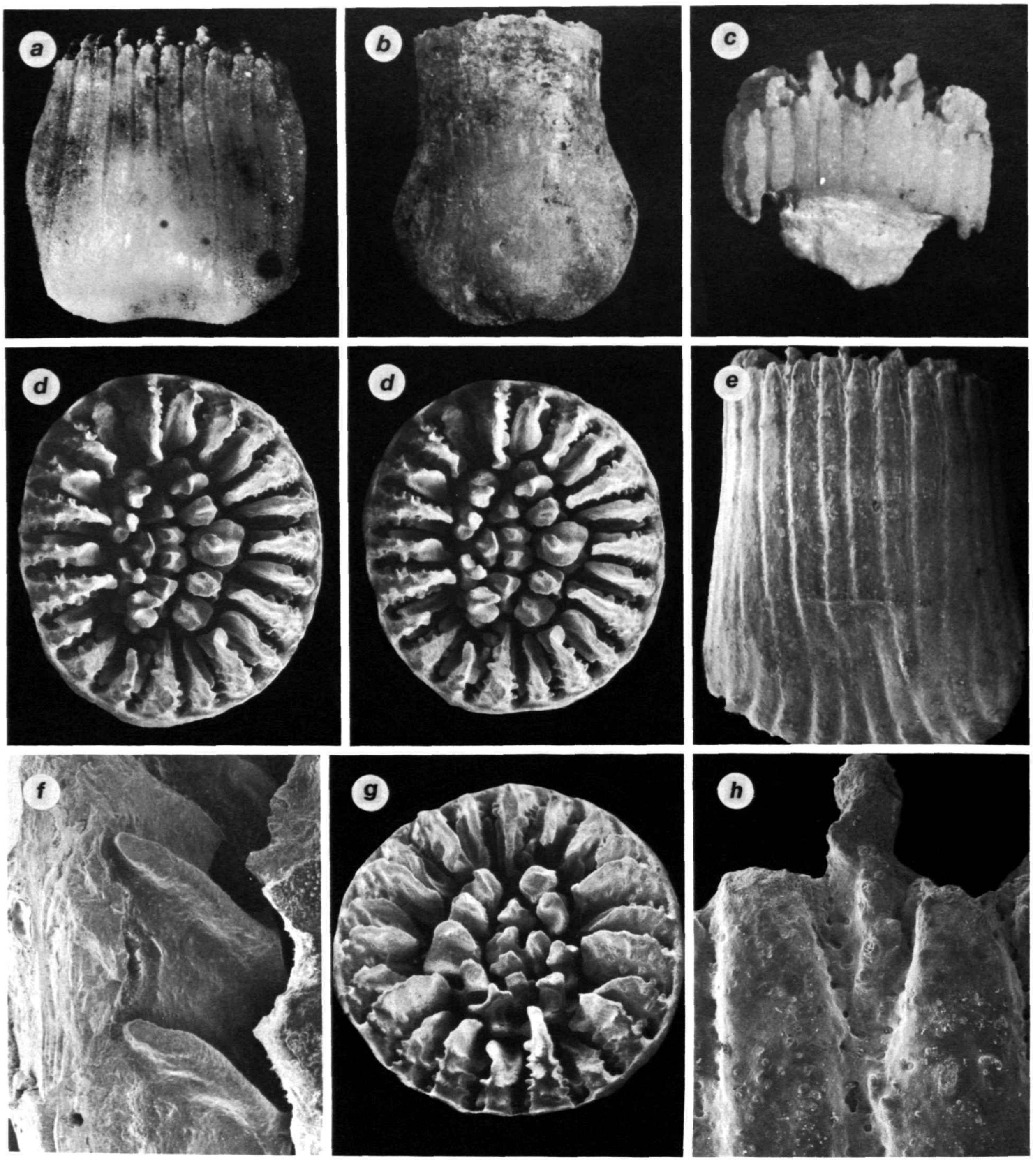

PLATE 18.—*Idiotrochus kikutii* (*a,d-h*, MUSORSTOM 2-33, USNM 81911; *b*, MUSORSTOM 2-32, MNHNP): ***a,b,e***, lateral views of three coralla (anthocyathi), ×11.8, ×7.4, ×20, respectively; ***d,g***, calicular views of coralla, ×16, ×18, respectively (*d* is a stereo pair); *f*, septal carinae, ×60; *h*, outer calicular edge, showing intercalation of septum between two costae, ×125. *Idiotrochus perexigua*: *c*, syntype of *S. emarciatus* var. *perexigua*, east of Neptune Island, 45 fms, South Australian Museum, juvenile anthocyathus still attached basally to remnant of anthocaulus, ×14.7.

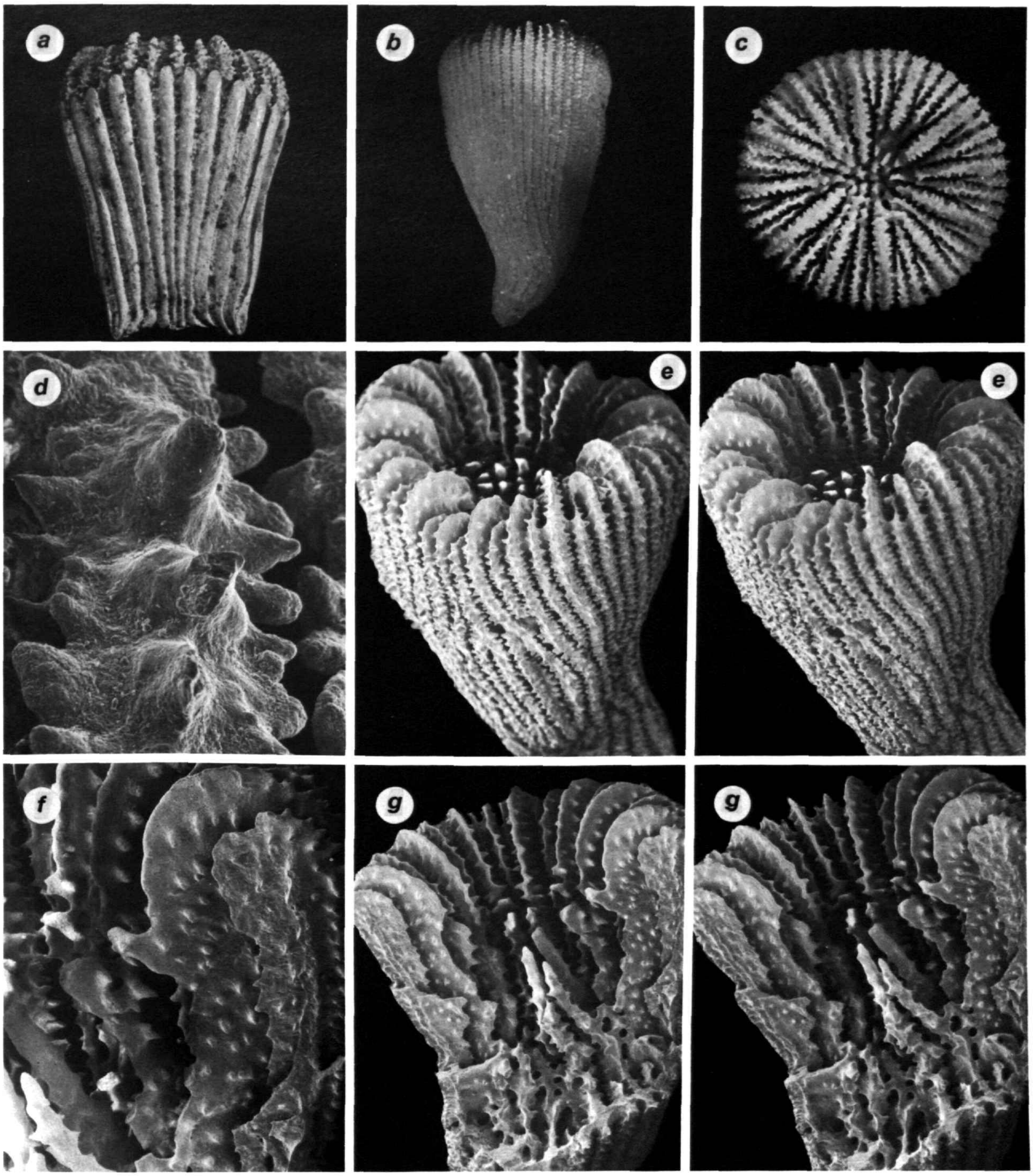

PLATE 19.—*Idiotrochus emarciatus*: *a*, lateral view of specimen from USGS 10820 (Muddy Creek, Victoria, Australia, Miocene), USNM 77060, ×6.6. *Thrypticotrochus multilobatus*, new species (*b,c*, holotype; *d,e*, ALB-5301, USNM 81903, paratype; *f,g*, ALB-5217, USNM 81902, paratype): *b,c*, lateral and calicular views of holotype, ×7.0, ×12.3, respectively; *d*, costal granulation, ×18.5; *e*, stereo view of corallum, ×15.8; *f*, paliform lobes, ×38; *g*, stereo view of damaged corallum revealing columella and paliform lobes, ×18.4.

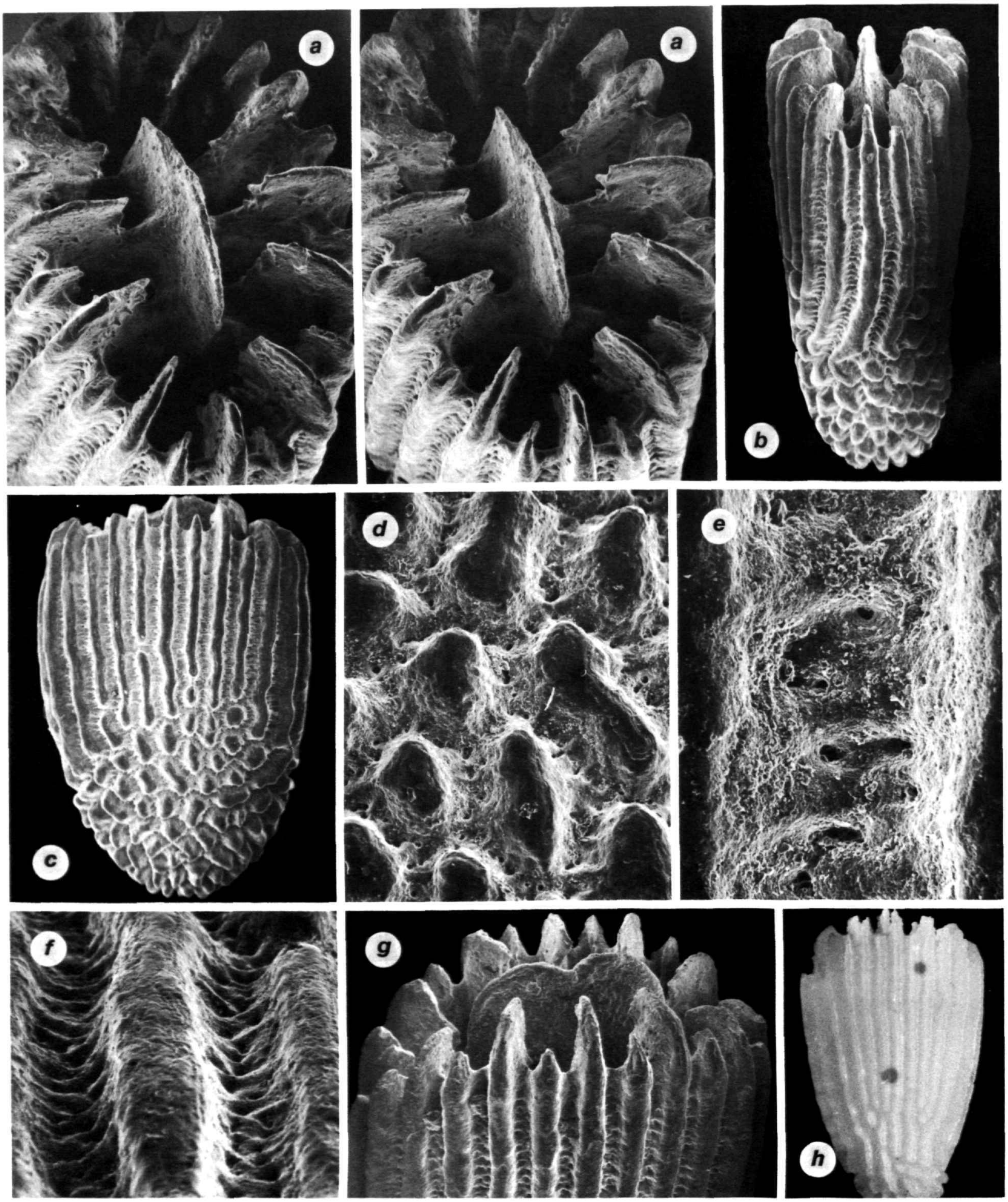

PLATE 20.—*Sphenotrochus hancocki* (*a*–*g*, ALB-5311, USNM 81897; *h*, holotype): *a*, stereo calicular view illustrating columella and septal granulation, ×37; *b,c*, edge and lateral views of corallum, ×18.5, ×17.5, respectively; *d*, discontinuous costal granules on lower half of corallum, ×77; *e*, intercostal groove showing tiny coenosteal pits, ×265; *f*, costae and intercostal grooves, also showing coenosteal pits, ×107; *g*, oblique view of calice showing exsert columella, ×27.8; *h*, lateral view of holotype, ×13.6.

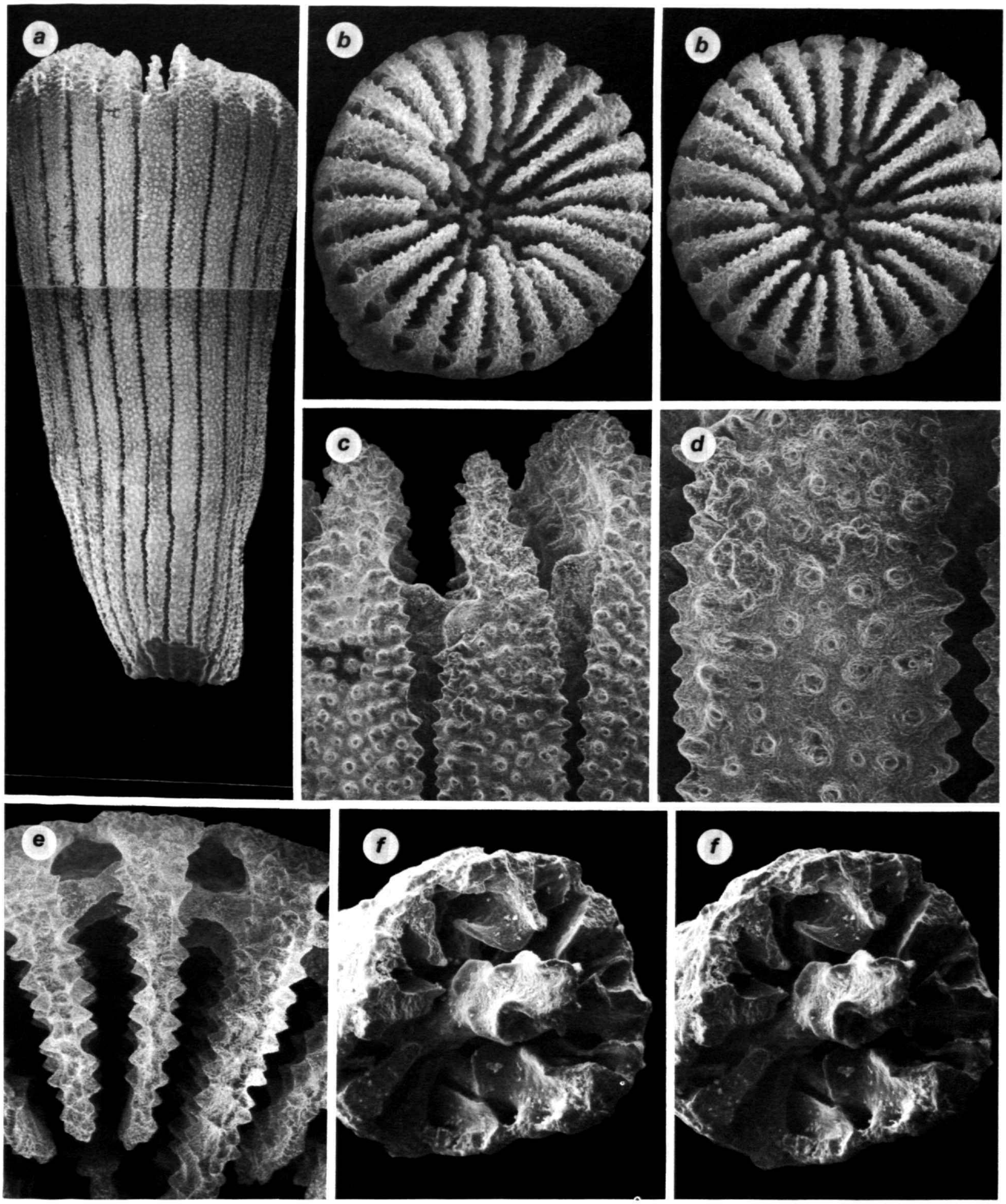

PLATE 21.—*Endocyathopora laticostata*, new species (*a–e*, holotype): *a,b,* lateral and stereo calicular views, ×20, ×23, respectively; *c,d,* costal granulation, ×80, ×170, respectively; *e,* edge of calice showing costae and theca from above, ×70. *Guynia annulata: f,* MUSORSTOM 2-33, MNHNP, stereo view of broken calice illustrating columella and inner septal sinuosity, ×46.

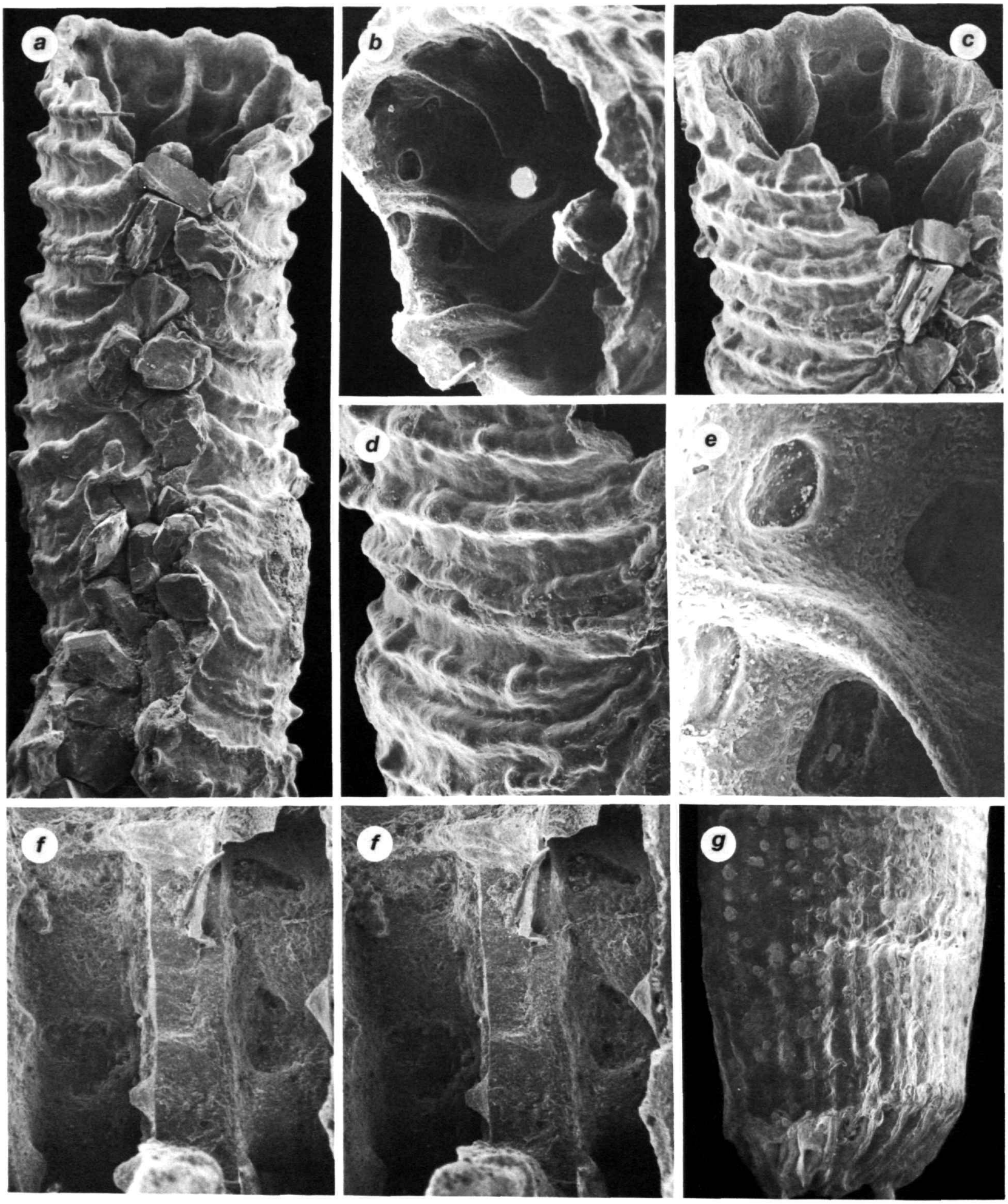

PLATE 22.—*Guynia annulata* (*a-e*, MUSORSTOM 2-33, MNHNP): *a*, lateral view of specimen attached to sand grains, ×46; *b,c*, oblique calicular views illustrating round thecal pores and tip of columella, ×68, ×46, respectively; *d*, costal annulation, ×77; *e*, higher magnification of four incipient thecal pores, ×220. *Truncatoguynia irregularis* (*f,g*, ALB-5311, USNM 81891, paratype): *f*, stereo view of broken septum flanked by pairs of thecal pores, ×72; *g*, lateral view of anthocyathus showing basal scar and exterior thecal spotting, ×9.7.

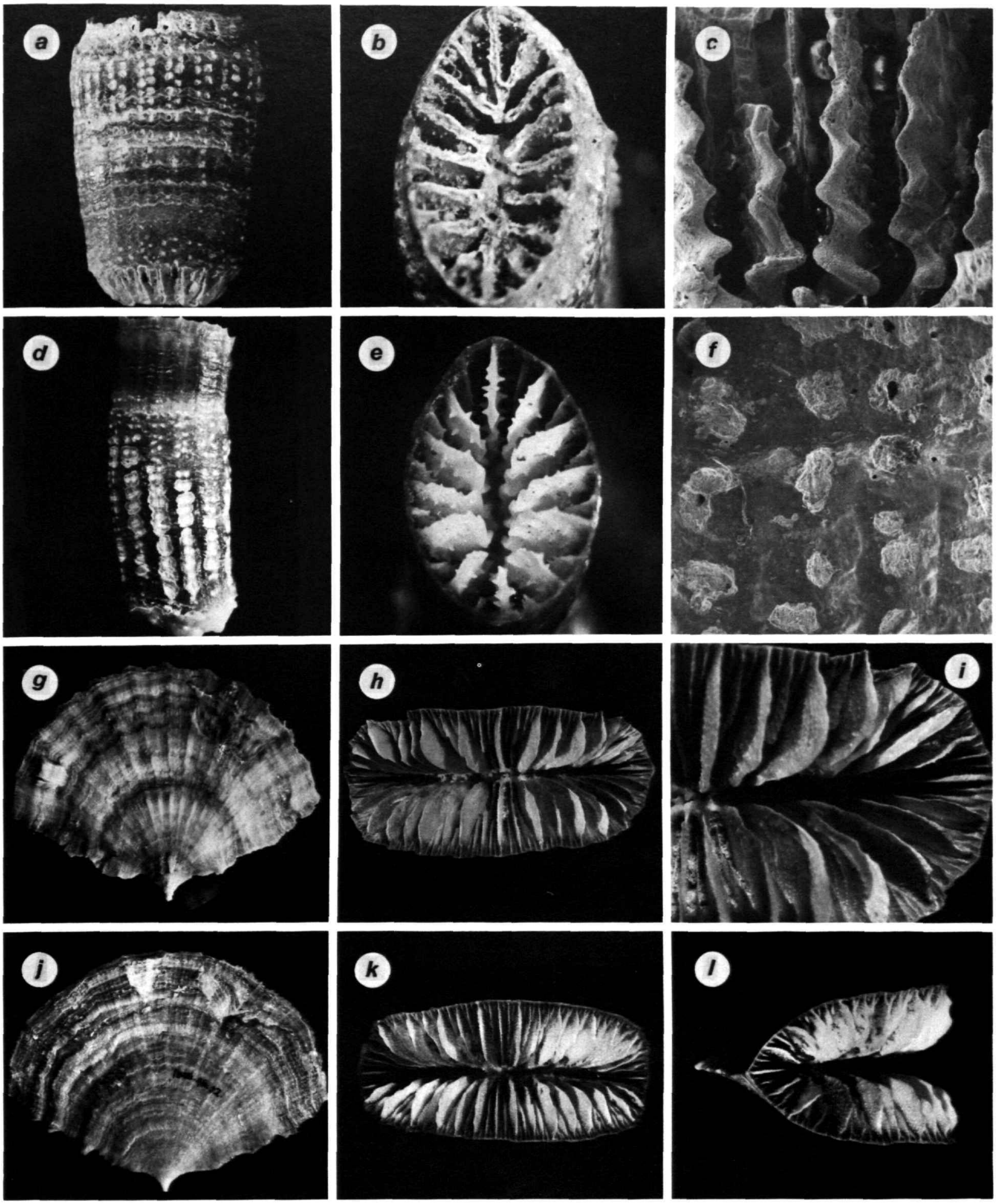

PLATE 23.—*Truncatoguynia irregularis*, new species (*a,b*, holotype; *c,f*, ALB-5311, USNM 81891, paratype): *a,b*, lateral and calicular views of holotype, ×5.3, ×8.9, respectively; *c*, sinuosity of lower inner septum, ×21; *f*, external thecal pitting, ×29. *Truncatoguynia* sp. (*d,e*, NZOI C531 (29°14′40″S, 178°02′W, 179 m), USNM 81893): *d,e*, lateral and calicular views of same corallum, ×6.1, ×13.7, respectively. *Flabellum pavoninum* (*g–i*, lectotype of *Flabellum pavoninum*, MNHNP 372; *j–l*, lectotype of *F. distinctum*, BM 1840.4.6.82): *g–i*, lateral and calicular views of lectotype, ×1.0, ×1.0, ×2.0, respectively; *j–l*, lateral, calicular, and edge views of lectotype of *F. distinctum*, ×0.93, ×0.88, ×1.18, respectively.

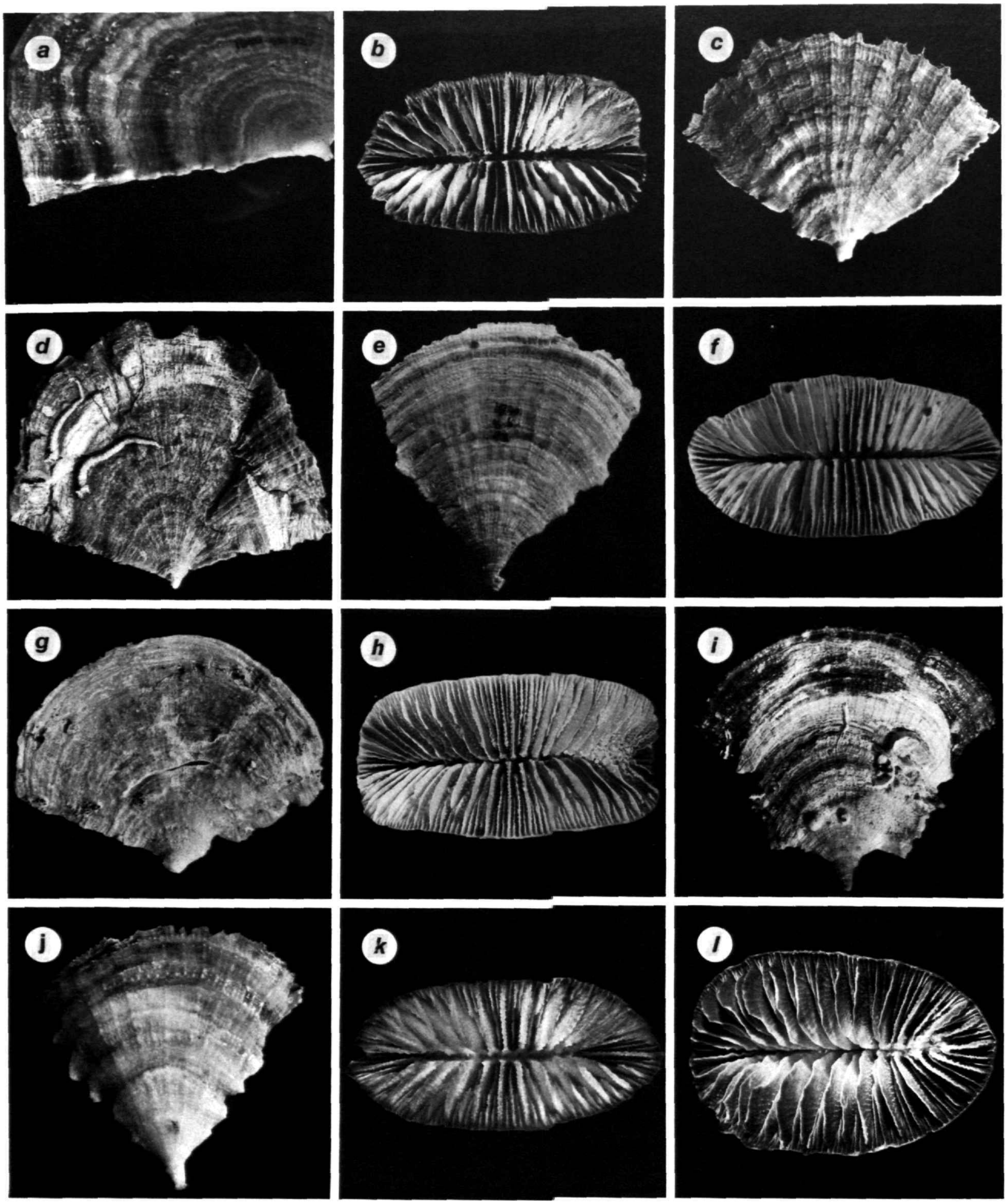

PLATE 24.—*Flabellum pavoninum* (*a*, lectotype of *F. distinctum*, BM 1880.4.6.82; *b*, paralectotype of *F. distinctum*, BM 1840.4.6.81; *c*, *F. distinctum* of Marenzeller (1889), MV 8197; *d*, *F. pavoninum* of Marenzeller (1889), MV 8201): *a*, corallum edge, ×1.6; *b*, calicular view, ×1.1; *c,d*, lateral views of Marenzeller's (1889) specimen from off Japan, both ×1.2. *Flabellum* sp.: *e,f*, paralectotype of *F. distinctum*, BM 1840.4.6.83, lateral and calicular views, ×1.75, ×1.45, respectively. *Flabellum pavoninum* of Gardiner (1902): *g,h*, BM 1950.1.11.30, lateral and calicular views, both ×1.2. *Flabellum coalitum* (*i,l*, *F. distinctum* of Yabe and Eguchi (1942a), TIUS 43409; *j,k*, holotype, MV 8196): *i,l*, lateral and calicular views, ×1.4, ×1.5, respectively; *j,k*, lateral and calicular views of holotype, ×1.6, ×1.8, respectively.

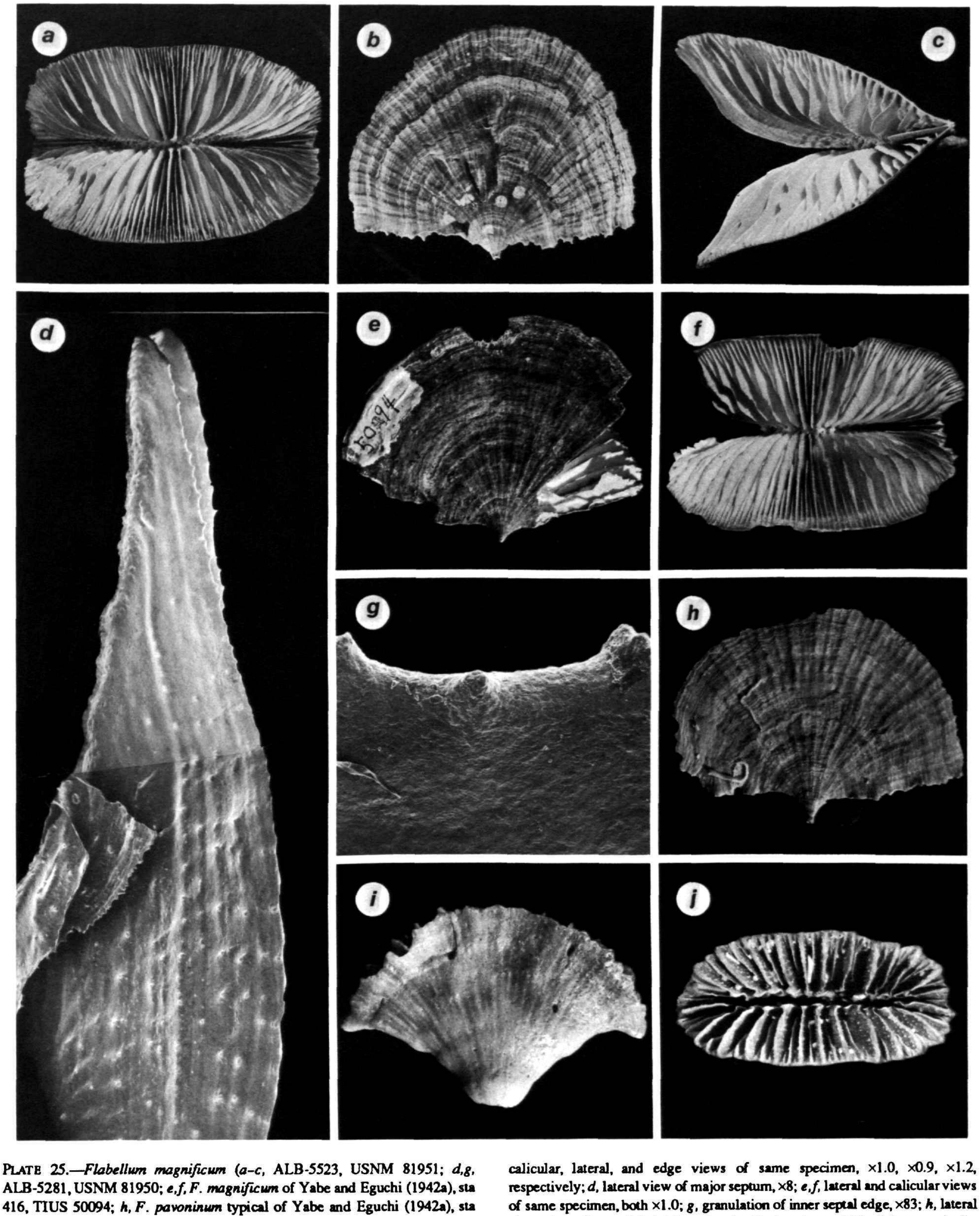

PLATE 25.—*Flabellum magnificum* (*a–c*, ALB-5523, USNM 81951; *d,g*, ALB-5281, USNM 81950; *e,f*, *F. magnificum* of Yabe and Eguchi (1942a), sta 416, TIUS 50094; *h*, *F. pavoninum* typical of Yabe and Eguchi (1942a), sta 439, TIUS 43448; *i,j*, holotype of *F. suluense*, *Siboga*-100, ZMA 1231): *a–c*, calicular, lateral, and edge views of same specimen, ×1.0, ×0.9, ×1.2, respectively; *d*, lateral view of major septum, ×8; *e,f*, lateral and calicular views of same specimen, both ×1.0; *g*, granulation of inner septal edge, ×83; *h*, lateral view of corallum, ×1.2; *i,j*, lateral and calicular views, ×2.6, ×2.2, respectively.

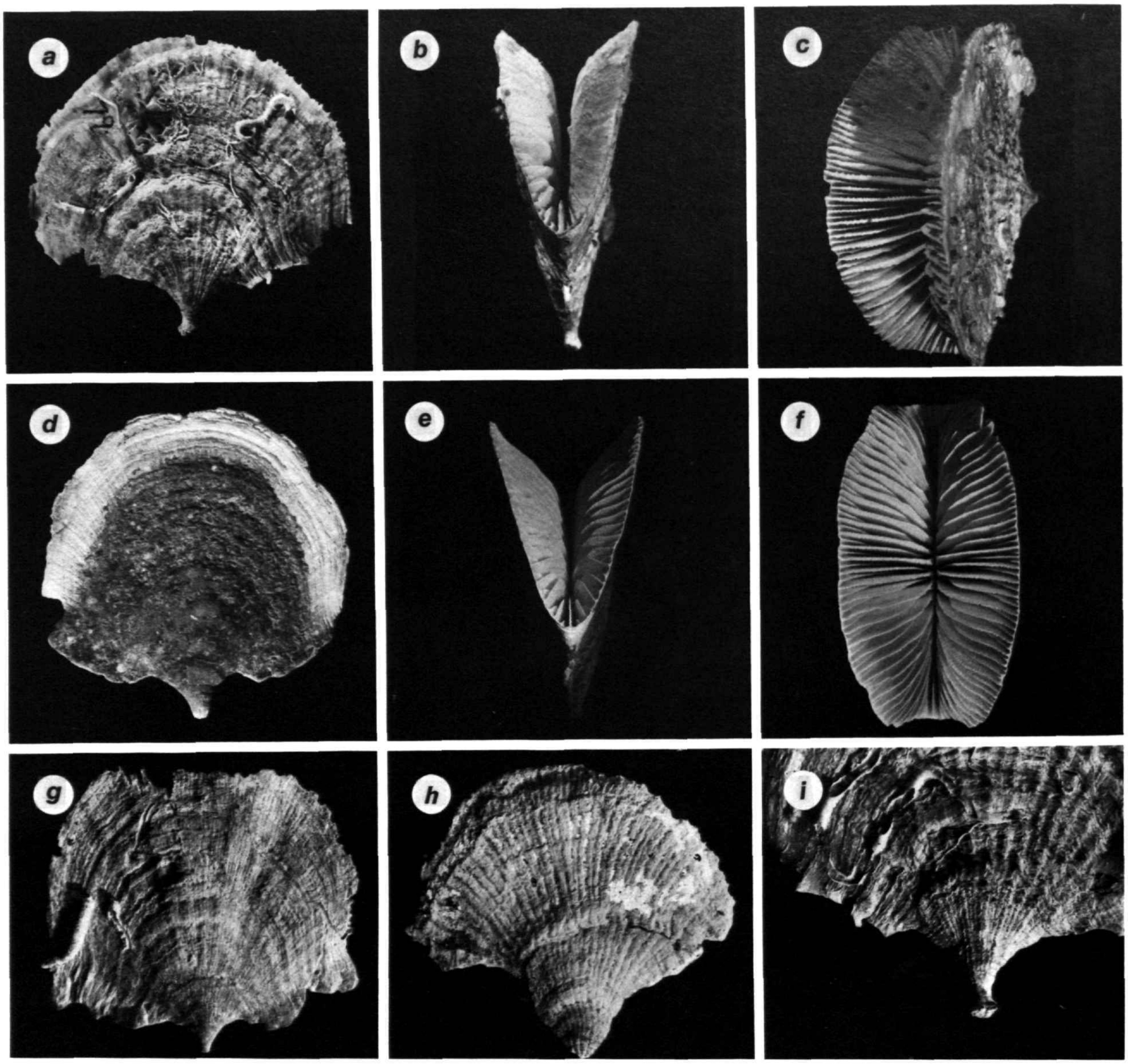

PLATE 26.—*Flabellum patens* (*a–c,i*, lectotype; *d–f*, ALB-5289, USNM 40745; *g*, *F. pavoninum paripavoninum* of Yabe and Eguchi (1942a), sta 419, TIUS 43441; *h*, *F. pavoninum distinctum* of Umbgrove (1950), RGM 77842, Pleistocene of Java): *a–c*, lateral, edge, and calicular views of lectotype, ×1.2, ×0.8, ×1.0, respectively; *d–f*, lateral, edge, and calicular views of same corallum, ×1.2, ×1.2, ×1.35, respectively; *g,h*, lateral views of Japanese and Pleistocene Javanese specimens, ×1.3, ×2.5, respectively; *i*, pedicel and lateral edge of lectotype, ×2.1.

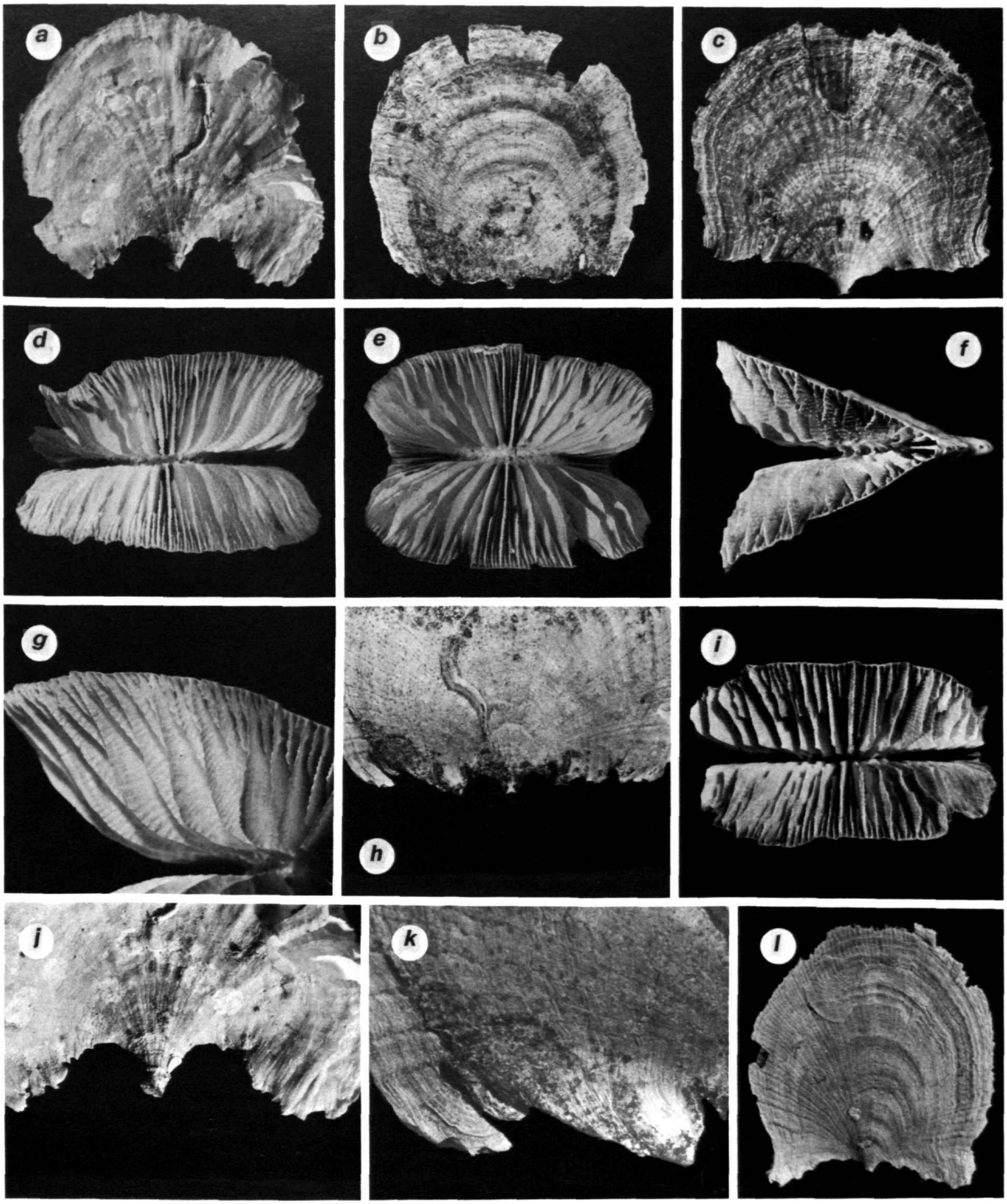

PLATE 27.—*Flabellum lamellulosum* (*a,d,g,j*, holotype, *Siboga*-251, ZMA 1215; *b,e,h,k*, ALB-5393, USNM 40754; *c,f*, paralectotype of *F. pavoninum*, MNHNP 372; *i*, different paralectotype of *F. pavoninum*, MNHNP 372; *l*, ALB-5212, USNM 40744): *a,d,g,j*, lateral, calicular, septal profile, and pedicel views of holotype, ×1.3, ×1.4, ×2.5, ×1.8, respectively; *b,e*, lateral and calicular views of same specimen, ×0.9, ×1.1, respectively; *h,k*, lateral edge costal eversions, ×1.2, ×2.7, respectively; *c,f,i*, lateral, edge, and calicular views of two specimens, ×1.6, ×1.5, ×1.1, respectively; *l*, lateral view of corallum, ×0.9.

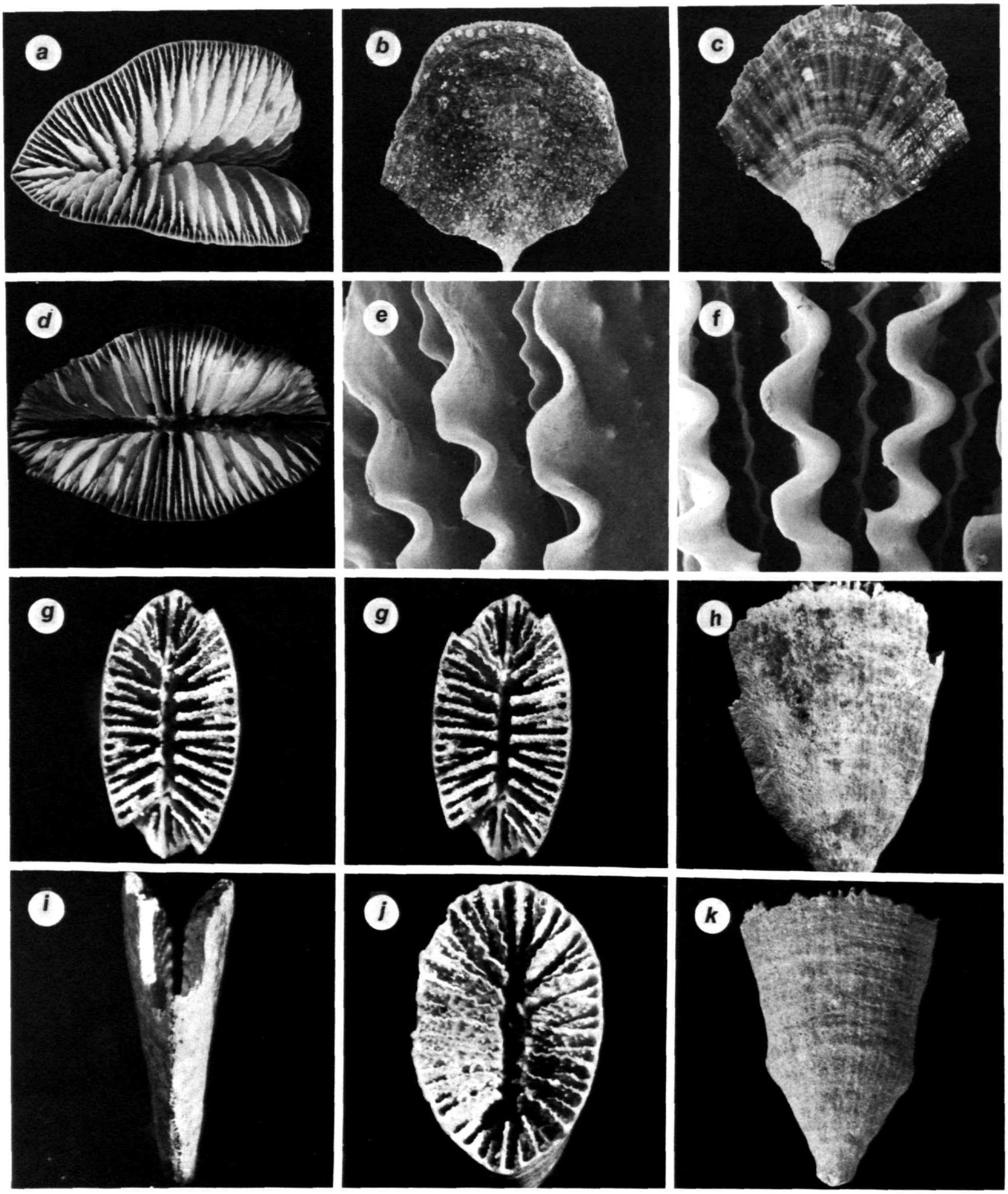

PLATE 28.—*Flabellum politum*, new species (*a,b*, holotype; *c*, ALB-5391, USNM 40724, paratype; *d*, paralectotype of *F. patens*, BM 1880.11.25.79; *e,f*, ALB-5393, USNM 81946, paratype): *a,b*, calicular and lateral views of holotype, ×1.9, ×1.3, respectively; *c*, small corallum illustrating thecal pigmentation pattern, ×2.0; *d*, calicular view, ×2.0; *e,f*, two views of inner septal sinuosity, ×12.5, ×14.7, respectively. *Flabellum dens* (*g–i*, Alcock's (1902a) figured syntype, *Siboga*-95, ZMA 1209; *j,k*, another syntype, *Siboga*-95, ZMA 1449): *g,h,i*, calicular, lateral, and edge views of same specimen, ×4.0, ×3.5, ×3.5, respectively (*g* is a stereo pair); *j,k*, calicular and lateral views, ×3.8, ×2,3, respectively.

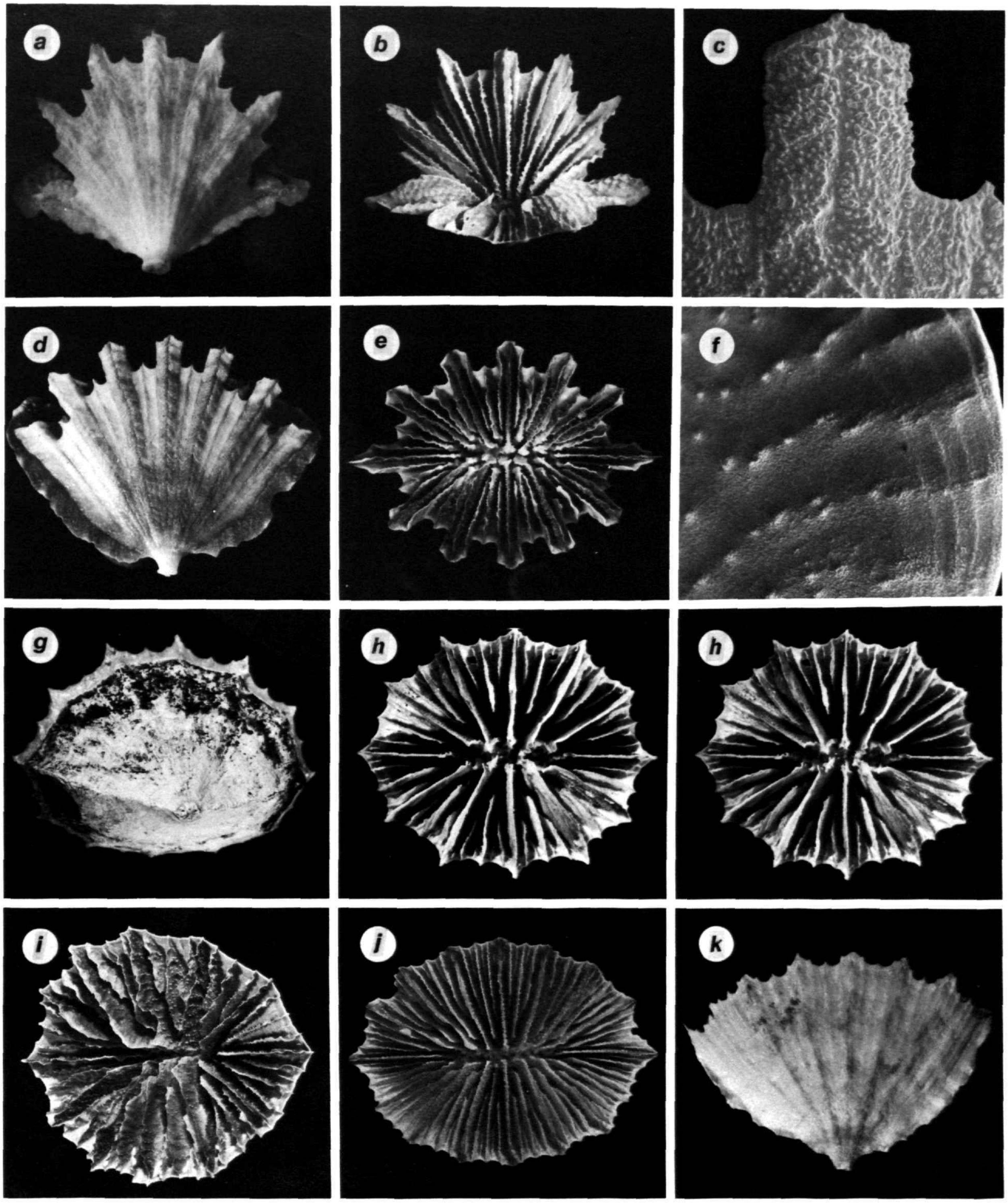

PLATE 29.—*Flabellum deludens* (*a,b*, syntype from *Valdivia*-185, ZMB 7086; *c-f*, ALB-5453, USNM 40768): *a,b*, lateral and calicular views of syntype, both ×2.25; *c*, thecal extension, ×16; *d,e*, lateral and calicular views of same specimen, ×2.2, ×2.1, respectively; *f*, septal face granulation, ×14.5. *Flabellum japonicum* (*g,h*, syntype, BM; *i*, ALB-5221, USNM 40690): *g,h*, basal and stereo calicular views of a syntype, magnification unknown but approximately same as *i*; *i*, oblique calicular view, ×1.2. *Flabellum japonicum* of Hoffmeister (1933): *j,k*, E5557, off Gabo Island to Cape Everard, USNM 82012, calicular and lateral views of same specimen, both ×1.4.

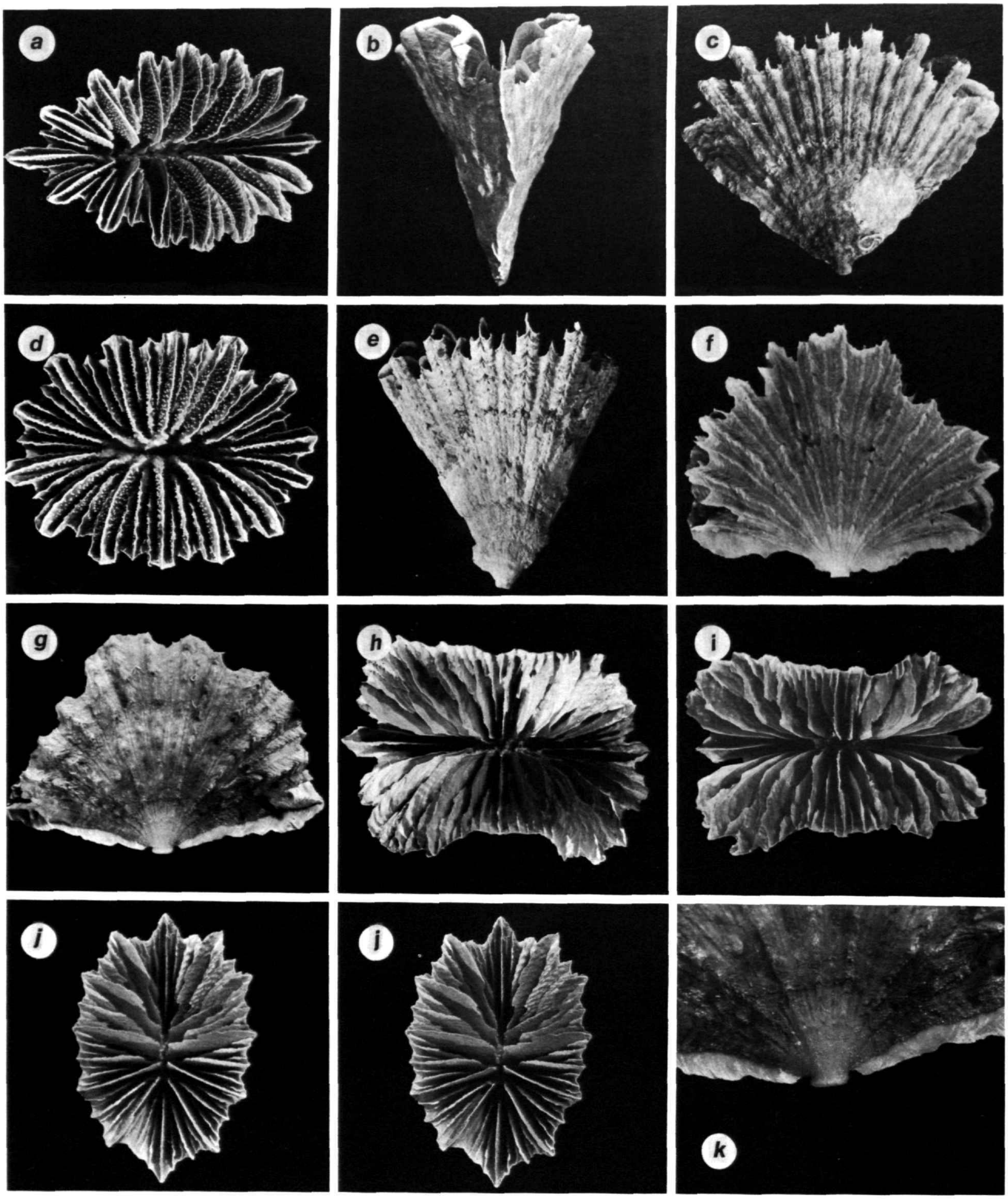

PLATE 30.—*Flabellum marenzelleri*, new species (*a-c*, holotype; *d,e*, aberrant paratype from ALB-5268, USNM 81887): *a-c*, calicular, edge, and lateral views of holotype, all ×1.6; *d,e*, calicular and lateral views, ×1.8, ×1.5, respectively. *Flabellum messum* (*f,i*, unknown ALB station in Philippine Islands, USNM 81937; *g,h,k*, syntype of *F. laciniatum* var. *messum*, *Siboga*-314, ZMA 1214): *f,i*, lateral and calicular views of same specimen, ×1.2, ×1.5, respectively; *g,h*, lateral and calicular views of a syntype, ×1.2, ×1.3, respectively; *k*, enlargement of pedicel and adjacent lateral edges of syntype illustrating edge crest, ×2.3. *Flabellum sexcostatum*, new species: *j*, holotype, stereo view of calice, ×1.2.

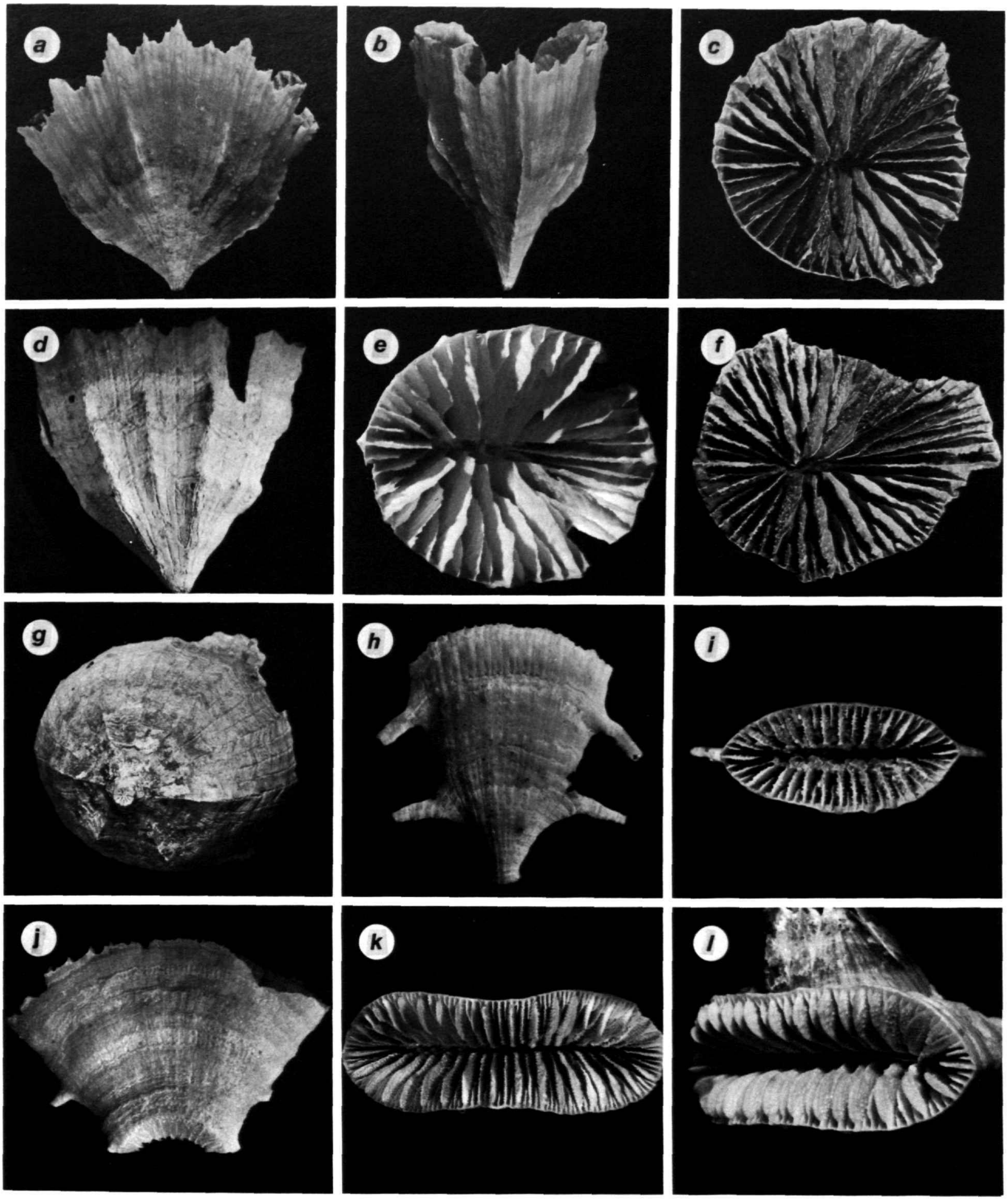

PLATE 31.—*Flabellum sexcostatum*, new species: *a,b*, lateral and edge views of holotype, ×1.2, ×1.4, respectively. *Flabellum conuis* (*c,f,g*, ALB-5428, USNM 81936; *d,e*, holotype): *c,g*, calicular and basal views of same specimen, both ×1.5; *f*, calicular view of different specimen, ×1.5; *d,e*, lateral and calicular views of holotype, both ×1.8. *Truncatoflabellum aculeatum* (*h,i*, holotype of *F. aculeatum*; *j-l*, syntype of *F. variabile*, MV 8205): *h*, holotype, represented by anthocaulus and short, still-attached anthocyathus, ×2.9; *i*, calice of holotype, ×3.3; *j-l*, lateral, calicular, and oblique calicular views of syntype of *F. variabile*, ×1.5, ×1.5, ×2.1, respectively (*l* shows notching of septa near calicular edge).

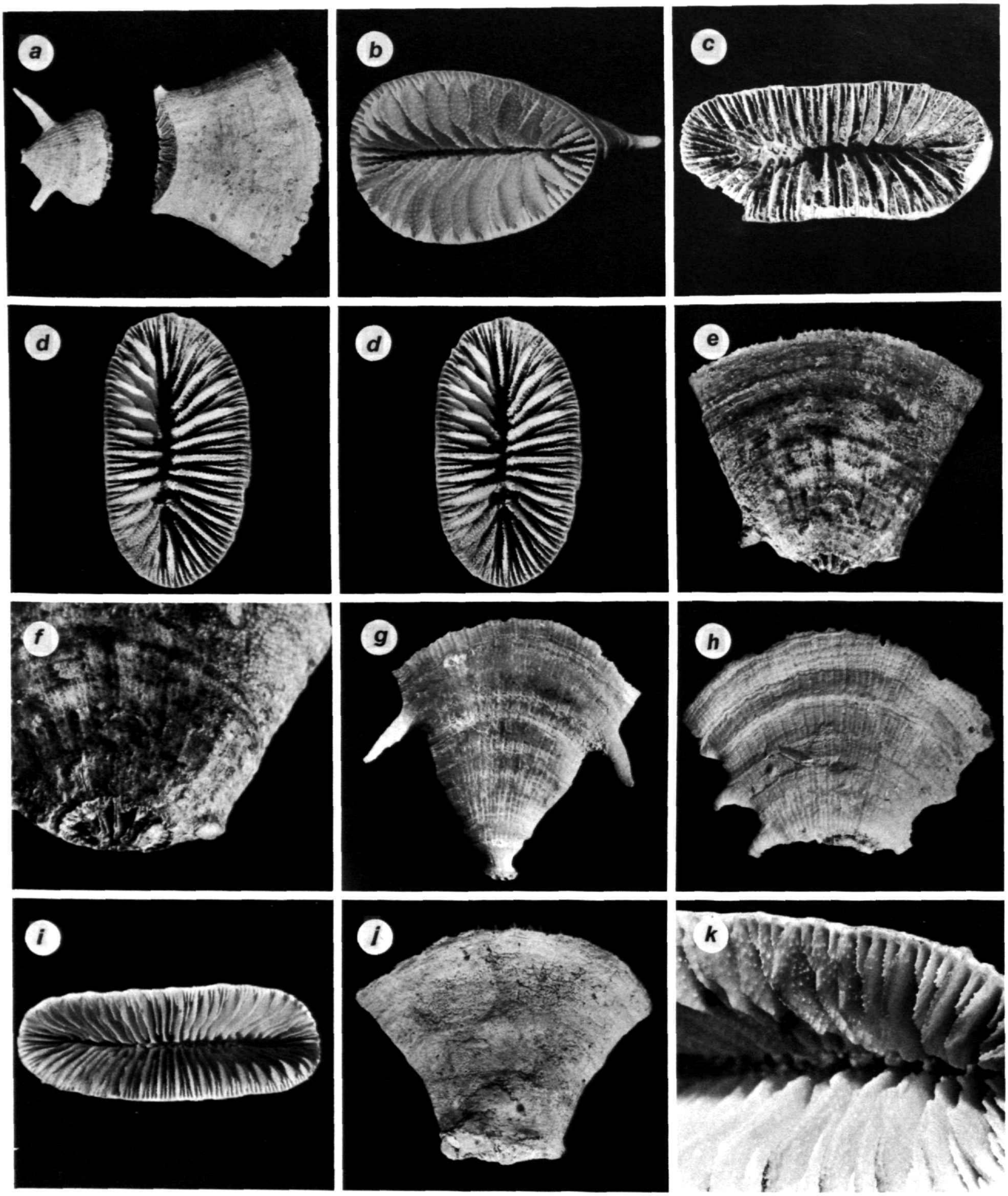

PLATE 32.—*Truncatoflabellum aculeatum* (*a,b*, ALB-5156, USNM 40781; *c*, *F. rubrum* of Umbgrove (1938), RGM 35461, Pleistocene of Talaud): *a*, anthocaulus and anthocyathus of presumably the same specimen, ×1.5; *b*, calicular view of anthocyathus, ×2.4; *c*, calice of fossil specimen, ×2.4. *Truncatoflabellum crassum*: *d-f*, stereo calicular, lateral, and calicular views of holotype (anthocyathus), ×1.8, ×2.0, ×3.1, respectively. *Truncatoflabellum spheniscus* (*g*, syntype of *F. debile*, BM 1855.12.27.2; *h*, *F. rubrum stokesi* of Yabe and Eguchi (1942a), sta 339, TIUS 50228; *i-k*, syntype of *F. spheniscus*, USNM 89): *g*, lateral view of anthocaulus, ×2.7; *h*, lateral view of anthocyathus, ×2.3; *i-k*, calicular, lateral, and enlarged calicular views of same specimen, ×1.6, ×1.6, ×5.6, respectively.

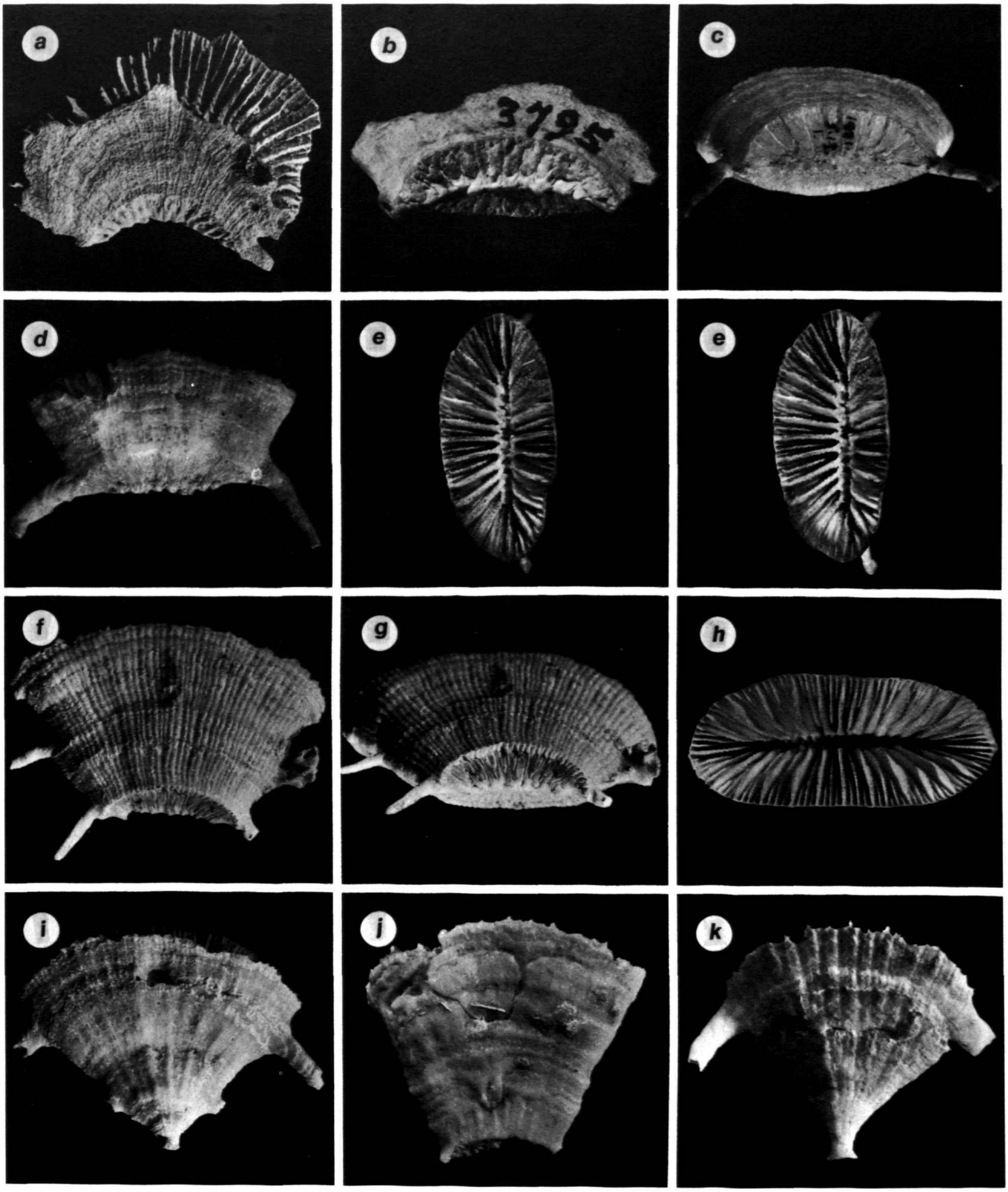

PLATE 33.—*Flabellum (= Truncatoflabellum) variabile* of Gerth (1921): *a*, RGM 3796, Miocene of Java, lateral view of anthocyathus, ×1.5. *Truncatoflabellum stokesi* (*b*, *F. stokesi* of Gerth (1921), RGM 3795, Miocene of Java; *c–e*, holotype, BM 1981.5.12.1; *f–h*, *F. stokesi* of Moseley (1881), *Challenger*-190, BM 1880.11.25.78; *i*, *F. stokesi* of Moseley (1881), *Challenger*-188, BM 1880.11.25.77; *j*, supposed type of *F. magnificum*, ZMB 5088): *b*, basal view of anthocyathus, ×3.2; *c–e*, basal, lateral, and stereo calicular view of holotype, ×2.6, ×2.3, ×2,2, respectively; *f–h*, lateral, basal, and calicular views of anthocyathus, ×2.0, ×2.1, ×1.8, respectively; *i*, anthocaulus, magnification unknown (approximately ×3.7); *j*, anthocyathus, ×1.4. *Truncatoflabellum bairdi*: *k*, holotype of *Flabellum sumatrense*, anthocaulus and basalmost anthocyathus, MNHNP 374, ×3.3.

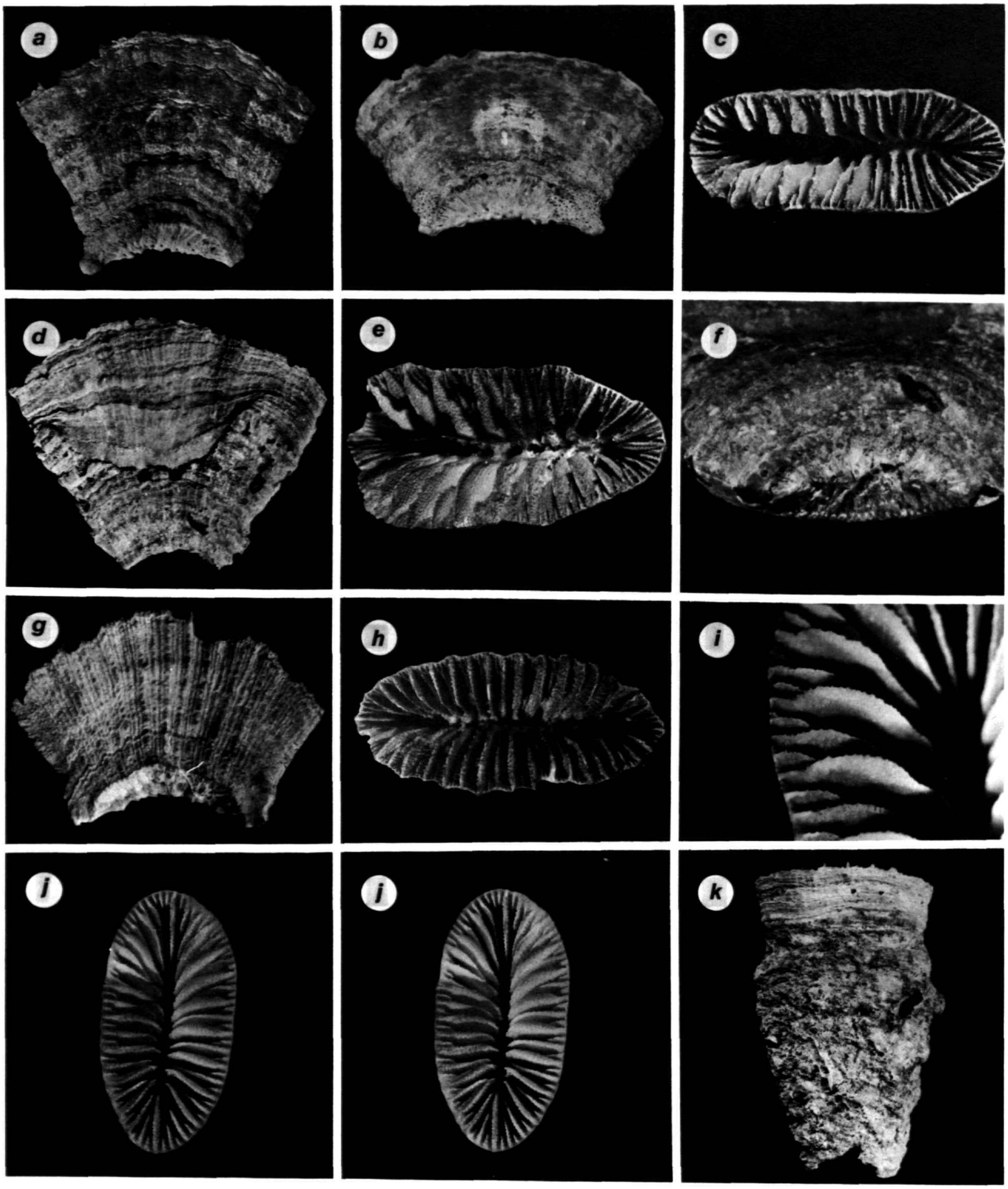

PLATE 34.—*Truncatoflabellum bairdi: a–c,* lateral, basal, and calicular views of holotype, ×2.1, ×2.5, ×2.2, respectively. *Truncatoflabellum profundum* (*d–f,* holotype of *F. profundum; g,h,* holotype of *F. crenulatum*): *d–f,* lateral, calicular, and basal views of holotype, ×1.2, ×1.4, ×2.4, respectively; *g,h,* lateral and calicular views, ×2.1, ×2.0, respectively. *Truncatoflabellum irregulare* (*i,j,* syntype, MV 15507; *k,* syntype, MV 8199): *i,* oblique view of septa showing dentate septal notches, ×7.2; *j,* stereo calicular view, ×2.4; *k,* lateral view, ×1.8.

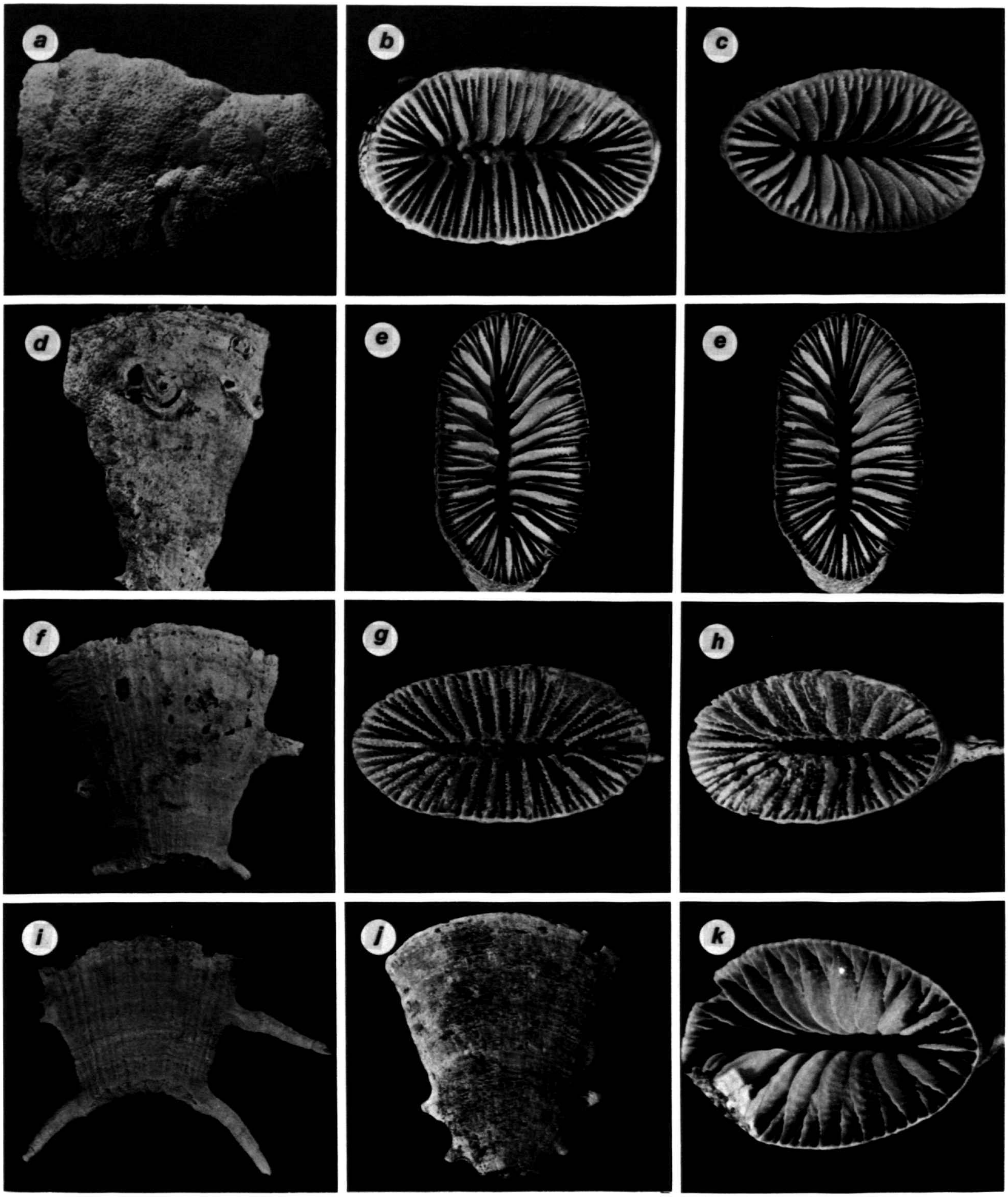

PLATE 35.—*Truncatoflabellum irregulare* (*a,b,* ALB-5145, USNM 81975; *c,* syntype, MV 8199): *a,b,* lateral and calicular views of same specimen having 20 primary septa, ×1.3, ×1.9, respectively; *c,* calicular view of specimen with 16 primary septa, ×2.5. *Truncatoflabellum incrustatum,* new species: *d,e,* lateral and stereo views of holotype, ×1.6, ×2.1, respectively. *Truncatoflabellum cumingi* (*f–h,* neotype; *i, Te Vega* 1-54, USNM 81977): *f–h,* lateral, calicular, and oblique views of neotype, ×2.2, ×2.7, ×2.7, respectively; *i,* lateral view of anthocyathus with relatively intact thecal spines, ×2.5. *Truncatoflabellum formosum,* new species: *j,k,* lateral and calicular views of holotype, ×2.4, ×3.3, respectively.

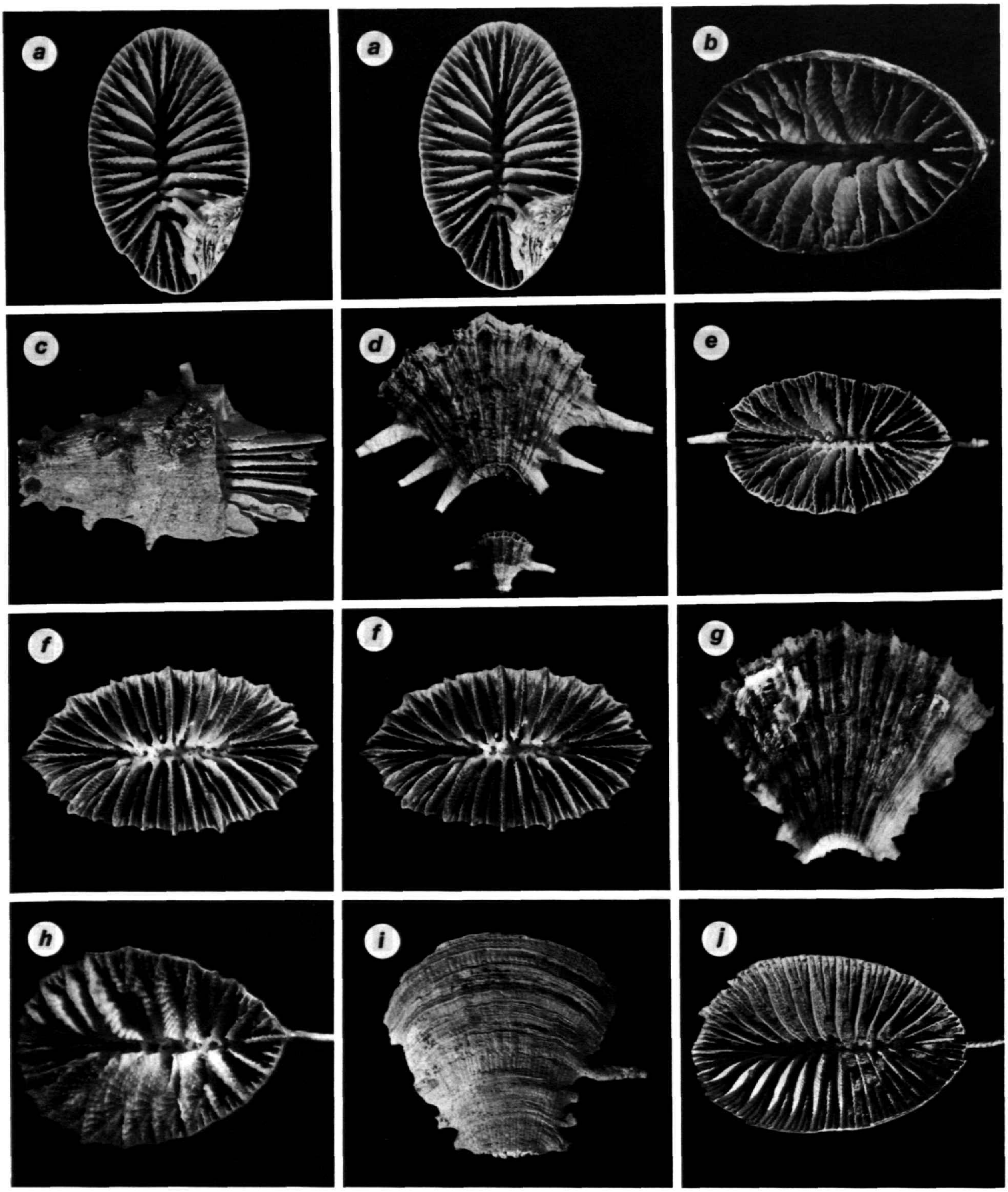

Plate 36.—*Truncatoflabellum formosum* (*a*, holotype; *b*, *F. rubrum* of Yabe and Eguchi (1942a), sta 465, TIUS 50229): *a*, stereo view of calice, ×2.5; *b*, calicular view of Japanese specimen, ×3.8. *Truncatoflabellum vanuatu: c*, USGS 25715, USNM 71861, paratype, Pleistocene of Vanuatu, lateral view, ×1.5. *Truncatoflabellum candeanum* (*d,e*, neotype; *f,g*, holotype of *F. elegans; h, F. candeanum* of Marenzeller (1889), off Japan, MV 8194): *d*, lateral view of anthocaulus and anthocyathus of same specimen, ×2.2; *e*, calice of anthocyathus of *d*, ×2.2; *f,g*, stereo calicular and lateral views of same specimen, ×1.7, ×1.9, respectively; *h*, oblique calicular view, ×3.0. *Truncatoflabellum candeanum* of Duncan (1870): *i,j*, USGS 10809, USNM 353592, Mornington, Victoria, Australia, Miocene, lateral and calicular views, ×1.4, ×1.6, respectively.

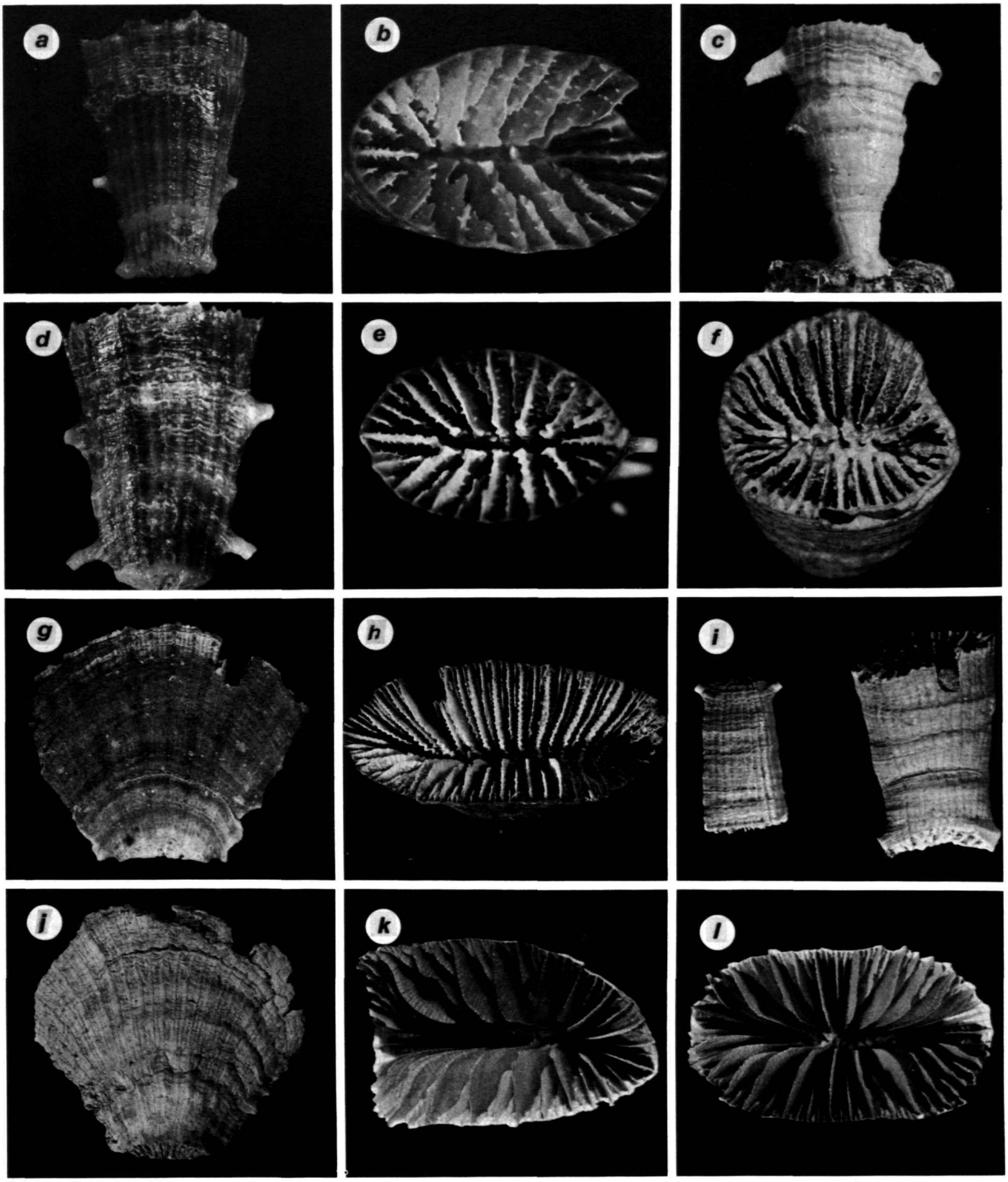

PLATE 37.—*Truncatoflabellum pusillum*, new species (*a,b*, holotype; *c–e*, paratype, ALB-5178, USNM 81979): *a,b*, lateral and calicular views of holotype (anthocyathus), ×4.5, ×8.3, respectively; *c*, anthocaulus, ×6.7; *d,e*, lateral and calicular views of same specimen, ×6.1, ×7.8, respectively. *Flabellum (= Truncatoflabellum) irregulare* of Gerth (1921): *f*, specimen from Miocene of Java, RGM 3784, calicular view, ×3.8. *Flabellum paripavoninum* of Wells (1984): *g,h*, USGS 25715, USNM 71858, Pleistocene of Vanuatu, lateral and calicular views, ×2.0, ×2.1, respectively. *Truncatoflabellum victoriae*: *i*, USNM 353582, Balcomb's Bay, Victoria, Australia, Miocene, lateral view of two anthocyathi, ×3.4. *Truncatoflabellum paripavoninum*: *j–l*, ALB-5648, USNM 40728, lateral, oblique calicular, and calicular views of an anthocyathus, ×1.3, ×1.7, ×1.6, respectively.

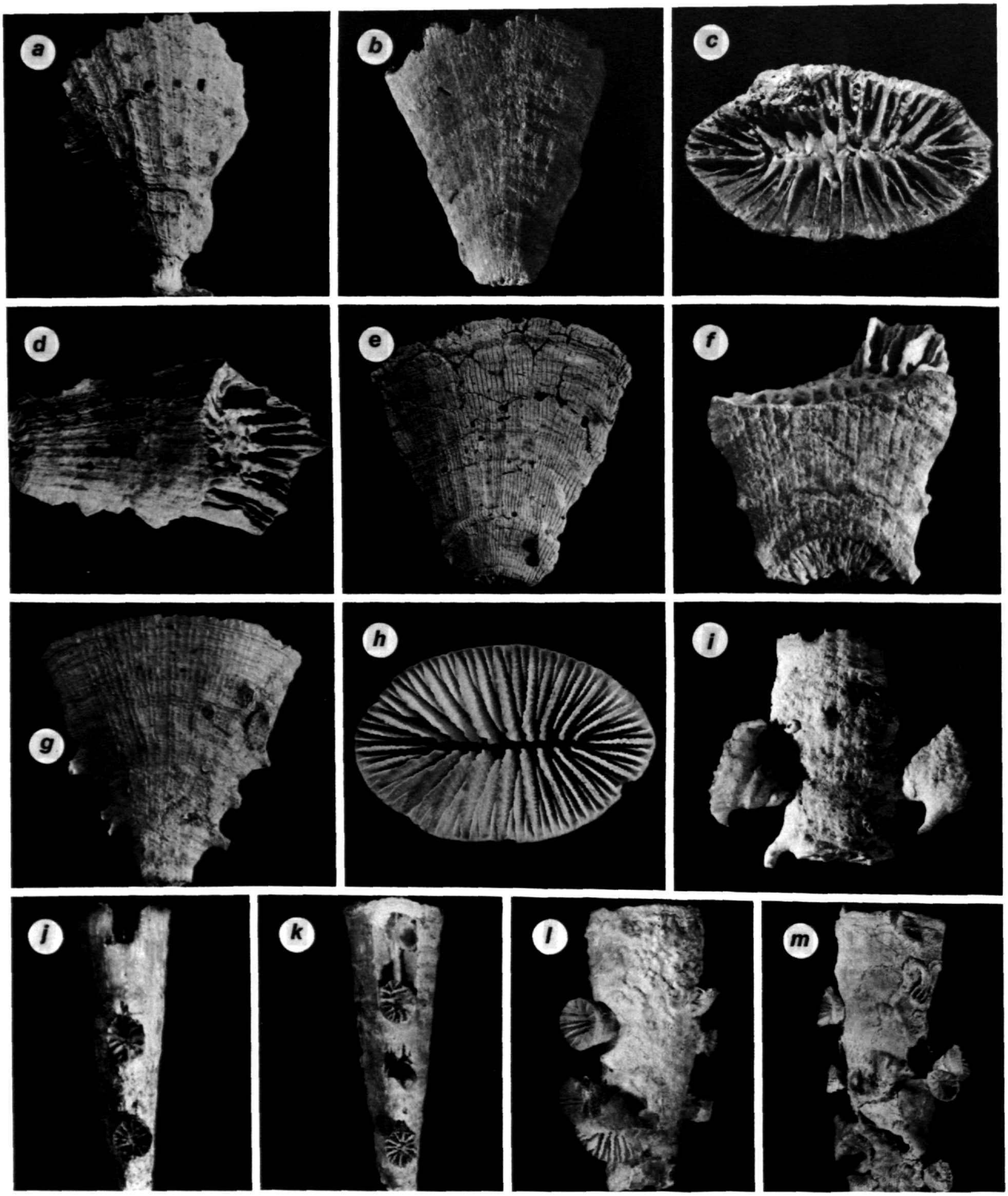

PLATE 38.—*Truncatoflabellum paripavoninum: a*, ALB-5658, USNM 40729, anthocaulus with still-attached basalmost section of anthocyathus (two sections separated by two irregularly shaped pores lying on the incipient fracture plane), ×2.8. *Truncatoflabellum carinatum*, new species (*b,c*, holotype; *d, F. rubrum* of Yabe and Eguchi (1942a), Tonohama, Pliocene, TIUS 43434; *e, F. rubrum* of Umbgrove (1950), Pleistocene of Java, RGM 77860): *b,c*, lateral and calicular views of holotype, ×1.8, ×2.4, respectively; *d,e*, lateral views of anthocyathi, ×6.6, ×1.6, respectively. *Flabellum variabile* var. *alta* Gerth (1921): *f*, holotype from Miocene of Java, RGM 3799, lateral view, ×2.7. *Truncatoflabellum* sp.: *g,h, F. rubrum* of Yabe and Eguchi (1942a), sta 107, TIUS 50231, lateral and calicular views, ×1.9, ×2.1, respectively. *Blastotrochus nutrix* (*i,j*, two of six syntypes, BM 1855.12.27.6; *k–m*, specimens reported by Semper (1872) from Bohol, Philippines, MV 15500): *i,j*, lateral and edge views of two syntypes illustrating anthoblasts, ×3.9, ×2.7, respectively; *k–m*, edge and lateral views of different specimens also illustrating anthoblasts, all ×2.7.

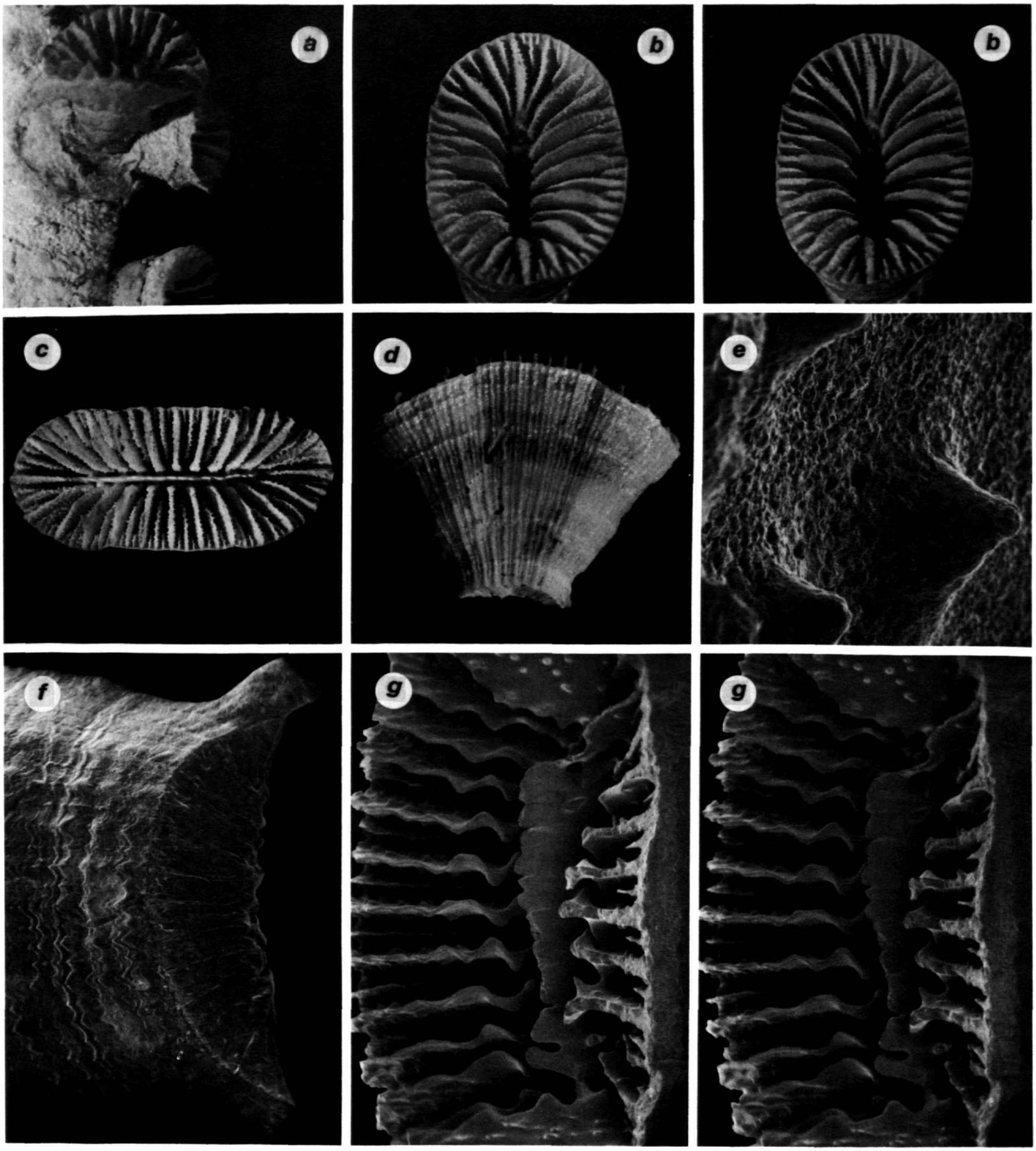

PLATE 39.—*Blastotrochus nutrix* (*a,b*, Semper's (1872) specimen illustrated previously in Plate 38*l*, MV 15500): *a*, enlargement of lateral anthoblasts, ×5.6; *b*, stereo view of calice, ×6.1. *Placotrochus laevis* (*c,d*, ALB-5107, USNM 81980; *e–g*, *Alpha Helix* 79-M-14, USNM 81995): *c,d*, calicular and lateral views of same corallum, ×3.0, ×2.8, respectively; *e*, septal granulation, ×150; *f*, basal anthocyathus scar, ×9.2; *g*, stereo view of broken corallum revealing septal sinuosity and lamellar columella, ×10.5.

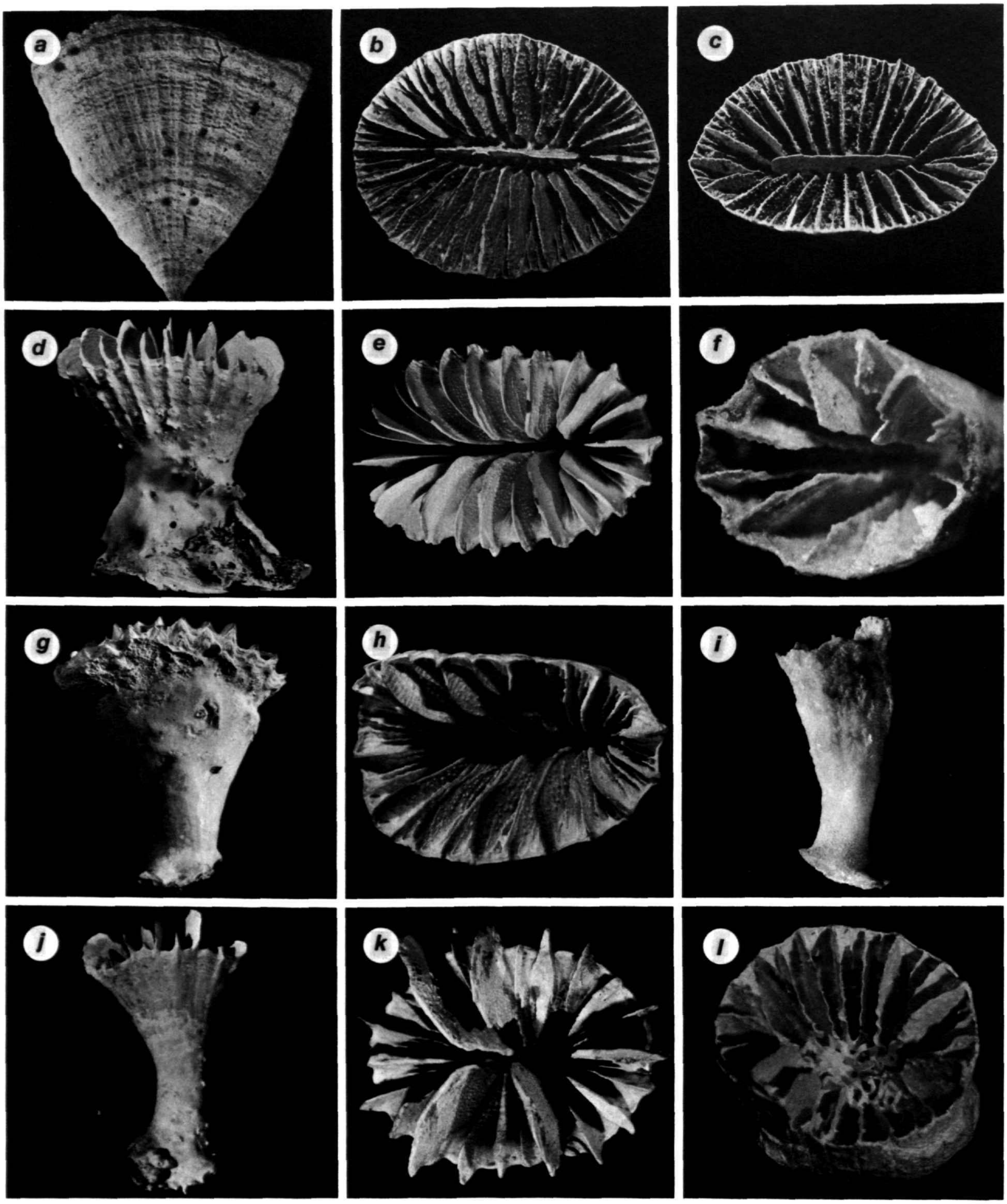

PLATE 40.—"*Placotrochus*" *deltoideus* (*a–c*, USNM 67953, Balcomb's Bay, Victoria, Australia, Miocene): *a,b*, lateral and calicular views of same specimen, ×1.9, ×2.0, respectively; *c*, slightly oblique calicular view of different specimen illustrating lamellar columella, ×2.3. *Javania insignis* (*d,e*, Izu Oceanic Park, Japan, 46 m, USNM 81985; *g,h*, *Flabellum* "*weberi*" ms name, "type," *Siboga*-310, ZMA 1232; *j–k*, ALB-5255, USNM 81986): *d,e,g,h,j,k*, lateral and calicular views of three specimens: ×1.8, ×2.4; ×2.1, ×2.6; ×1.4, ×2.0, respectively. "*Desmophyllum*" (= *?Javania*) *alabastrum*: *f,i*, holotype, *Siboga*-95, ZMA 1252, calicular and lateral views, ×13.8, ×5.7, respectively. *Placotrochides scaphula*: *l*, MUSORSTOM 2-25, MNHNP, calicular view, ×5.3.

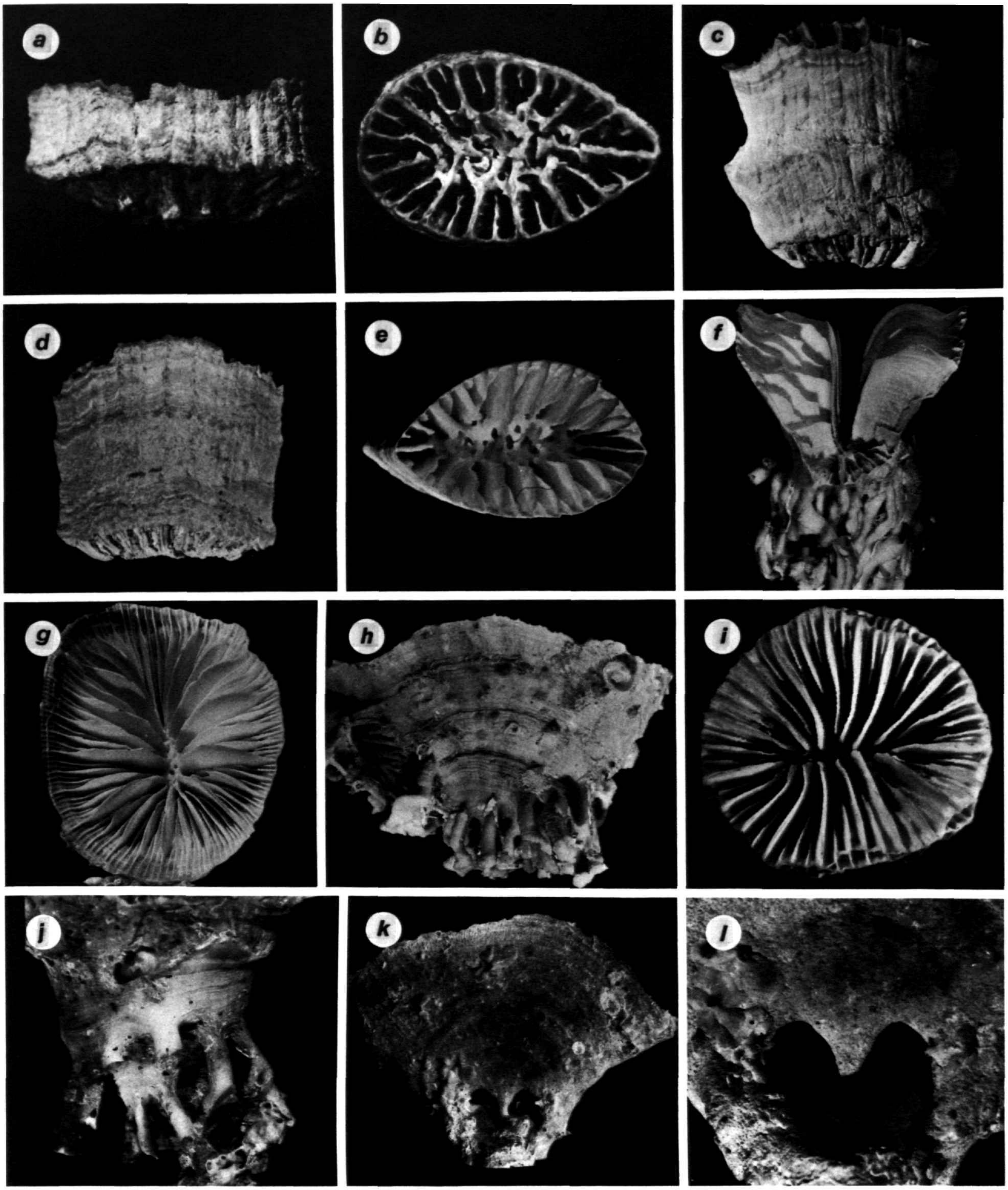

PLATE 41.—*Placotrochides scaphula* (*a,b*, holotype; *c–e*, ALB-5582, USNM 81996): *a,b*, lateral and calicular views of holotype (anthocyathus), both ×8.5; *c*, lateral view of anthocyathus, ×3.7; *d,e*, lateral and calicular views of the same specimen, ×3.3, ×4.0, respectively. *Rhizotrochus typus* (*f*, ALB-5593, USNM 82001; *g,h*, ALB-5357, USNM 82000; *i,j*, specimen from unknown locality, BM 1851.2.19.2): *f*, damaged corallum revealing septal outline and basal rootlets, ×1.0; *g,h*, calicular and lateral views of same specimen, ×1.1, ×1.3, respectively; *i,j*, calicular and basal views of same specimen, magnification unknown (approximately ×1.2, ×1.7, respectively). *Rhizotrochus flabelliformis*, new species: *k,l*, holotype (*Flabellum latum* of Alcock (1902a)), *Siboga*-105, ZMA 1216, lateral views of corallum illustrating rootlets and pedicel, ×1.0, ×2.3, respectively.

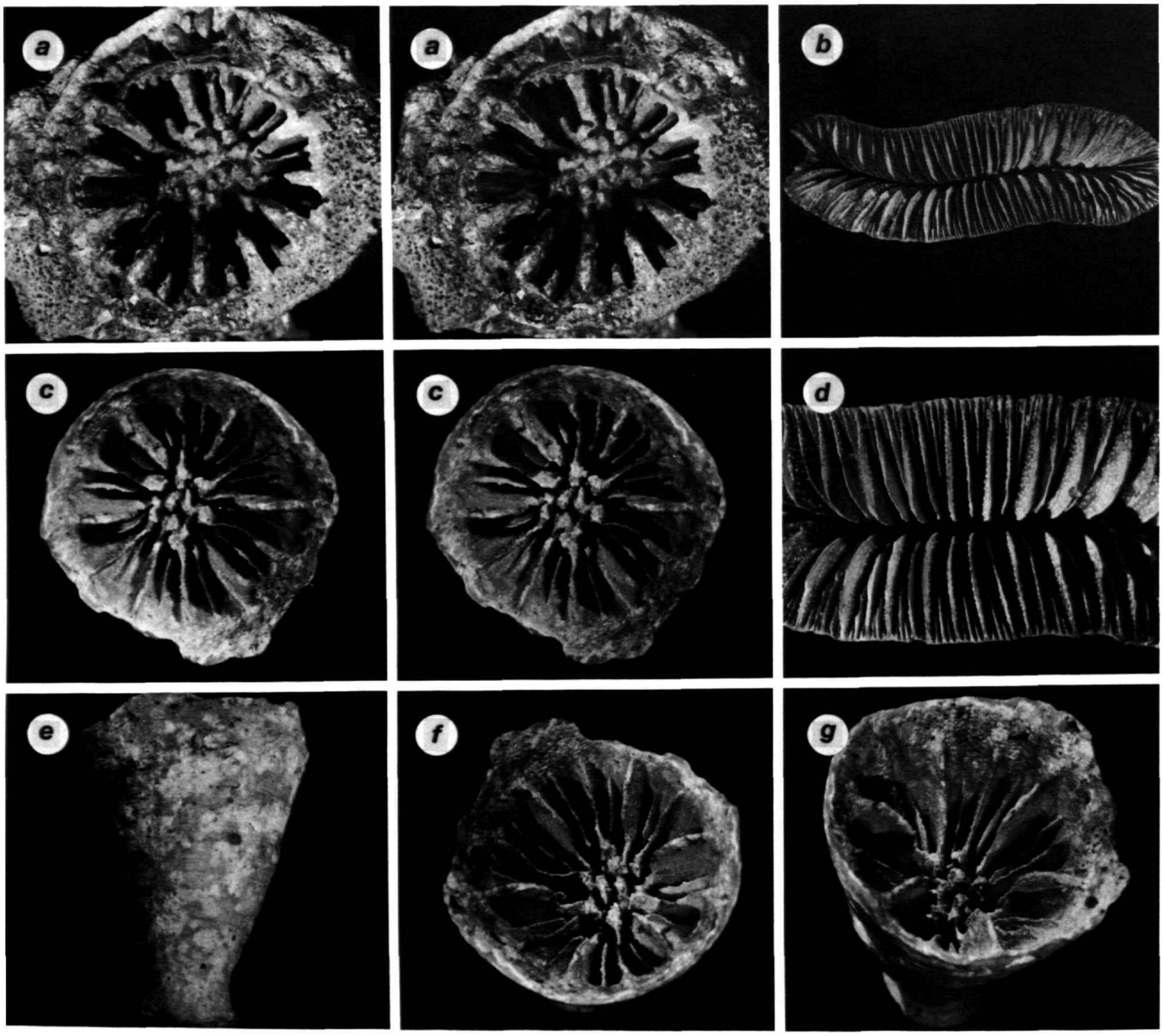

PLATE 42.—*Gardineria philippinensis*, new species: *a*, stereo calicular view of holotype, ×3.6. *Rhizotrochus flabelliformis*, new species: *b,d*, calicular views of holotype, ×1.0, ×2.1, respectively. *Gardineria musorstomica*, new species: *c, e–g*, stereo calicular, lateral, and two oblique views of holotype, ×3.6, ×3.0, ×3.6, ×3.6, respectively.

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